The structural and thermal properties of avian cup-shaped nests

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“Those who admire the freedom of birds have never built a nest”

~ Anonymous
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>TABLE OF CONTENTS</td>
<td>i</td>
</tr>
<tr>
<td>TABLE OF FIGURES</td>
<td>vii</td>
</tr>
<tr>
<td>TABLE OF TABLES</td>
<td>x</td>
</tr>
<tr>
<td>LIST OF ABBREVIATIONS</td>
<td>xii</td>
</tr>
<tr>
<td>ABSTRACT</td>
<td>xv</td>
</tr>
<tr>
<td>DECLARATION</td>
<td>xvii</td>
</tr>
<tr>
<td>ACKNOWLEDGEMENTS</td>
<td>xviii</td>
</tr>
<tr>
<td>CHAPTER 1</td>
<td>1</td>
</tr>
<tr>
<td>(a) Life-history theory and energetic trade-offs</td>
<td>1</td>
</tr>
<tr>
<td>(b) The energetic cost of reproduction</td>
<td>1</td>
</tr>
<tr>
<td>(c) Incubation and associated costs</td>
<td>1</td>
</tr>
<tr>
<td>(d) Reduction of energetic costs during incubation</td>
<td>2</td>
</tr>
<tr>
<td>(e) Thesis and chapter objectives</td>
<td>2</td>
</tr>
<tr>
<td>CHAPTER 2</td>
<td>5</td>
</tr>
<tr>
<td>STATEMENT OF AUTHORSHIP</td>
<td>6</td>
</tr>
<tr>
<td>ABSTRACT</td>
<td>7</td>
</tr>
<tr>
<td>1. INTRODUCTION</td>
<td>8</td>
</tr>
<tr>
<td>2. METHODS</td>
<td>11</td>
</tr>
<tr>
<td>(a) Nest dimensions</td>
<td>12</td>
</tr>
<tr>
<td>(b) Total nest conductance</td>
<td>13</td>
</tr>
<tr>
<td>(c) Surface-specific nest conductance</td>
<td>16</td>
</tr>
<tr>
<td>(d) Nest thermal conductivity</td>
<td>16</td>
</tr>
<tr>
<td>(e) Parent mass</td>
<td>16</td>
</tr>
<tr>
<td>(f) Hemispherical nest model</td>
<td>16</td>
</tr>
<tr>
<td>i. General assumptions</td>
<td>17</td>
</tr>
<tr>
<td>ii. Heat loss scaling</td>
<td>17</td>
</tr>
<tr>
<td>iii. Isometric scaling</td>
<td>18</td>
</tr>
<tr>
<td>iv. Structural scaling</td>
<td>19</td>
</tr>
<tr>
<td>Section</td>
<td>Page</td>
</tr>
<tr>
<td>------------------------------------------------------------------------</td>
<td>------</td>
</tr>
<tr>
<td>1. INTRODUCTION</td>
<td>53</td>
</tr>
<tr>
<td>2. METHODS</td>
<td></td>
</tr>
<tr>
<td>(a) Egg measurements</td>
<td>57</td>
</tr>
<tr>
<td>(b) Egg photography</td>
<td>57</td>
</tr>
<tr>
<td>(c) Egg image processing</td>
<td>58</td>
</tr>
<tr>
<td>(d) Egg macro</td>
<td></td>
</tr>
<tr>
<td>i. Bodies and surfaces of revolution</td>
<td>59</td>
</tr>
<tr>
<td>ii. The shape of an egg</td>
<td>61</td>
</tr>
<tr>
<td>iii. Interpretation of the parameters</td>
<td>61</td>
</tr>
<tr>
<td>iv. The area and volume of an egg</td>
<td>64</td>
</tr>
<tr>
<td>v. The egg shape macro</td>
<td>67</td>
</tr>
<tr>
<td>vi. Macro testing</td>
<td>69</td>
</tr>
<tr>
<td>(e) Clutch size</td>
<td>70</td>
</tr>
<tr>
<td>(f) Nest dimensions</td>
<td>70</td>
</tr>
<tr>
<td>3. RESULTS</td>
<td>21</td>
</tr>
<tr>
<td>4. DISCUSSION</td>
<td>27</td>
</tr>
<tr>
<td>ACKNOWLEDGEMENTS</td>
<td>29</td>
</tr>
<tr>
<td>POST-PUBLICATION ADDITIONS</td>
<td>30</td>
</tr>
<tr>
<td>SUPPLEMENT 2.1: PUBLISHED VERSION OF CHAPTER 2</td>
<td>31</td>
</tr>
<tr>
<td>SUPPLEMENT 2.2: THE LENGTH OF THE GREY FANTAIL (Rhipiduridae: <em>Rhipidura albiscapa</em>) NEST PENDULUM</td>
<td>38</td>
</tr>
<tr>
<td>SUPPLEMENT 2.3: ALLOMETRIC RELATIONS OF AVIAN CUP-SHAPED NESTS</td>
<td>40</td>
</tr>
<tr>
<td>SUPPLEMENT 2.4: A PHYLOGENETIC VIEW OF THE ALLOMETRIC RELATIONSHIP FOR THE STRUCTURE AND THERMAL PROPERTIES OF AVIAN CUP-SHAPED NESTS</td>
<td>42</td>
</tr>
<tr>
<td>SUPPLEMENT 2.5: THE INFLUENCE OF SEXUAL SIZE DIMORPHISM ON THE STRUCTURE AND THERMAL PROPERTIES OF AVIAN CUP-SHAPED NESTS</td>
<td>44</td>
</tr>
<tr>
<td>SUPPLEMENT 2.6: AVIAN CUP-SHAPED NEST DESIGN CONTAINS A PHYLOGENETIC SIGNAL</td>
<td>48</td>
</tr>
<tr>
<td>CHAPTER 3</td>
<td>51</td>
</tr>
<tr>
<td>STATEMENT OF AUTHORSHIP</td>
<td>52</td>
</tr>
<tr>
<td>ABSTRACT</td>
<td>53</td>
</tr>
</tbody>
</table>

The structural and thermal properties of avian cup-shaped nests
ABSTRACT

1. INTRODUCTION 111

2. METHODS 116
   (a) Nest dimensions and thermal properties 117
   (b) Altitude and climate data 117
   (c) Parent mass 119
   (d) Statistical analyses
      i. Nest material use 120
      ii. Principal component analyses 120
      iii. Phylogenetic analyses 120
      iv. Multiple linear regression analyses 121
      v. Model assumptions and data transformation 122

3. RESULTS 123

4. DISCUSSION 129
   (a) Climate 129
   (b) Altitude 131
   (c) Summary 132

ACKNOWLEDGEMENTS 134

CHAPTER 5 135

STATEMENT OF AUTHORSHIP 136

ABSTRACT 139

1. INTRODUCTION 140

2. METHODS 142
   (a) Nest collection 142
   (b) Descriptive properties and dimensions of nests 144
   (c) The effect of water on nest thermal properties 145
      i. Water content and rate of evaporation 145
      ii. Total nest conductance 147
      iii. Surface-specific nest conductance 148
      iv. Nest material thermal conductivity 148
   (d) Measurement frequency 148
(e) Statistical analyses

3. RESULTS

(a) Descriptive properties and dimensions of nests
(b) Water content and rate of evaporation
(c) Nest thermal properties

4. ENERGY EXPENDITURE MODEL

(a) Model components and assumptions
   i. Nest temperature
   ii. Ambient temperature and precipitation
   iii. Recess length and frequency
   iv. Nest conductance
   v. Determination of heat loss and energy expenditure
(b) Model outcomes
(c) Model accuracy and improvements

5. DISCUSSION

CHAPTER 6

STATEMENT OF AUTHORSHIP

ABSTRACT

1. INTRODUCTION

2. METHODS

(a) Study species
(b) Nest dimensions
(c) Wind tunnel
(d) Total nest conductance
(e) Surface-specific nest conductance
(f) Thermal conductivity
(g) Statistical analyses

3. RESULTS

4. DISCUSSION

(a) Still conditions
(b) The effect of wind
   i. Sealed nests
   ii. Open nests
   iii. No nest
(c) Summary

ACKNOWLEDGEMENTS

SUPPLEMENT 6.1: PUBLISHED VERSION OF CHAPTER 6

CHAPTER 7

APPENDICES

APPENDIX 1: IMAGES OF CUP-SHAPED NESTS OF AUSTRALIAN PASSERINES

APPENDIX 2: THE THERMAL PROPERTIES OF AVIAN CUP-SHAPED NESTS

APPENDIX 3: THE PHYSICAL DIMENSIONS AND MASS OF AVIAN CUP-SHAPED NESTS

APPENDIX 4: THE VOLUME, DENSITY AND SURFACE AREAS OF AVIAN CUP-SHAPED NESTS

APPENDIX 5: IMAGES OF EGGS OF AUSTRALIAN PASSERINES

APPENDIX 6: OOMORPHOLOGY MACRO

APPENDIX 7: ELECTRONIC SUPPLEMENTARY MATERIAL

APPENDIX 8: SHAPE PARAMETERS OF AVIAN EGGS

APPENDIX 9: AVIAN EGG SIZE

APPENDIX 10: MATERIAL USE IN AVIAN CUP-SHAPED NESTS

APPENDIX 11: METHODS OF ATTACHMENT BETWEEN CUP-SHAPED NESTS AND HOST BRANCH

APPENDIX 12: COLLECTION LOCATION, ATTACHMENT METHOD, WEAVE AND NEST MATERIAL USE FOR CUP-SHAPED NESTS OF AUSTRALIAN PASSERINES

APPENDIX 13: NESTS OF GLICIPHILA MELANOPS

REFERENCES
### TABLE OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.1</td>
<td>A diagram representative of a nest showing the dimensions used to calculate nest surface area. Both internal (light grey) and external (dark grey) nest surface area were calculated to obtain the geometric mean surface area.</td>
<td>12</td>
</tr>
<tr>
<td>2.2</td>
<td>Diagram of the equipment used to measure nest thermal conductance.</td>
<td>14</td>
</tr>
<tr>
<td>2.3</td>
<td>Relationship between parent mass and a – total nest conductance and b – nest mass for cup-shaped birds’ nests.</td>
<td>23</td>
</tr>
<tr>
<td>2.4</td>
<td>Relationship between parent mass and a – nest surface area, b – nest thickness, c – internal diameter and external diameter and d – internal height and external height.</td>
<td>25</td>
</tr>
<tr>
<td>2.5</td>
<td>Relationship between parent mass and a – surface-specific nest conductance and b – nest thermal conductivity for cup-shaped birds’ nests.</td>
<td>26</td>
</tr>
<tr>
<td>S2.2.1</td>
<td>Image of a <em>R. albiscapa</em> nest.</td>
<td>38</td>
</tr>
<tr>
<td>S2.2.2</td>
<td>Diagram showing standard nest dimensions in addition to the length of the pendulum.</td>
<td>39</td>
</tr>
<tr>
<td>3.1</td>
<td>Diagram of the measurements made on egg samples, including egg length and egg width.</td>
<td>57</td>
</tr>
<tr>
<td>3.2</td>
<td>Diagram of camera set-up used to photograph egg samples, as shown in profile.</td>
<td>58</td>
</tr>
<tr>
<td>3.3</td>
<td>Diagram of the image adjustment steps for egg photographs, where a – original egg photograph, b – egg vector created in CorelDraw, c – egg image with adjusted contrast, d – egg outline following use of the Find Edges tool and e – egg outline following image inversion.</td>
<td>59</td>
</tr>
<tr>
<td>3.4</td>
<td>a – The plotted curve of a surface of revolution for b – a horizontally rotated surface and c – a vertically rotated surface.</td>
<td>60</td>
</tr>
<tr>
<td>3.5</td>
<td>Plots of the parameter b.</td>
<td>62</td>
</tr>
<tr>
<td>3.6</td>
<td>Plots of the parameter c.</td>
<td>63</td>
</tr>
<tr>
<td>3.7</td>
<td>Plots of the parameter d.</td>
<td>63</td>
</tr>
<tr>
<td>3.8</td>
<td>Plots of the parameter e.</td>
<td>64</td>
</tr>
<tr>
<td>3.9</td>
<td>Close-up of an egg outline showing blurred outlines and errant pixels.</td>
<td>67</td>
</tr>
<tr>
<td>3.10</td>
<td>Diagram showing the direction of slicing for egg images in the trapezoidal integration process.</td>
<td>68</td>
</tr>
<tr>
<td>3.11</td>
<td>Diagram showing the aerial diagrammatic representation of a nest, where the clutch profile area ($PA_{C}$, cm$^2$) is equal to that of the white surfaces and the nest opening surface area ($A_{LID}$, cm$^2$) is equal to the surface area of the light grey circle. Note that specific arrangement of eggs does not represent actual arrangement in a nest, rather is for graphical purposes only.</td>
<td>70</td>
</tr>
<tr>
<td>3.12</td>
<td>Informal supertree showing the phylogenetic relationships between bird species.</td>
<td>74</td>
</tr>
</tbody>
</table>
Figure 3.13. Diagram showing replicate egg profiles for individual species, where egg height has been standardised.

Figure 3.14. Plotted curves of egg outlines, based on rescaled shape parameters (a, b0, c0, d0, e0).

Figure 3.15. Relationship between female body mass and a – circular distortion and elliptical distortion; b – egg length and width; c – profile area of the egg and clutch; d – surface area of the egg and clutch and e – volume of the egg and clutch.

Figure 3.16. Relationship between female mass and sexual size dimorphism and egg volume.

Figure 3.17. Relationship between a – female mass and clutch size and b – sexual size dimorphism and clutch size.

Figure 3.18. Relationship between a – nest height and log egg width residuals; b – nest opening surface area and clutch profile area; c – internal nest surface area and clutch surface area; d – nest cup volume and clutch volume and e – log nest mass residuals and clutch volume.

Figure S3.1.1. Diagram of the egg outline function.

Figure S3.1.2. Diagram of a potential set-up to measure egg tip to plate distances.

Figure 4.1. Informal supertree showing the phylogenetic relationships between bird species.

Figure 4.2. Maps showing the altitude, mean annual temperature and annual precipitation with respect to nest collection location.

Figure 4.3. Residual-residual (interaction) plots for temperature and precipitation and the relationship with a – nest conductance and b – material conductivity.

Figure 4.4. The relationship between altitude and nest conductance for cup-shaped birds’ nests.

Figure 5.1. Climate recorded at Keith, South Australia, for a – total precipitation per month; b – days of precipitation and c – mean maximum and minimum temperatures each month through the average Gliciphiila melanops breeding season.

Figure 5.2. Diagram of the equipment used to measure nest thermal properties at varying levels of water content.

Figure 5.3. Relationship between the time elapsed since initial saturation and water content for cup-shaped nests of Gliciphila melanops.

Figure 5.4. Relationship between the water content and conductance for cup-shaped nests of Gliciphila melanops.

Figure 5.5. Relationship between the water content and material conductivity for cup-shaped nests of Gliciphila melanops.

Figure 5.6. Daily fluctuation in energy expenditure on a day in July without rain or with rain and in December without rain or with rain.

Figure 5.7. Modelled daily energy expenditure on a day without rain or with rain in July and December.
Figure 6.1. A nest of *Acanthagenys rufogularis* and *Manorina flavigula*. 167
Figure 6.2. The wind tunnel used to alter experimental wind conditions. 168
Figure 6.3. The equipment used to measure nest thermal conductance. 170
Figure 6.4. The effect of wind speed on nest conductance. 175
Figure 6.5. The effect of wind speed on heat loss from nests. 177
Figures A1.1 to A1.36. Images of cup-shaped nests of Australian passerines. 198
Figures A5.1 to A5.36. Images of eggs of Australian passerines. 242
Figure A13.1. Lateral view of a nest of *Gliciphilla melanops*, showing the medium weave of the outer layer. 305
Figure A13.2. Arial view of a nest of *Gliciphilla melanops*, showing the dense inner lining. 306
Figure A13.3. Nest of *Gliciphilla melanops*. 307
TABLE OF TABLES

Table 2.1. Model output for the allometric relationship between parent mass (M, g) and the dimensions and thermal properties of a hemispherical object according to $y = aM^b$ for heat loss, isometric and structural scaling 20

Table 2.2. Allometric relationships between parent mass (M, g) and the dimensions and thermal properties of avian cup-shaped nests according to $y = aM^b$ 22

Table 2.3. Model predictions for the allometric relationship between parent mass (M, g) and the dimensions and thermal properties of a hemispherical object according to $y = aM^b$ for heat loss, isometric and structural scaling, and tests for significant differences between actual scaling exponents (Table 2.1) and predictions 24

Table S2.3.1. Allometric relationships between parent mass (M, g) and the dimensions of avian cup-shaped nests according to $y = aM^b$ 41

Table S2.4.1. Phylogenetic analysis of the allometric relationships between parent mass (M, g) and the dimensions and thermal properties of avian cup-shaped nests according to $y = aM^b$ 43

Table S2.4.2. Phylogenetically corrected allometric relationships between parent mass (M, g) and the dimensions of avian cup-shaped nests according to $y = aM^b$ 43

Table S2.5.1. Phylogenetic analysis of the allometric relationships between parent mass (M, g), sexual size dimorphism (SDI) and the dimensions and thermal properties of avian cup-shaped nests according to $y = aM^b$ SDI $b$ 46

Table S2.5.2. Statistics for the regression of nest dimensions and thermal properties against body mass (M, g) and sexual size dimorphism index (SDI) according to $y = aM^b$ SDI $b$ 47

Table S2.6.1. Statistics for the relationship between nest morphology and phylogeny 49

Table 3.1. Statistics for the relationship between egg morphology and phylogeny 77

Table 3.2. Comparative phylogenetics statistics for the regression of egg morphology against female body mass ($M_F$, g) and sexual size dimorphism index (SDI) according to $y = aM_F^b$ SDI $b$ 78

Table 3.3. Statistics for the regression of egg morphology against female body mass ($M_F$, g) and sexual size dimorphism index (SDI) according to $y = aM_F^b$ SDI $b$ 79

Table 3.4. Statistics for the relationship between egg morphology and nest morphology 82

Table 3.5. Model predictions for the allometric relationship between parent mass (M, g) and the dimensions and thermal properties of a hemispherical object according to $y = aM^b$ for heat loss, isometric and structural scaling, and tests for significant differences between actual scaling exponents and predictions 85

Table S3.2.1. Statistics for the relationship between egg morphology and phylogeny 97

Table S3.3.1. Relationship between clutch size (E) and the morphology of avian eggs 100

Table S3.6.1. Relationship between parental care (C) and the size and shape of avian eggs 106
Table 4.1. Bioclimatic variables for temperature and precipitation with associated eigenvalues

Table 4.2. Comparative phylogenetics statistics for the relationship between nest structural and thermal properties and model variables

Table 4.3. Statistics for the regression of the dimensions and thermal properties of nests against altitude and breeding season climate

Table 4.4. Comparative phylogenetics estimate and supporting statistics for the relationship between nest conductance (inverse-logarithm) and model variables at the breeding season level

Table 4.5. Non-phylogenetic regression estimates and supporting statistics for the relationship between nest conductance (inverse-logarithm) and model variables at the breeding season level

Table 4.6. Indicator species analysis output for materials found in nests from climate and altitude categories

Table 5.1. Collection dates and locations for nests of Gliciphila melanops used to determine the effect of water content on nest thermal properties

Table 5.2. Mean nest dimensions for Gliciphila melanops

Table 6.1. Comparison of wind speeds between open and sealed treatments for nests of Acanthagenys rufogularis and Manorina flavigula

Table 6.2. Nest dimensions for cup-shaped nests of Acanthagenys rufogularis and Manorina flavigula

Table 6.3. Indicator species analysis output for materials found in Acanthagenys rufogularis and Manorina flavigula nests

Table 6.4. Comparison of the structural and thermal properties of nests of Acanthagenys rufogularis and Manorina flavigula under each wind speed treatment

Table A10.1. Indicator species analysis output for materials found in nests
## LIST OF ABBREVIATIONS

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Φ</td>
<td>Heat production rate (mW)</td>
</tr>
<tr>
<td>Φ&lt;sub&gt;FAN&lt;/sub&gt;</td>
<td>Fan heat production rate (mW)</td>
</tr>
<tr>
<td>Φ&lt;sub&gt;GLOBE&lt;/sub&gt;</td>
<td>Globe heat production rate (mW)</td>
</tr>
<tr>
<td>λ</td>
<td>Lambda, an indicator of the strength of a phylogenetic relationship</td>
</tr>
<tr>
<td>η</td>
<td>Night length (h)</td>
</tr>
<tr>
<td>τ</td>
<td>Time coefficient (h)</td>
</tr>
<tr>
<td>A</td>
<td>Nest surface area (cm&lt;sup&gt;2&lt;/sup&gt;)</td>
</tr>
<tr>
<td>Ā</td>
<td>Geometric mean of the internal and external nest surface area (cm&lt;sup&gt;2&lt;/sup&gt;)</td>
</tr>
<tr>
<td>ΔAIC</td>
<td>Akaike Information Criterion difference (phylogenetic – non-phylogenetic)</td>
</tr>
<tr>
<td>ΔAIC&lt;sub&gt;c&lt;/sub&gt;</td>
<td>Second-order Akaike Information Criterion difference (phylogenetic – non-phylogenetic)</td>
</tr>
<tr>
<td>AIC</td>
<td>Akaike Information Criterion</td>
</tr>
<tr>
<td>AIC&lt;sub&gt;c&lt;/sub&gt;</td>
<td>Second-order Akaike Information Criterion</td>
</tr>
<tr>
<td>A&lt;sub&gt;lid&lt;/sub&gt;</td>
<td>Surface area of the nest opening (cm&lt;sup&gt;2&lt;/sup&gt;)</td>
</tr>
<tr>
<td>A&lt;sub&gt;R&lt;/sub&gt;</td>
<td>Area of the region R (cm&lt;sup&gt;2&lt;/sup&gt;)</td>
</tr>
<tr>
<td>b&lt;sub&gt;0&lt;/sub&gt;</td>
<td>Egg shape parameter, representing deviation from spherical</td>
</tr>
<tr>
<td>C</td>
<td>Curve in the Euclidean plane R&lt;sup&gt;2&lt;/sup&gt;</td>
</tr>
<tr>
<td>c&lt;sub&gt;0&lt;/sub&gt;</td>
<td>Egg shape parameter, representing sharpness of the egg poles</td>
</tr>
<tr>
<td>d</td>
<td>Nest diameter (cm)</td>
</tr>
<tr>
<td>d&lt;sub&gt;0&lt;/sub&gt;</td>
<td>Egg shape parameter, representing the squareness of the egg</td>
</tr>
<tr>
<td>D&lt;sub&gt;C&lt;/sub&gt;</td>
<td>Distortion from circular</td>
</tr>
<tr>
<td>D&lt;sub&gt;E&lt;/sub&gt;</td>
<td>Distortion from elliptical</td>
</tr>
<tr>
<td>d&lt;sub&gt;E&lt;/sub&gt;</td>
<td>External nest diameter (cm)</td>
</tr>
<tr>
<td>DEE</td>
<td>Daily energy expenditure (KJ d&lt;sup&gt;-1&lt;/sup&gt;)</td>
</tr>
<tr>
<td>d&lt;sub&gt;i&lt;/sub&gt;</td>
<td>Internal nest diameter (cm)</td>
</tr>
<tr>
<td>DL</td>
<td>Day length (h)</td>
</tr>
<tr>
<td>e&lt;sub&gt;0&lt;/sub&gt;</td>
<td>Egg shape parameter, a general shape modifier</td>
</tr>
<tr>
<td>e</td>
<td>Eccentricity</td>
</tr>
<tr>
<td>E</td>
<td>Clutch size</td>
</tr>
<tr>
<td>EE</td>
<td>Rate of energy expenditure (J s&lt;sup&gt;-1&lt;/sup&gt;)</td>
</tr>
<tr>
<td>f</td>
<td>Function</td>
</tr>
<tr>
<td>G</td>
<td>Nest thermal conductance (mW °C&lt;sup&gt;-1&lt;/sup&gt;)</td>
</tr>
<tr>
<td>G&lt;sub&gt;0%&lt;/sub&gt;</td>
<td>Nest conductance at 0 % water content (i.e. dry, mW °C&lt;sup&gt;-1&lt;/sup&gt;)</td>
</tr>
<tr>
<td>G&lt;sub&gt;100%&lt;/sub&gt;</td>
<td>Nest conductance at 100 % water content (i.e. saturated, mW °C&lt;sup&gt;-1&lt;/sup&gt;)</td>
</tr>
</tbody>
</table>
\( G_{x\%} \) = Nest conductance at x \% water content (mW °C\(^{-1}\))
\( G_A \) = Surface-specific nest conductance (W °C\(^{-1}\) m\(^{-2}\))
\( G_{A-LID} \) = Surface-specific Styrofoam lid thermal conductance (W °C\(^{-1}\) cm\(^{-2}\))
\( G_{LID} \) = Styrofoam lid thermal conductance (mW °C\(^{-1}\))
\( G_{ST} \) = Standardised nest conductance
\( G_t \) = Nest conductance at time, t (mW °C\(^{-1}\))
\( G_{TOT} \) = Nest system thermal conductance (mW °C\(^{-1}\))
\( h \) = Nest height (cm)
\( h_E \) = External nest height (cm)
\( h_i \) = Internal nest height (cm)
\( %H_2O_t \) = Water content in a nest at time, t (\%)
\( HP_{0\%} \) = Heat production at 0 \% water content (W or J s\(^{-1}\))
\( HP_{x\%} \) = Heat production at measured water content, x (W or J s\(^{-1}\))
\( H_V \) = Latent heat of vaporization, 2.259 (J mg\(^{-1}\))
\( I \) = Current (A)
\( k \) = Nest material thermal conductivity (mW °C\(^{-1}\) m\(^{-1}\))
\( K \) = Blomberg et al.’s (2003) K-statistic, representing phylogenetic signal
\( L \) = Egg length (cm)
\( LSH \) = The time at which the maximum solar height occurs (h)
\( M \) = Mean parent body mass (g)
\( M_C \) = Clutch mass (g)
\( M_F \) = Female body mass (g)
\( \dot{M}H_2O \) = Rate of evaporation (mg s\(^{-1}\))
\( M_{H_2O_{evap}} \) = Mass of the evaporated water (g)
\( M_{H_2O_{saturated}} \) = Mass of water in the nest when saturated (g)
\( M_{H_2O_t} \) = Mass of water in the nest at time, t (g)
\( M_M \) = Male body mass (g)
\( M_N \) = Nest mass (g)
\( M_{N_{dry}} \) = Mass of the nest when desiccated (g)
\( M_{N_{saturated}} \) = Mass of the nest when saturated (g)
\( M_{N_t} \) = Mass of the nest at time, t (g)
\( NEE \) = Nesting energy expenditure (KJ)
\( P \) = Delay in maximum temperature with respect to the time of maximum solar height (h)
\( \rho \) = Nest wall density (g cm\(^{-3}\))
\( PA_C \) = Clutch profile area (cm\(^2\))
\( PA_E \) = Egg profile area (cm\(^2\))
The structural and thermal properties of avian cup-shaped nests

PCs = Principal components

R = Region on the Euclidean plane that is rotated about an axis that does not pass through that region

RHE = Relative humidity of the CT cabinet

SAC = Clutch surface area (cm²)

SAE = Egg surface area (cm²)

SAH = Area of the surface generated by curve, C, when rotated about the x-axis

SAv = Area of the surface generated by curve, C, when rotated about the y-axis

SDI = Sexual size dimorphism index

ΔT = Temperature difference (°C)

t = Time elapsed (h)

TA = Ambient temperature (°C)

TE = External nest temperature (°C)

TEGG = Egg heater surface temperature (°C)

Ti = Internal nest temperature (°C)

Tk = Effect of buoyancy (°C)

tm = Rescaled value of xm

TN = Nest temperature (°C)

tS = Sunset time (h)

V = Voltage (V)

VB = Bird volume (mL)

VC = Clutch volume (cm³)

VCUP = Nest cup volume (cm³)

VE = Egg volume (cm³)

VN = Nest wall volume (cm³)

VR = Volume of the solid generated by rotating R about the x-axis (cm³)

VV = Volume of the solid generating by rotating R about the y-axis (cm³)

W = Egg width (cm)

x = Explanatory variable in a function, f

X = Mean nest thickness (cm)

XB = Nest base thickness (cm)

XW = Nest wall thickness (cm)

xm = The distance of the centre of egg mass from the point of origin, representing deviation from an ellipse (cm)

y = Response variable in a function, f

zm = Width of the egg at point xm (cm)
ABSTRACT

Incubation in birds is energetically demanding and the energy invested to maintain egg temperature can influence the outcome of a reproductive event and therefore the lifetime reproductive success of birds. It is reasonable that heat loss can be minimised by optimising the physical structure and location of the nest. We assess the structural and thermal properties of nests across 36 species of Australian passerines, assessing variables against parent mass, egg and clutch size, once accounting for phylogenetic relationships. The surface area and volume of the nest cup increases with the surface area and volume of the clutch, as well as the size of the incubating parent. Sexual size dimorphism influences the mass and density of nests, while structural support for the parent and clutch is the primary factor driving nest thickness. A change in nest thickness with the combined mass of the parent and clutch has a direct influence on the conductance of nests, such that structurally adequate nests achieve a lower thermal conductance (higher insulation) than expected, as they increase in size. When exposed to wind or rain, the rate of heat loss from the nest increases, which is likely to have direct consequences on the energetics of the incubating parent. However, birds breeding in warm and wet conditions select materials for nest construction that have a high thermal conductivity to facilitate the nest drying process and reduce the overall cost of incubation.
The structural and thermal properties of avian cup-shaped nests
DECLARATION

I, Caragh Heenan, certify that this work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

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The structural and thermal properties of avian cup-shaped nests
CHAPTER 1

INTRODUCTION

(a) Life-history theory and energetic trade-offs

Life-history theory is based on the notion that for any given individual, resources available within the environment are finite and that there is variation in how individual organisms allocate those resources between self-maintenance, growth, activity and reproduction (Reid et al. 2002b). There may be trade-offs such that there is a cost of reproduction – defined as the extent to which investment in one reproductive event reduces the capacity of a parent to invest elsewhere.

Reproduction is often thought of as one of the most energetically costly periods of the life-cycle (Dawson et al. 2005). Therefore, it is of interest to understand the resource limitations and fitness costs associated with the various aspects of reproduction and therefore the life-history strategies of an organism (Reid et al. 2002b).

(b) The energetic cost of reproduction

For birds, the reproductive requirements include the energy and matter deposited in the egg, the energy retained by the oviduct, as well as any additional heat produced to maintain a stable temperature for developing young (Robbins 1983). In addition, energy can be expended during reproduction for territorial defence and courtship.

There are several distinct periods during the reproductive cycle of birds that can be potentially costly for the parents, which can be separated into the stages of nest construction, egg production, incubation and brooding (including feeding chicks) (Hansell 2000). This study concerns the energetic costs associated with incubating young, regularly considered as being a phase of low energetic demand compared to other reproductive phases, according to the peak demand hypothesis (Tinbergen and Williams 2002; Williams 1988). However, for some species, incubation can be as energetically demanding as the brooding phase or even more so (Tatner and Bryant 1993; Williams 1996).

(c) Incubation and associated costs

Incubation is the process by which eggs are kept at temperatures suitable for embryonic development with most of the heat energy supplied by the incubating bird and not from the environment (Deeming 2002b). Maintenance of an appropriate nest temperature is important for the development and growth of young, however, this requires the deployment of parental resources in terms of time and energy (Deeming and Ferguson 1991; Reid et al. 2002b). Not only can incubation come at a cost due to the heat energy required to regulate the embryo’s developmental environment but also because the process of incubation requires parents to spend considerable time sitting on the nest (Deeming 2002a; Haftorn and Reinertsen 1985). This restricts the time available for further activities, such as foraging and finding mates, which can in turn influence parental
The structural and thermal properties of avian cup-shaped nests

fitness (Reid et al. 2002b; Robbins 1983). On the other hand, allocating too much time to activities away from the nest can expose the young to unfavourable conditions, reducing embryo development and thereby compromising the outcome of the reproductive attempt (Reid et al. 2002b; Skutch 1976).

(d) **Reduction of energetic costs during incubation**

Parents can reduce the cost of incubation to some extent by constructing a nest with sufficient insulation to minimise heat loss, appropriate nest site selection and brood patch development for efficient transfer of heat to the young (Bailey 1952; Walsberg 1978). However, variation in the effectiveness of such factors as well as ambient climate conditions means that the energetic demand of incubation varies within and between species (Reid et al. 2002b). It is therefore important to have detailed knowledge of microclimate variables when conducting studies concerning the costs of incubation (Tinbergen and Williams 2002).

The energetic cost of incubation to the breeding bird has been analysed in a number of species (Biebach 1981; Croxall 1982; Gessaman and Findell 1979; Gloutney et al. 1996; Grant and Whittow 1983; Hamilton and Gessaman 1981; Thomson et al. 1998; Vleck 1981; Weathers and Sullivan 1985); however, the contribution of the nest to reducing energetic expenditure has largely been overlooked. Furthermore, our understanding of how the local microclimate influences the design of nests is limited. Nest insulation has generally only been qualitatively addressed and studies have focused on only a few species (Kern 1984; Kern and Van Riper 1984; Skowron and Kern 1980; Whittow and Berger 1977).

(e) **Thesis and chapter objectives**

The aim of this dissertation is to detail investigations made into the structural and thermal properties of avian nests. Specifically, the question is asked: Does the nest provide sufficient insulation to ameliorate heat loss from the parent? In addition, what factors influence nest insulation and hence the energetics of the incubating parent?

Nest insulation is expressed in terms of the conductance of heat through the nesting material, where well-insulated nests have low conductance and vice-versa. The total nest conductance is the rate of heat flux (watts) moving across the nest wall per degree of temperature difference between the inside and outside of the nest, based on Newton’s Law of Cooling (Calder III and King 1974; Tracy 1972). Nest conductance is influenced by the thermal conductivity of the nest materials, the surface area of the nest cup and the thickness of the nest wall. Therefore, a well-insulated nest can be achieved by selecting strongly insulating material or large quantities of insulating material (Hilton et al. 2004). I quantify each of these parameters for a range of nests and assess the factors that influence nest design and hence the thermal value of a nest, including the mass of the parent, egg morphology and the ambient microclimate. The following summaries briefly detail the individual approaches used to assess the energetic cost of incubation in birds.

Chapter two presents the results of a study concerning the effect of parent size on the structural and thermal properties of cup-shaped nests. The research is based on 213 cup-shaped nests, from 36 Australian species weighing 8 to 360 g. The nest dimensions and thermal conductance was measured for the nests and
related to the body mass of the incubating adult, using allometric scaling methods. The main findings are discussed and related to three hypothetical models to show that structural support, not insulation, is the primary driver for avian cup-shaped nest design.

Chapter three presents the results of a study concerning the size and shape of avian eggs and how they relate to the design of the nest. The research is based on 36 Australian species weighing 8 to 360 g. A total of ten eggs from each species were assessed – egg length and width were measured and the eggs photographed for digital analyses. A macro script was developed in conjunction with a mathematician to determine the surface area and volume of eggs from photographs. These values were then multiplied out by the number of eggs in a clutch to gain an understanding of how clutch volume relates to the nest cup volume and heat loss from the nest, among other comparisons. The parameters of interest are also assessed against incubating adult body mass using allometric scaling techniques.

Chapter four presents the results of a study on the structural and thermal properties of nests for birds breeding in different temperature, precipitation and altitude conditions. The research is based on 201 cup-shaped nests, from 36 Australian species weighing 8 to 360 g. The nest dimensions and thermal conductance was measured for the nests and related to climate and altitude data obtained from GIS climate maps. The analysis takes the mass of the incubating parent into account due to the known allometric relationships observed in chapter 2. The analysis focuses on breeding season climate using mean temperature and precipitation values, however annual level bioclimatic variables are also considered. The main findings are discussed in relation to nest material choice and nest site selection.

Chapter five outlines the findings of a study on the thermal properties of tawny-crowned honeyeater (Gliciphilla melanops) nests at various levels of water saturation. The research is based on seven nests collected from Ngarkat Conservation Park in South Australia, where G. melanops is known to incubate during inclement weather conditions. The nest dimensions and the thermal conductance were measured for the nests prior to saturation treatments to gain a baseline level of heat loss from the nests. Each nest was then saturated with water and the thermal conductance was again measured at intervals while the nest dried. The thermal conductance, thermal conductivity, vapour conductance and the rate of evaporation from nests at different levels of saturation show variation between nests – a consequence of differences in nest dimensions, which is discussed in relation to the current literature. The effect of water saturation on nest conductance and the consequence of this for the energetics of the incubating parent are examined to reinforce the view that nest site selection is crucial for birds.

Chapter six describes the effect of wind (forced convection) on the rate of heat loss from avian cup-shaped nests. The study involves assessing the thermal conductance of nests of the spiny-cheeked honeyeater (Acanthagenys rufogularis) and yellow-throated miner (Manorina flavigula) under three wind speed conditions. Comparisons are made between the rates of heat loss from nests that are covered with a layer of Styrofoam to represent nests attended by parents, as well as those that are open to represent incubation.
The structural and thermal properties of avian cup-shaped nests recesses. The consequence of the differences in thermal conductance with each treatment is related to the energetics of the incubating parent. The importance of selecting a sheltered nest site is discussed.

Chapter seven reintroduces the importance of the studies, discusses and summarises the findings of Chapters two through to six and puts the findings of each chapter in context with the rest of the findings. There is scope for further research that was not considered in Chapters two to six and these options are also discussed in Chapter seven.

The thesis concludes with a host of appendices, including additional analyses regarding nest design and egg size that supplement the main chapters, as well as species-mean tables, material use and images of nests and eggs to facilitate the understanding of nest design within and between a species.
CHAPTER 2

STRUCTURAL SUPPORT, NOT INSULATION, IS THE PRIMARY DRIVER
FOR AVIAN CUP-SHAPED NEST DESIGN

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STATEMENT OF AUTHORSHIP

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HEENAN, C. B. (Candidate)

Lead study design, constructed equipment, collected all data and performed statistical analyses, interpreted data, wrote manuscript and acted as corresponding author

I hereby certify that the statement of contribution is accurate.

Signed Date 27/02/2013

SEYMOUR, R. S.

Provided feedback on study design, supervised development of work, helped in data interpretation and manuscript evaluation

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis.

Signed Date 27/02/2013
ABSTRACT

The nest microenvironment is a widely studied area of avian biology, however, the contribution of nest conductance (the inverse of insulation) to the energetics of the incubating adult and offspring has largely been overlooked. Surface-specific thermal conductance (W °C⁻¹ cm⁻²) has been related to nest dimensions, wall porosity, height above ground and altitude, but the most relevant measure is total conductance (G, mW °C⁻¹). This study is the first to analyse conductance allometrically with adult body mass (M, g), according to the form G = aMᵇ. We propose three alternative hypotheses to explain the scaling of conductance. The exponent may emerge from: heat loss scaling (M⁰.⁴⁸) in which G scales with the same exponent as thermal conductance of the adult bird, isometric scaling (M⁰.₃₃) in which nest shape is held constant as parent mass increases, and structural scaling (M⁰.₂₅) in which nests are designed to support a given adult mass. Data from 213 cup-shaped nests, from 36 Australian species weighing 8 to 360 g, show conductance is proportional to M⁰.₂₅. This allometric exponent is significantly different from those expected for heat loss and isometric scaling and confirms the hypothesis that structural support for the eggs and incubating parent is the primary factor driving nest design.

Keywords: bird nest design; insulation; thermal conductance; scaling; allometry; reproductive energetics
1. INTRODUCTION

Birds’ nests have evolved into many shapes and sizes, but all function to provide a secure substrate for eggs and hatchlings, camouflage and defence from predators, as well as moderate the microenvironment (temperature, humidity, gas composition) surrounding the eggs and hatchlings (Ar and Sidis 2002; Collias and Collias 1984; Hansell 2000). Of the variables that influence the nest microenvironment, nest temperature is among one of the most widely studied (Bartholomew et al. 1976; Caccamise and Weathers 1977; Hadley 1969; Howell and Dawson 1954; Orr 1970; Ricklefs and Hainsworth 1969; Webb 1987; White et al. 1975), because of its importance for development and growth of young (Ar and Sidis 2002; Deeming and Ferguson 1991). Maintenance of nest temperature may conflict with the life demands of the parent birds – such as the need to leave the nest to forage and to conserve energy while incubating (Ar and Sidis 2002). Whether the parent’s energy requirement increases during incubation of eggs is not clear. Some studies show an increase in metabolic heat production (Gloutney et al. 1996; Haftorn and Reinertsen 1985; Töien et al. 1986), while others show that resting metabolism of incubating birds can be lower than that of non-incubating individuals due to the insulation provided by the nest and appropriate nest site selection (Hilton et al. 2004; Walsberg 1978; Walsberg and King 1978). Furthermore, the energy demands of the parent and offspring may increase after hatching (Ricklefs 1983; Williams 1996). Therefore, in addition to attenuating changes in egg temperature, well-insulated nests may also provide an environment in which the energy reserves of the parents and hatchlings may be conserved at low ambient temperatures.

It is reasonable that heat loss can be minimised by optimising the physical structure and location of the nest (Hilton et al. 2004; Reid et al. 2000b). The energy invested to maintain egg temperature and re-warm clutches that have cooled during incubation recesses can influence the outcome of current or subsequent breeding attempts (Reid et al. 2000b; Tinbergen and Williams 2002). A reduced energetic demand of incubation can enable parents to invest more to care of the offspring later in the breeding attempt, in turn increasing fledging success, or have indirect fitness consequences such as an increase in clutch size and decreased incubation periods (Reid et al. 2000b; Tinbergen and Williams 2002). The energetic demand of incubation largely depends on the rate at which heat energy is lost from the clutch and incubating parent (Hilton et al. 2004). Therefore nest insulation is arguably important to the lifetime reproductive success of birds. Yet, it is surprising that there are few investigations of the thermal properties of nests.

Nest insulation is expressed in terms of the conductance of heat through the nesting material, where well-insulated nests have low conductance and vice-versa. Surface-specific nest conductance has been investigated in a number of studies that have reported relationships with nest mass (Kern 1984), thickness (Kern 1984; Skowron and Kern 1980; Whittow and Berger 1977), depth (Kern 1984), wall porosity (Kern 1984; Kern and Van Riper 1984; Skowron and Kern 1980), surface area, height above ground (Kern 1984) and elevation above sea level (Kern and Van Riper 1984). However surface-specific conductance is an inadequate descriptor of the quality of a nest in terms of the amount of energy that the incubating bird has to
expend to maintain the nest temperature. More important to the energetics of the bird is the total conductance of the nest, which is the total quantity of heat that passes through the nest per degree of temperature difference between the inside and outside, based on Newton’s Law of Cooling (Calder III and King 1974; Tracy 1972). Remarkably, total conductance has been measured in only one species, the Eurasian tree sparrow (*Passer montanus*) (Pinowski et al. 2006). That study measured total conductance of the parent and nest and found that nest-lining within a nest-box decreased conductance from the bird by 23 to 36 percent, in comparison to an empty nest-box that decreased heat loss by 18 percent.

Two nests could have the same surface-specific conductance, but have greatly different rates of heat loss under the same conditions, if they were different sizes. Therefore the only way to assess the thermal qualities of nests of different sizes is to measure total conductance and analyse it allometrically, that is in relation to size. Allometric relationships are of the form \( y = aM^b \), where \( y \) is the measured variable of interest and \( M \) is body mass (Schmidt-Nielsen 1984). The ‘\( a \)’ value defines the elevation (height) of the curve and the exponent ‘\( b \)’ describes the way the curve bends. Allometric relationships with a positive exponent describe an increase in the variable of interest as body mass increases, whereas negative exponents describe a decrease. Examination of the scaling exponents provides insights to the factors that affect nest construction. In particular, we pose three alternative hypotheses and test the data against them.

**Heat loss scaling:** If insulation is a major factor in the evolution of nest design, thermal conductance would be related to the heat transfer from the incubating parent, which is in turn a function of plumage conductance (Wolf and Walsberg 2000). Therefore, thermal conductance would scale with adult bird body mass with an exponent of 0.48 (Schleucher and Withers 2001). Such scaling would support an insulating function.

**Isometric scaling:** If nest size is proportional to bird size, then the nest should increase isometrically, in which case thermal conductance would scale to the 0.33 power. This exponent emerges because conductance \( (M^{0.33}) \) is proportional to the ratio of surface area \( (M^{0.67}) \) divided by thickness \( (M^{0.33}) \).

**Structural scaling:** If structural considerations of nest construction are of primary importance, then the nest must be able to support the combined weight of the bird, the young and the nest itself, which are assumed to be proportional to the body mass of the adult bird. In this case, nest thermal conductance would be secondarily related to nest mass.

According to engineering principles, the mass of supporting structures scales to the mass of the supported object with an exponent of 1.33 (Schmidt-Nielsen 1984). The exponent deals with an entirely self-supporting structure, similar to the ideal mass of the skeleton to support an animal’s mass (Prange et al. 1979). In the case of a nest, the exponent takes into account support of not only the nest itself, but also the clutch and parent. The exponent stems from the fact that the mass of the object must be proportional to the surface area that supports them. To normalise the stress on the cross-sectional surface area of a supporting structure, its area should scale proportionally with mass, that is, with an exponent of 1.0. However area is two-
dimensional and therefore the third linear dimension, which scales with mass to the exponent 0.33, must be added to achieve the three-dimensional, self-supporting structure (Schmidt-Nielsen 1984).

Assuming that (1) the nest is a thick-walled hemisphere made of a material with a constant thermal conductivity, (2) the nest maintains the same shape as it increases in size, and (3) the nest wall volume scales with bird mass to the 1.33 power (Prange et al. 1979; Schmidt-Nielsen 1984), then the total conductance should scale with bird mass to the 0.25 power. This exponent emerges from geometry because conductance ($M^{0.25}$) is proportional to geometric mean surface area ($M^{0.77}$) divided by nest thickness ($M^{0.52}$). The higher exponent for nest volume ($M^{1.33}$) increases the external diameter of the nest. This in turn raises the exponents for nest thickness and surface area above what would be expected based on isometric scaling.
2. METHODS

Nests used in this study were borrowed from the South Australian Museum and Queensland Museum ornithology collections. A total of 213 nests (from 36 species) were included in the study, of which 189 nests (across 36 species) were from the South Australian Museum ornithological collection and 24 nests (across 8 species) were from the Queensland Museum ornithological collection (nest images in Appendix 1).

Nests were measured from species that construct cup-shaped nests over a range of parent sizes from 8 to 360 g. Nests were selected for measurement if they were in a good condition and had no branches obscuring the opening of the nest. Nests that were damaged were excluded from analyses. Nests that were soiled with chick faeces were not excluded from analyses as the data did not influence the slope \( F_{1,43} = 0.55, P = 0.46, N = 47 \) or elevation \( F_{1,44} = 0.42, P = 0.52, N = 47 \) of the nest conductance relationship. An analysis of covariance showed no significant difference between the regressions of the entire data set and a reduced data set with \( n > 3 \) nests per species \( F_{1,32} = 0.19, P = 0.66, N = 36 \) and so all species were included in the allometric analyses. We acknowledge the small number of replicates for some species in this study and suggest that museums should try to increase the number of samples in their collections, as this will aid further comparative studies.

It is reasonable that as hatchlings grow, they may compact the nest and therefore influence the thermal properties of the nest. However, we found no significant difference between nests that had been occupied by hatchlings or those that had been collected during the incubation period with respect to nest thickness (among slopes: \( F_{1,19} = 0.18, P = 0.68, N = 23 \); among elevations: \( F_{1,20} = 0.01, P = 0.93, N = 23 \)) or nest conductance (among slopes: \( F_{1,19} = 0.69, P = 0.42, N = 23 \); among elevations: \( F_{1,20} = 0.14, P = 0.71, N = 23 \)). Furthermore, many of the nests did not have information supporting the use of the nest. Therefore, data were pooled for analyses and no differentiation was made between nests that had been occupied by hatchlings or those that had been collected prior to egg-laying.

The influence of clutch mass was not taken into account in this study. The total mass of the nest \( (M^{1.36}) \), clutch \( (M^{0.61}) \) and incubating parent \( (M^{0}) \) has an exponent of between 1.07 (biparental care) to 1.11 (uniparental care) during incubation (Saether 1985). If we assume that chick mass is close to parent mass just prior to fledging, the exponent for nest contents at this time ranges from 1.04 for a clutch of five chicks to 1.08 for a clutch of one. As this covers the clutch size range of the species included in this study and the exponents are close to that of parent mass alone \( (M^{0}) \), it is clear that clutch mass is unlikely to significantly influence the outcome of the study (Marchant and Higgins 2001; 2002; 2006).

To ensure that there was no bias in the data arising from nest degradation within the collection, individual nests with time information available were analysed according to the year the nest was collected, as well as the year the nest was catalogued in the collection. There was no significant influence of nest age (years) on the thermal conductivity of the nest materials (year collected: \( F_{1,144} = 1.58, P = 0.21, N = 186 \); year catalogued: \( F_{1,136} = 3.55, P = 0.06, N = 180 \)). In addition, all nests included in this study were from museum collections,
stored in a similar way. Therefore consistency in the storage methods should help to eliminate any bias resulting from degradation and storage. A repeated measures analysis of nest conductance, immediately following the breeding season and after an extended period of storage, may assist in the understanding of nest degradation for further comparative studies.

(a) Nest dimensions

The physical dimensions of the nests were measured (Figure 2.1), including the nest thickness (X) and internal / external diameter (d) and height (h), to enable calculations of the nest surface area (A). Nest dimensions were accurately measured with callipers and a micrometer to the nearest millimetre. Nests were weighed on a Mettler digital analytical balance (model AE163, Zürich, Switzerland). Those with supporting structures still attached were excluded from nest weight analyses. The pendulum of *Rhipidura albiscapa* nests was not included in nest dimension measurements, but is reported in Supplement 2.2.

![Diagram of nest dimensions](image.png)

*Figure 2.1. A diagram representative of a nest showing the dimensions used to calculate nest surface area. Both internal (light grey) and external (dark grey) nest surface area were calculated to obtain the geometric mean surface area.*

The internal and external nest surface area (A) was approximated using the equation for half of a prolate spheroid (Equation 2.1).

\[
A = \pi \left( \frac{d^2}{4} + \frac{dh}{2e} \sin^{-1} e \right)
\]

(2.1)

where:

- **A** = Surface area (cm\(^2\))
- **d** = Nest diameter (cm)
- **h** = Nest height (cm)
- **e** = Eccentricity = \( \sqrt{1 - \left( \frac{d^2}{4h^2} \right)} \)
Internal surface area was calculated using values for internal height and diameter, while external surface area was calculated using values for external height and diameter (Figure 2.1). Average surface area (\( \bar{A} \)) is the geometric mean of the internal and external surface area. The geometric mean is used as this normalises the ranges being averaged and represents the central tendency of the two surface areas.

(b) **Total nest conductance**

The total thermal conductance (\( G, \text{ mW} \; ^\circ\text{C}^{-1} \)) of the nests was measured by placing an artificial heat source inside the nest and measuring the heat flow out through the wall (\( \Phi \)), in relation to the temperature difference (\( \Delta T \)).

To prevent forced convection by the fan through the nest, they were lined with aluminium foil (Figure 2.2). The surface of the foil was heated to 40 °C with a 10 W (12 V, 0.83 A) globe. The heated air within the aluminium hemisphere was circulated with a 2.5 cm fan, mounted above the heat source. The opening of the nest was insulated with a 23 mm thick layer of Styrofoam and cotton padding sealed the lip against air leaks. The temperature inside the hemisphere was measured with a LM35DZ temperature sensor and the power supplied to the globe was varied to achieve constant temperature. This occurred automatically, as the globe and temperature sensor were connected to a custom-built controlled temperature power monitor employing a feedback system.

The voltage supplied to the globe was recorded in a chart application using AD Instruments Powerlab (model ML750, Castle Hill, Australia) and the current sent through the globe was measured with a Tektronix TX3 multimeter (Beaverton, U.S.A.). The power used to operate the fan (\( \Phi_{\text{FAN}} \)) is released as heat and this offsets the power requirement of the globe (\( \Phi_{\text{GLOBE}} \)). Consequently, the voltage and current sent through the fan was determined using a Tektronix TX3 multimeter prior to the study. The total power (\( \Phi \)) required to keep a stable nest temperature was calculated by multiplying the voltage and current from the globe and adding this to the product of voltage and current from the fan, according to Equation 2.2.

\[
\Phi = (VI)_{\text{GLOBE}} + (VI)_{\text{FAN}} \quad (2.1)
\]

where:

- \( \Phi \) = Heat production rate (W)
- \( V \) = Voltage (V)
- \( I \) = Current (A)
The structural and thermal properties of avian cup-shaped nests


The measurements were carried out in a 5 °C constant temperature cabinet. Air flow around the nest was minimised to eliminate the effect of convection on the measurements by placing a large cardboard box around the equipment within the cabinet.

Three thermocouples were placed inside the nest and three outside the nest, against the nest, to measure the average temperature gradient across the nest wall. To determine thermocouple placement, nest height was divided into thirds and each thermocouple was positioned such that it rested in the centre of each 1/3 height division. This was done for each nest to accurately represent the mean temperature gradient across the nest. Temperatures were logged on a data logger (model 1023, Grant Instruments, Cambridge, England).

The equipment was set up to heat the nest with measurements obtained following equilibration of the heat production rate data trace in the AD Instruments chart application. Equilibration took between 30 and 120 min.

Using the temperature gradient across the nest wall and the power required to keep a stable nest temperature, the thermal conductance of the nest (G, mW °C⁻¹) was calculated using Equation 2.3, based on Newton’s Law of Cooling (Calder III and King 1974; Tracy 1972).

\[ G = \frac{\Phi}{T_i - T_e} \]  

(2.2)
where the new symbols are:

\( G \) = Nest thermal conductance (mW °C⁻¹)
\( T_I \) = Internal temperature (°C)
\( T_E \) = External temperature (°C)

and the new units used are:

\( \Phi \) = Heat production rate (mW)

The total conductance of the system is equal to the sum of the nest conductance and the Styrofoam lid conductance. The conductance of the lid (\( G_{\text{LID}} \)) was calculated by replacing the nest with a polystyrene coffee cup and measuring the conductance of the system before adding a second and a third cup. Adding a second cup halved the conductance of the ‘nest’ or cup portion of the system, allowing the conductance of the lid to be calculated, according to Equation 2.4. The Styrofoam lid conductance was confirmed for each measurement by adding a third cup and calculating lid conductance according to Equations 2.5 and 2.6.

\[
G_{\text{LID}} = \left( \frac{2\Phi}{T_I - T_E} \right)_{2\text{cups}} - \left( \frac{\Phi}{T_I - T_E} \right)_{1\text{cup}}
\]

(2.3)

\[
G_{\text{LID}} = \left( \frac{3\Phi}{T_I - T_E} \right)_{3\text{cups}} - \left( \frac{2\Phi}{T_I - T_E} \right)_{2\text{cups}}
\]

(2.4)

\[
G_{\text{LID}} = \frac{\left( \frac{3\Phi}{T_I - T_E} \right)_{3\text{cups}} - \left( \frac{\Phi}{T_I - T_E} \right)_{1\text{cup}}}{2}
\]

(2.5)

where the new symbols are:

\( G_{\text{LID}} \) = Lid thermal conductance (mW °C⁻¹)

This process was repeated eight times and the average lid conductance was then determined from the conductance values obtained from each calculation (Equation 2.4, 2.5 and 2.6, \( N = 24 \)). Surface-specific conductance for the Styrofoam lid (\( G_{A-LID} \)) was then determined from the average lid conductance divided by the surface area of the cup opening (Equation 2.7).

\[
A_{\text{LID}} = \pi \frac{d_{I}^2}{4}
\]

(2.6)

where the new symbols are:

\( A_{\text{LID}} \) = Surface area of the cup or nest opening (cm²)
\( d_{I} \) = Internal nest diameter (cm)
For each nest, the surface-specific lid conductance was then multiplied by the surface area of the nest opening \( (A_{\text{LID}}, \text{Equation } 2.7) \), in order to obtain the total lid conductance \( (G_{\text{LID}}) \) for each nest. This was then subtracted from the total conductance of the nest system to obtain a value for nest conductance \( (G) \).

(c) **Surface-specific nest conductance**

The surface-specific conductance \( (G_A, W \, °C^{-1} \, m^{-2}) \) was calculated by dividing the total conductance by the geometric mean surface area of the nest.

(d) **Nest thermal conductivity**

The thermal conductivity \( (k, mW \, °C^{-1} \, m^{-1}) \) of the materials used in each nest was calculated using the surface area and thickness of the nest, according to Equation 2.8.

\[
k = G \frac{X}{\bar{A}}
\]

where the new symbols are:

- \( k \) = Material thermal conductivity \( (mW \, °C^{-1} \, m^{-1}) \)
- \( X \) = Mean nest thickness \( (m) \)
- \( \bar{A} \) = Geometric mean of the internal and external surface area \( (m^2) \)

Thermal conductivity relates to the nest alone (nest material and air spaces between materials) in the present study, as thermocouples were placed against the internal and external surfaces of the nest wall. While there are likely to be boundary layer effects that influence the thermal properties of nests, these were not accounted for due to the indefinite limits of boundary layers and increasing boundary layer thickness with nest size.

(e) **Parent mass**

Parent mass values for each species were obtained from the Handbook of Australian, New Zealand and Antarctic Birds resource series (Marchant and Higgins 2001; 2002; 2006) to enable allometric analyses. The mean of the male and female mass values was used for each species where reported. For those where a mean value was not reported, the mean of the minimum and maximum mass values was used.

(f) **Hemispherical nest model**

A model was developed to explain the allometric relationships between the mass of an incubating bird and the structural and thermal properties of a nest. The hemispherical nest properties were calculated according to heat loss scaling, isometric proportionality and structural support scaling. This was conducted to determine which factor has the most influence on the physical dimensions and thermal properties of the nests measured in this study.
**i. General assumptions**

The modelled nest was assumed to be a hemisphere with a geometric mean surface area between the inside and outside surfaces of the hemisphere. The nest was assumed to have uniform wall strength and thickness and for the weight of contents to push out uniformly from within and against the inner surface of the nest. The nest was assumed to maintain shape as it increases in size. The incubating bird was assumed to be a sphere with a density of 0.9 (median of the minimum and maximum values for 12 species of wet and plucked birds) \( (\text{Hamershock et al. 1993}) \) and volume \( (V_B) \) equal to bird mass divided by density.

Nest thermal conductivity was assumed to be equal to the average for all nests measured in the study irrespective of species \( (k = 1.467 \text{ mW °C}^{-1} \text{ cm}^{-1}) \) and independent of parent mass. Initial nest thickness \( (X, M = 1 \text{ g}) \) used in the model was obtained from the allometric intercept at \( M = 1 \text{ g} \) for nest thickness obtained in this study \( (X = 0.3 \text{ cm}) \). Input assumptions and conditions for thickness and thermal conductivity were used for all modelled comparisons.

The internal diameter and height was calculated for the hemispherical nest model according to Equations 2.9 and 2.10. The internal diameter and height was used for all three hypotheses.

\[
d_i = 2 \left( \frac{3V_B}{4\pi} \right)^{0.33} \tag{2.8}
\]

\[
h_i = \left( \frac{3V_B}{4\pi} \right)^{0.33} \tag{2.9}
\]

where the new symbols are:

\[
V_B = \text{Bird volume (mL)} = \frac{\text{Bird mass}}{\text{Bird density}}
\]

\[
h_i = \text{Internal nest height (cm)}
\]

**ii. Heat loss scaling**

If insulation is a major factor in the evolution of nests then thermal conductance would be related to the heat transfer from the incubating parent, which is in turn a function of plumage conductance \( (\text{Wolf and Walsberg 2000}) \). Therefore, thermal conductance would scale with adult bird body mass with an exponent of 0.48 \( (\text{Schleucher and Withers 2001}) \). Plumage conductance was assumed to be equal to the wet thermal conductance of birds in the rest phase. Consequently, nest conductance was modelled using Equation 2.11, where ‘a’ is the value of conductance at \( M = 1 \text{ g} \) \( (16.6 \text{ mW °C}^{-1} \text{ m}^{-1}) \). The dimensions of a hemispherical nest under heat loss scaling were modelled, including the external diameter (Equation 2.12), nest mass (Equation 2.13), external height (Equation 2.14), thickness (Equation 2.15) and surface area (Equation 2.16). Equations
The structural and thermal properties of avian cup-shaped nests

2.12 to 2.16 were derived from stepwise transpositions of standard equations for the dimensions of a hemispherical shell and Equation 2.8.

\[ G = aM^{0.48} \]  
\[ d_E = -\left(\frac{d_i G}{\pi d_k} - G\right) \]  
\[ M_N = \pi \left(\frac{d_E^3 - d_i^3}{12}\right) \]  
\[ h_E = \left(\frac{3M_N}{2\pi} + h_i^3\right)^{0.33} \]  
\[ X = \frac{d_E - d_i}{2} \]  
\[ \bar{\Lambda} = \pi \frac{d_E d_i}{2} \]

where the new symbols are:
- \( d_E \) = External nest diameter (cm)
- \( M_N \) = Nest mass (g), equivalent to nest volume (\( V_N \), mL), assuming 1 g = 1 mL
- \( h_E \) = External nest height (cm)

and the new units used are:
- \( X \) = Mean nest thickness (cm)
- \( \bar{\Lambda} \) = Geometric mean of the internal and external surface area (cm\(^2\))

### iii. Isometric scaling

If nest size is proportional to bird size, then the nest dimensions should increase isometrically. Isometric (‘iso’ = same, ‘metric’ = measure) scaling refers to the concept of geometric similarity, which is governed by the square-cube law (Galilei 1914). That is, if an object exhibits a constant shape regardless of size, then the surface area and linear dimensions and volume will be related to each other, as well as to the mass of the object (Schmidt-Nielsen 1984). As a result, linear functions should scale to the 0.33 power (\( M^{1/3} \)) and surface area to the 0.67 power (\( M^{2/3} \)) of nest volume. Nest thickness was modelled using Equation 2.17, where ‘a’ is the nest thickness at \( M = 1 \) g from the nest data. The dimensions of a hemispherical nest under isometric scaling were modelled using stepwise transpositions of standard equations for the dimensions of a
hemispherical shell, including nest mass (Equation 2.13), surface area (Equation 2.16), external diameter (Equation 2.18), external height (Equation 2.19). Nest conductance was then modelled according to Equation 2.20 (a transposition of Equation 2.8).

\[ X = aM^{0.33} \quad (2.16) \]

\[ d_e = d_i + 2X \quad (2.17) \]

\[ h_e = h_i + X \quad (2.18) \]

\[ G = \frac{\bar{A}}{X} \quad (2.19) \]

where the new units used are:

\[ k \quad = \text{Material thermal conductivity (mW} \ °C^{-1} \ \text{cm}^{-1}) \]

iv. Structural scaling

The mass of supporting structures scales to the mass of the supported object with an exponent of 1.33 (Prange et al. 1979; Schmidt-Nielsen 1984). This exponent stems from the fact that the mass of the object must be proportional to the surface area that supports them. Cross-sectional surface area of a supporting structure should scale with mass to the exponent of 1.0, however, it is two-dimensional and therefore the linear dimension, which scales with mass to the exponent 0.33, must be added to achieve the three-dimensional nest. Consequently, nest mass was modelled according to Equation 2.21, where ‘a’ is the value for nest mass at \( M = 1 \text{ g} \) (1.2 g). The dimensions of a hemispherical nest under structural scaling were then modelled using stepwise transpositions of standard equations for the dimensions of a hemispherical shell, including the external height (Equation 2.14), nest thickness (Equation 2.15), surface area (Equation 2.16) and external diameter (Equation 2.22). Nest dimensions and thermal conductivity were then used to model nest conductance according to Equation 2.20 (a transposition of Equation 2.8).

\[ M_N = aM^{1.33} \quad (2.20) \]

\[ d_e = 2\left(\frac{12M_N + d_i^3}{8\pi}\right)^{0.33} \quad (2.21) \]

Modelled dimensions for hemispherical nests ranging in size were regressed against mass of the model bird. The scaling exponent values produced by the model (Table 2.1) were then used to inform us as to whether total nest conductance and dimensions are related to heat loss from the parent or structural support.
Table 2.1. Model output for the allometric relationship between parent mass (M, g) and the dimensions and thermal properties of a hemispherical object according to $y = aM^b$ for heat loss, isometric and structural scaling

<table>
<thead>
<tr>
<th>Nest parameter</th>
<th>Heat loss scaling</th>
<th>Isometric scaling</th>
<th>Structural scaling</th>
</tr>
</thead>
<tbody>
<tr>
<td>Internal diameter / height (d_i / h_i, cm)</td>
<td>$M^{0.33}$</td>
<td>$M^{0.33}$</td>
<td>$M^{0.33}$</td>
</tr>
<tr>
<td>External diameter / height (d_e / h_e, cm)</td>
<td>$M^{0.30}$</td>
<td>$M^{0.33}$</td>
<td>$M^{0.43}$</td>
</tr>
<tr>
<td>Thickness (X, cm)</td>
<td>$M^{0.15}$</td>
<td>$M^{0.33}$</td>
<td>$M^{0.52}$</td>
</tr>
<tr>
<td>Surface area (Å, cm²)</td>
<td>$M^{0.64}$</td>
<td>$M^{0.67}$</td>
<td>$M^{0.77}$</td>
</tr>
<tr>
<td>Volume (V, ml) or mass (M_N, g)</td>
<td>$M^{0.78}$</td>
<td>$M^{1.00}$</td>
<td>$M^{1.33}$</td>
</tr>
<tr>
<td>Total nest conductance (G, mW °C⁻¹)</td>
<td>$M^{0.48}$</td>
<td>$M^{0.33}$</td>
<td>$M^{0.25}$</td>
</tr>
</tbody>
</table>

Nest model output values represent the exponent (slope, b) of the regression mean according to the allometric relationship $y = aM^b$. N = 81 for all comparisons. Scaling exponents were derived from modelled hemispherical object dimensions (Equations 2.9 to 2.22), regressed against model bird mass.

(g) Statistical analyses

Statistical analyses on allometric relationships were performed in JMP IN (SAS Institute (2001), version 4.0.4) using linear regression techniques on log-transformed data. ANCOVA techniques were used to test if multiple regression slopes differed and to test the model output values against nest data. Residuals of the data met the assumptions required for parametric linear regression tests of normality (Shapiro-Wilk W Test) and equal variance (constant spread of the residuals). The significance value was set at 0.05 for all analyses. Data are expressed as mean ± 95 % C.I.
3. RESULTS

Nest thermal properties are significantly correlated with parent mass (Table 2.2). Values for each species are listed in Appendix 2. Nest conductance scales positively with parent mass (Figure 2.3.a). The scaling exponent is 0.25, which is equivalent to the expected exponent for a load-bearing structure, but differs significantly from that of an isometric object and an object designed to prevent heat loss (Table 2.3). The scaling exponent of nest mass is 1.36 (Figure 2.3.b), which is also not significantly different from the expected exponent of 1.33, on structural grounds (Table 2.3). Nest dimensions are also significantly correlated with parent mass (Table 2.2). Values for each species are listed in Appendix 3. Nest thickness (M^{0.49}, Figure 2.4.b) and external diameter (M^{0.42}, Figure 2.4.c) have a scaling exponent higher than that of isometric or heat loss scaling but not significantly different to that of a structural object (Table 2.3). Internal diameter (M^{0.35}, Figure 2.4.c) has a scaling exponent higher than would be expected based on isometric, structural and heat loss scaling. On the other hand, the scaling exponent for internal nest height (M^{0.26}, Figure 2.4.d) is statistically lower than that for isometric, structural and heat loss scaling. The scaling exponent for external nest height (M^{0.32}, Figure 2.4.d) is statistically similar to isometric and heat loss scaling but differs significantly from scaling of a structural object. Furthermore, the scaling exponent for nest surface area (M^{0.68}, Figure 2.4.a) is statistically indistinguishable from that of an isometric object; however it differs significantly from that of a structural object as well as an object designed to prevent heat loss.

There is a distinct pattern for nest diameter to increase at a greater rate in comparison to nest height as bird mass increases. This is true for both internal (F_{1,68} = 9.35, P = 0.003, N = 72) and external (F_{1,38} = 4.23, P = 0.04, N = 72) dimensions. Therefore large birds build nests that are shallower than the nests of small birds.

Surface-specific conductance scales negatively with parent mass (Figure 2.5.a). Large birds build nests that have a lower conductance per unit area compared to small birds. On the other hand, the conductance value of the materials used in the nest, as determined by the thermal conductivity, is independent of parent mass (Figure 2.5.b).
Table 2.2. Allometric relationships between parent mass (M, g) and the dimensions and thermal properties of avian cup-shaped nests according to $y = aM^b$

<table>
<thead>
<tr>
<th>nest parameter</th>
<th>intercept, a</th>
<th>scaling exponent, b</th>
<th>$R^2$</th>
<th>$F$ ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>internal diameter ($d_i$, cm)</td>
<td>2.03 ± 1.09</td>
<td>0.35 ± 0.02</td>
<td>0.96</td>
<td>865.23*</td>
</tr>
<tr>
<td>external diameter ($d_e$, cm)</td>
<td>2.35 ± 1.18</td>
<td>0.42 ± 0.04</td>
<td>0.91</td>
<td>352.99*</td>
</tr>
<tr>
<td>internal height ($h_i$, cm)</td>
<td>1.74 ± 1.24</td>
<td>0.26 ± 0.06</td>
<td>0.70</td>
<td>78.65*</td>
</tr>
<tr>
<td>external height ($h_e$, cm)</td>
<td>2.05 ± 1.34</td>
<td>0.32 ± 0.08</td>
<td>0.66</td>
<td>65.12*</td>
</tr>
<tr>
<td>thickness ($X$, cm)</td>
<td>0.30 ± 1.64</td>
<td>0.49 ± 0.14</td>
<td>0.61</td>
<td>53.24*</td>
</tr>
<tr>
<td>nest mass ($M_N$, g)</td>
<td>0.17 ± 3.77</td>
<td>1.36 ± 0.39</td>
<td>0.67</td>
<td>51.09*</td>
</tr>
<tr>
<td>surface area ($\bar{A}$, cm$^2$)</td>
<td>11.65 ± 1.29</td>
<td>0.68 ± 0.07</td>
<td>0.92</td>
<td>394.33*</td>
</tr>
<tr>
<td>total nest conductance ($G$, mW °C$^{-1}$)</td>
<td>43.98 ± 1.31</td>
<td>0.25 ± 0.08</td>
<td>0.57</td>
<td>44.59*</td>
</tr>
<tr>
<td>surface-specific nest conductance ($G_s$, W °C$^{-1}$ m$^{-2}$)</td>
<td>37.74 ± 1.42</td>
<td>-0.44 ± 0.10</td>
<td>0.71</td>
<td>81.44*</td>
</tr>
<tr>
<td>thermal conductivity ($k$, mW °C$^{-1}$ m$^{-1}$)</td>
<td>111.61 ± 1.50</td>
<td>0.06 ± 0.11</td>
<td>0.03</td>
<td>1.09</td>
</tr>
</tbody>
</table>

Statistics include the intercept of the regression mean (a) and scaling exponent (slope, b) according to the allometric relationship $y = aM^b$, as well as the correlation coefficient ($R^2$) and $F$ ratio. The intercept and scaling exponent values represent the mean ± 95% C.I. for all species.

* Indicates that there is a significant effect of parent mass on the variable ($P < 0.0001$ at $\alpha = 0.05$) in all cases with exception to thermal conductivity which was not significantly related to mass ($P = 0.30$).

N = 36 and DF = 1,34 for all comparisons except nest mass which has N = 27 and DF = 1,25. The replicate for the nest mass measurements is lower as some nests were excluded from analysis due to the attachment of supporting branches.
Figure 2.3. Relationship between parent mass (M, g) and a – total nest conductance (mW °C⁻¹, $G = 43.98 \times M^{0.25}$) and b – nest mass (g, $M_N = 0.17 \times M^{1.36}$) for cup-shaped birds' nests. Each point represents the mean ± 95% C.I. for a species of bird (N[a] = 36, N[b] = 27). Solid lines (-----) represent the regression mean. Black dashed lines (.........) represent the 95% confidence bands for the regression mean. Grey lines represent the modelled regression for heat loss scaling (.........), isometric scaling (---) and structural scaling (-- -- --).
Table 2.3. Model predictions for the allometric relationship between parent mass ($M$, g) and the dimensions and thermal properties of a hemispherical object according to $y = aM^b$ for heat loss, isometric and structural scaling, and tests for significant differences between actual scaling exponents (Table 2.1) and predictions

<table>
<thead>
<tr>
<th>Nest parameter</th>
<th>Heat loss scaling</th>
<th>Isometric scaling</th>
<th>Structural scaling</th>
</tr>
</thead>
<tbody>
<tr>
<td>Internal diameter (d$_i$, cm)</td>
<td>$M^{0.33}$</td>
<td>$F = 7.41, P = 0.01^*$</td>
<td>$F = 7.41, P = 0.01^*$</td>
</tr>
<tr>
<td>External diameter (d$_e$, cm)</td>
<td>$M^{0.30}$</td>
<td>$F = 65.18, P &lt; 0.001^*$</td>
<td>$F = 34.48, P &lt; 0.001^*$</td>
</tr>
<tr>
<td>Internal height (h$_i$, cm)</td>
<td>$M^{0.33}$</td>
<td>$F = 16.69, P &lt; 0.001^*$</td>
<td>$F = 16.69, P &lt; 0.001^*$</td>
</tr>
<tr>
<td>External height (h$_e$, cm)</td>
<td>$M^{0.30}$</td>
<td>$F = 0.63, P = 0.43$</td>
<td>$F = 0.20, P = 0.66$</td>
</tr>
<tr>
<td>Thickness (X, cm)</td>
<td>$M^{0.15}$</td>
<td>$F = 62.58, P &lt; 0.001^*$</td>
<td>$F = 13.92, P &lt; 0.001^*$</td>
</tr>
<tr>
<td>Surface area (A, cm$^2$)</td>
<td>$M^{0.64}$</td>
<td>$F = 4.80, P = 0.03^*$</td>
<td>$F = 0.57, P = 0.45$</td>
</tr>
<tr>
<td>Volume (V, ml) or mass (M$_N$, g)</td>
<td>$M^{0.78}$</td>
<td>$F = 33.94, P &lt; 0.001^*$</td>
<td>$F = 13.41, P &lt; 0.001^*$</td>
</tr>
<tr>
<td>Total nest conductance (G, mW °C$^{-1}$)</td>
<td>$M^{0.48}$</td>
<td>$F = 99.12, P &lt; 0.001^*$</td>
<td>$F = 13.36, P &lt; 0.001^*$</td>
</tr>
</tbody>
</table>

Nest thermal properties model output values represent the exponent (slope, $b$) of the regression mean according to the allometric relationship $y = aM^b$. The scaling exponent values represent the mean for all masses. Accompanying statistics include the $F$-ratio and $P$-value for the ANCOVA comparisons between the model predictions and real nest data.

* Indicates that the scaling exponent for the model output and real nest data are statistically different at the specified alpha value ($\alpha = 0.05$) following Bonferroni adjustment.

N = 117 and DF = 1,113 for all comparisons, except nest mass, which has N = 108 and DF = 1,104. The replicate for the nest mass measurements is lower as some nests were excluded from analysis due to the attachment of supporting branches.
Figure 2.4. Relationship between parent mass (M, g) and a – nest surface area (cm$^2$, $\bar{A} = 11.65 \times M^{0.68}$), b – nest thickness (cm, $X = 0.30 \times M^{0.49}$), c – internal (●, solid black line) diameter (cm, $d_i = 2.03 \times M^{0.35}$) and external (Φ, solid grey line) diameter (cm, $d_e = 2.35 \times M^{0.42}$) and d – internal (●, solid black line) height (cm, $h_i = 1.74 \times M^{0.26}$) and external (Φ, solid grey line) height (cm, $h_e = 2.05 \times M^{0.32}$). Each point represents the mean ± 95% C.I. for a species of bird (N = 36). Black dashed lines (…………) represent the 95% confidence bands for the regression mean. Grey lines represent the modelled regression for heat loss scaling (…………), isometric scaling (– – – –) and structural scaling (– – – –).
Figure 2.5. Relationship between parent mass (M, g) and a – surface-specific nest conductance (mW °C⁻¹ m⁻², $G_\alpha = 37.74 \times M^{-0.44}$) and b – nest thermal conductivity (mW °C⁻¹ m⁻¹, $k = 111.61 \times M^{0.06}$) for cup-shaped birds’ nests. Each point represents the mean ± 95 % C.I. for a species of bird (N = 36). Solid lines represent the regression mean. Dashed lines represent the 95 % confidence bands for the regression mean.
4. DISCUSSION

This study indicates that the requirement for adequate structural support is the primary selective influence on nest construction, not the requirement for insulation. As birds increase in size, nest surface area increases isometrically, however, nests become much thicker than what we would expect based on isometric or heat loss scaling. The thick walls provide structural support for the parent and clutch, with the consequence that the exponent for thermal conductance has to decrease, according to the relationship outlined in Equation 2.20.

Because the measured scaling exponent for thermal conductance is 0.25, but the hypothetical exponent for heat loss scaling is 0.48, it is clear that structurally adequate nests achieve a lower thermal conductance (higher insulation) than expected, as they increase in size. The consequence of this is that thermal conductance would be important only in small birds, if at all. Exactly how small is not clear, but this study focuses on nests from birds weighing between 8 g and 360 g, a range representing the largest proportion of the world’s birds (Blackburn and Gaston 1994). It is significant that there is little tendency for thermal conductance to drop below the regression line in the smallest nests of this study (Figure 2.3.a), which suggests that they are not overly insulated. Nevertheless, as nests become larger, they also become shallower, which may represent a relaxation of the role of insulation. This confirms previous suggestions by Ricklefs (1974, cited in Hansell 2000) regarding nest shape. Hansell (2000) further proposed that the change in shape means that eggs of small birds may be more protected from the elements. This may in turn offset the need for small birds, with high metabolic demands, to be so attentive to eggs, enabling them to forage more often.

There are over 9,000 species of birds worldwide, ranging in size from the bee hummingbird (Calypte helenae, 2 g) that constructs nests approximately two centimetres in diameter to the ostrich (Struthio camelus, 100 kg) that uses a one metre wide scrape in the ground in which to lay its eggs (Blackburn and Gaston 1994). Cup-shaped nests are but a fraction of the nest types used by birds. Nests can involve complicated construction such as the five metre wide incubation mounds of the mallee-fowl (Leipoa ocellata), the excavated cavities of the red-headed woodpecker (Melanerpes erythrocephalus) and underground burrows of the storm petrel (Hydrobates pelagicus) (Bolton 1996; Conner 1975; Frith 1962). Other species use pre-existing tree hollows (e.g. glossy-black cockatoo, Calyptorhynchus lathami halmaturinus), cliff edges (e.g. bank swallow, Riparia riparia) or scrapes on bare ground (e.g. piping plovers, Charadrius melodus) as their nesting substrate (Garnett et al. 1999; Mayer et al. 2009; Petersen 1955). For these species, structural support for the eggs is provided by a solid surface and the parent is less able to modify the insulation value of the nest. Furthermore, a few species do not use nests at all – such as the emperor penguin (Aptenodytes forsteri) that rests a single egg on their feet, which is then enfolded with their brood flap (Handrich 1989). In this case, support of the egg is paramount and incubation is constant – negating the need for an insulative nest altogether. When considering the above findings in the context of nests in general, it is not surprising that nest conductance is not driven by heat loss from the incubating parent, as bird species are able to employ...
different incubation strategies and utilise nests of various types to maintain an appropriate egg temperature for embryo development.

While this study shows that the requirement for structural support is the main driver on nest dimensions and therefore the thermal properties of nests across multiple species, it is possible that ambient temperature may still have some influence at a species-specific level. For example, the surface-specific conductance of nests of the Hawaiian honeycreeper (Hemignathus virens v.) at high elevations have more insulation than those at low elevations (Kern and Van Riper 1984). Nest insulation is clearly important for the nests of some birds, as a distinct layer of well-insulating materials can be found in the nests of many species (Hilton et al. 2004). The eider duck (Somateria mollissima) is a well-known example – females cover the eggs with down feathers prior to incubation recesses to reduce the extent of egg-cooling; however, the nests of this species are constructed on the ground where structural support of the eggs is inherent (Erikstad and Tveraa 1995). A nest that uses well-insulating materials or is lined with additional insulation is likely to play an important role in preventing heat loss from the nest during parental recesses in cool climates (Chapter 4) or inclement weather (Chapter 5).

This study was conducted on nests from within Australia and therefore it would be of interest to repeat the study using fresh samples and over greater geographic and climatic ranges. While further sampling seems unlikely to influence significantly the exponent of the allometric relationship with conductance, it may shed light on the full extent of variation in nest design by including species that nest in warmer and colder climates than those included in this analysis.

An understanding of the influence of climate (Chapter 4), rain (Chapter 5) and wind (Chapter 6) on nest thermal properties may help to clarify some of the within-species variation observed in this study. Greater knowledge regarding the influence of clutch size (Chapter 3) on nest dimensions and, in turn, the thermal properties of the nest may also prove useful.
ACKNOWLEDGEMENTS

We thank the South Australian Museum (in particular, Dr Philippa Horton) and Queensland Museum (mainly, Heather Janetzki) for use of their nest collections and Richard Norrish (the University of Adelaide) for designing and constructing the controlled temperature power monitor circuit. We thank the University of Queensland (principally, Dr Craig White) for allowing the use of their laboratory facilities. We also thank the reviewers for their useful comments and improving the clarity of the text.
POST-PUBLICATION ADDITIONS

Chapter 2 was published in February 2011. Following publication, several analyses were conducted that supplement the published information. The physical dimensions of the nests were used to calculate the nest cup volume ($V_{\text{CUP}}$), nest wall volume ($V_{\text{N}}$) and nest wall density ($\rho$). The species means for these dimensions are given in Appendix 4, along with nest opening surface area ($A_{\text{LID}}$) and internal/external nest surface areas ($A_{\text{I}}$ and $A_{\text{E}}$). These nest dimensions are analysed with respect to parent mass in Supplement 2.3. The allometric analyses conducted in Chapter 2 did not account for phylogenetic relationships and so phylogenetically-informed analyses of the allometric relationships are provided in Supplement 2.4. Chapter 3 finds an effect of sexual size dimorphism (SDI) on the size of eggs and so we repeat allometric analyses for nest dimensions, accounting for SDI, in Supplement 2.5. Finally, we assess nest dimensions against the phylogeny to test if nest morphology contains a phylogenetic signal (Supplement 2.6).
Heenan, C.B. & Seymour, R.S. (2011) Structural support, not insulation, is the primary driver for avian cup-shaped nest design. 
*Proceedings of the Royal Society B - Biological Sciences, v. 278 (1720), pp. 2924 -2929*

**NOTE:**
This publication is included on pages 31-37 in the print copy of the thesis held in the University of Adelaide Library.

It is also available online to authorised users at:

[http://dx.doi.org/10.1098/rspb.2010.2798](http://dx.doi.org/10.1098/rspb.2010.2798)
SUPPLEMENT 2.2: THE LENGTH OF THE GREY FANTAIL (RHIPIDURIDAE: *RHIPIDURA ALBISCAPA*) NEST PENDULUM

The nest of the grey fantail (Rhipiduridae: *Rhipidura albiscapa* Gould, 1840) typically is constructed from grass bound together with spider silk and the material is woven such that a pendulum hangs at the base (Figure S2.2.1) (Marchant and Higgins 2006). The functional significance of the fantail nest pendulum is unknown though some suggest that it may help to break up the shape of the nest to conceal the nest from predators. The dimensions of *R. albiscapa* nests, as reported in Chapter 2, did not include the length of the pendulum and hence we wish to define it here.

Nests used in this study were borrowed from the South Australian Museum ornithology collection. Of the 14 *R. albiscapa* nests studied, 5 lacked the characteristic tail. The length of the nest pendulum (Figure S2.2.2) of the remaining 9 nests was accurately measured with a micrometer to the nearest millimetre. The standard nest dimensions of *R. albiscapa* nests are reported in Appendix 3 and 4. In addition, the length of the nest pendulum is 2.86 ± 0.93 cm (mean ± 95 % C.I.). Of the nests that had a pendulum, the shortest was 1.00 cm and the longest was 6.45 cm.

*Rhipidura albiscapa* nests are typically constructed with a pendulum, though several of the nests included in the study of Chapter 2 lacked the characteristic tail. While the nests appeared to be in good condition, some may have been damaged by wind and rain prior to collection and hence the length of the nest pendulum as reported here should be considered a guide only.
Figure S2.2.2. Diagram showing standard nest dimensions in addition to the length of the pendulum. Note that the diagram is not to scale.
SUPPLEMENT 2.3: ALLOMETRIC RELATIONS OF AVIAN CUP-SHAPED NESTS

The understanding of how nest dimensions change with parent mass provides insight into the factors that affect nest construction, enables avian physiologists to identify species that differ from expected and make comparisons with other variables by employing exponents to derive mass-independent data. Making comparisons between mass and another variable is known as allometry. Allometric relationships are of the form \( y = aM^b \), where \( y \) is the measured variable of interest and \( M \) is body mass (Schmidt-Nielsen 1984). The ‘a’ value defines the elevation (height) of the curve and the exponent ‘b’ describes the way the curve bends. Allometric relationships with a positive exponent describe an increase in the variable of interest as body mass increases, whereas negative exponents describe a decrease. Our earlier study showed that nest structural and thermal properties scale with adult body mass (Chapter 2); however, here we describe the allometric relationships that were not reported previously.

Nest dimensions of internal and external nest surface area (\( A_I \) and \( A_E \)) were measured according to the methods of Chapter 2. The nest wall density (\( \rho \)) was measured in line with methods of Chapter 6. Nest volume (\( V_N \)) and nest cup volume (\( V_{CUP} \)) was measured using the methods of Chapter 3 and 5. Data were assessed against parent mass values from the Handbook of Australian, New Zealand and Antarctic Birds resource series (Marchant and Higgins 2001; 2002; 2006) using linear regression techniques on log-transformed data. Residuals of the data met the assumptions required for parametric linear regression tests of normality (Shapiro-Wilk \( W \) Test) and equal variance (constant spread of the residuals) in all but two cases. The residuals for internal nest surface area (\( W = 0.90, P<W = 0.003 \)) and nest cup volume (\( W = 0.90, P<W = 0.003 \)) were not normally distributed due to a potential outlier (\( Microeca fascinans \)). Removal of the problem species did improve the normality of residuals, however, did not greatly change the allometric relationship and so the author could see no other reason for its removal and retained the data point. The significance value was set at 0.05 for all analyses.

The nest dimensions are significantly related to the mass of the incubating parent (Table S2.3.1). Species-specific values can be found in Appendix 3. The internal and external nest surface area and nest opening surface area scale with parent mass with exponents that do not differ significantly from what would be expected for a surface area (\( M^{0.67} \)). The scaling exponent for nest volume is greater than expected (\( M^{1} \)); however, the volume of the nest cup does not differ from expected.

Nest dimensions reported here supplement the results of Chapter 2. Nest dimensions increase in proportion to the parent, as expected, with exception to nest volume which increases at a greater rate than expected for the volume of an isometric object. This is in line with our previous finding that avian nests are constructed primarily for structural support and hence walls are thicker than those of an isometric object, in turn inflating the nest wall volume (Chapter 2). In addition, nest wall density is independent of parent mass but more appropriate is the weave of the nest wall, which is more difficult to define.
### Table S2.3.1. Allometric relationships between parent mass ($M$, g) and the dimensions of avian cup-shaped nests according to $y = aM^b$

<table>
<thead>
<tr>
<th>nest parameter</th>
<th>intercept, a</th>
<th>scaling exponent, b</th>
<th>$R^2$</th>
<th>$F$ ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>internal nest surface area ($A_i$, cm$^2$)</td>
<td>9.95 ± 1.26</td>
<td>0.62 ± 0.06</td>
<td>0.92</td>
<td>393.07 *</td>
</tr>
<tr>
<td>external nest surface area ($A_e$, cm$^2$)</td>
<td>13.65 ± 1.39</td>
<td>0.74 ± 0.09</td>
<td>0.89</td>
<td>273.35 *</td>
</tr>
<tr>
<td>nest opening surface area ($A_{ULD}$, cm$^2$)</td>
<td>3.24 ± 1.19</td>
<td>0.71 ± 0.05</td>
<td>0.96</td>
<td>865.22 *</td>
</tr>
<tr>
<td>diameter:height ratio (d:h)</td>
<td>1.17 ± 1.24</td>
<td>0.10 ± 0.06</td>
<td>0.24</td>
<td>10.79 *</td>
</tr>
<tr>
<td>nest density ($\rho$, g cm$^{-3}$)</td>
<td>0.08 ± 2.46</td>
<td>0.05 ± 0.27</td>
<td>0.01</td>
<td>0.15</td>
</tr>
<tr>
<td>nest volume ($V_N$, cm$^3$)</td>
<td>3.05 ± 1.85</td>
<td>1.20 ± 0.17</td>
<td>0.86</td>
<td>204.20 *</td>
</tr>
<tr>
<td>nest cup volume ($V_{CUP}$, cm$^3$)</td>
<td>3.97 ± 1.40</td>
<td>0.94 ± 0.09</td>
<td>0.93</td>
<td>422.12 *</td>
</tr>
</tbody>
</table>

Statistics include the intercept of the regression mean ($a$) and scaling exponent (slope, $b$) according to the allometric relationship $y = aM^b$, as well as the correlation coefficient ($R^2$) and $F$ ratio. The intercept and scaling exponent values represent the mean ± 95% C.I. for all species.

* Indicates that there is a significant effect of parent mass on the variable ($P < 0.0001$ at $\alpha = 0.05$, except d:h which has $P = 0.0024$) in all cases with exception to nest wall density which was not significantly related to mass ($P = 0.70$).

$N = 36$ and $DF = 1,34$ for all comparisons except nest density which has $N = 27$ and $DF = 1,25$. The replicate for the nest density measurements is lower as some nests were excluded from analysis due to the attachment of supporting branches.
SUPPLEMENT 2.4: A PHYLOGENETIC VIEW OF THE ALLOMETRIC RELATIONSHIP FOR THE STRUCTURE AND THERMAL PROPERTIES OF AVIAN CUP-SHAPED NESTS

Our understanding of animal physiology is often improved through comparative studies; however, such studies can be statistically flawed through non-independence of data when phylogenetic relatedness is not taken into account (Blomberg et al. 2003; Garland and Adolph 1994). Consequently, we seek here to test if the allometric relationships for the structural and thermal properties of avian nests, as reported in Chapter 2, are influenced by phylogeny.

Allometric relationships for nest structure and thermal properties reported in Chapter 2 and Supplement 2.3 were assessed against the phylogeny of the species in R (Gentleman and Ihaka (2011), version 2.14.1) using linear regression techniques, whilst also accounting for phylogenetic relatedness, according to the methods of Chapter 3. Phylogenetic correlation was determined from the lambda (λ) value that maximised the likelihood of the model (Pagel 1999). The strength of the phylogenetic models was assessed by repeating analyses with λ equal to zero and comparing the second-order Akaike Information Criterion (AICc) values produced from the phylogenetic and non-phylogenetic models (Burnham and Anderson 2002). The need to account for phylogeny in the analysis of these data was supported if the AICc was lowest for the phylogenetic model, and if the ΔAICc difference (ΔAICc) between the phylogenetic and non-phylogenetic models was greater than four; the non-phylogenetic model was retained if the ΔAICc was less than four.

Nest dimensions and thermal properties are not influenced by phylogenetic relationships when regressed against parent mass (Table S2.4.1), with exception to nest mass and density (Table S2.4.2). The allometric relationship for nest mass (0.17M^{1.36}) represented in Chapter 2 does not account for phylogenetic relationships. The increase in the scaling exponent for nest mass (from 1.36 to 1.41), once accounting for phylogeny, indicates that nests may contain more material for structural support than previously suggested in Chapter 2. However, nest mass is also influenced by sexual size dimorphism (SDI) of the parents (Supplement 2.5), which is the ratio of male mass to female mass. When nest mass is regressed against parent mass and SDI simultaneously, the effect of phylogeny disappears and the slope of the relationship with parent mass increases further to 1.43. While nest density is influenced by phylogeny when regressed against parent mass, the regression itself is not significant. For nest mass, the phylogenetically-corrected allometric equation reported here can be used, but since sexual size dimorphism influences nest mass, we recommend using the multiple regression equation for nest mass where possible (see Supplement 2.5).
Table S2.4.1. Phylogenetic analysis of the allometric relationships between parent mass (M, g) and the dimensions and thermal properties of avian cup-shaped nests according to y = aM^b

<table>
<thead>
<tr>
<th>nest parameter</th>
<th>lambda (λ)</th>
<th>second-order Akaike Information Criterion (AICc)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>phylogenetic model</td>
<td>non-phylogenetic model</td>
</tr>
<tr>
<td>internal nest diameter (dᵢ, cm)</td>
<td>0.36</td>
<td>-144.2</td>
<td>-145 *</td>
</tr>
<tr>
<td>external nest diameter (dₑ, cm)</td>
<td>0</td>
<td>-98.6</td>
<td>-101.2 *</td>
</tr>
<tr>
<td>internal nest height (hᵢ, cm)</td>
<td>1.0</td>
<td>-81.2</td>
<td>-81.6 *</td>
</tr>
<tr>
<td>external nest height (hₑ, cm)</td>
<td>0</td>
<td>-56.2</td>
<td>-58.7 *</td>
</tr>
<tr>
<td>diameter:height ratio (d:h)</td>
<td>0.31</td>
<td>-80.1</td>
<td>-81.1 *</td>
</tr>
<tr>
<td>nest wall thickness (Xₜ, cm)</td>
<td>0.66</td>
<td>-22.3</td>
<td>-23.3 *</td>
</tr>
<tr>
<td>nest base thickness (Xₜ₀, cm)</td>
<td>0.15</td>
<td>5.9</td>
<td>4.3 *</td>
</tr>
<tr>
<td>mean nest thickness (X, cm)</td>
<td>0.07</td>
<td>-18.4</td>
<td>-20.7 *</td>
</tr>
<tr>
<td>internal nest surface area (Aᵢ, cm²)</td>
<td>1.0</td>
<td>-74.8</td>
<td>-76.1 *</td>
</tr>
<tr>
<td>external nest surface area (Aₑ, cm²)</td>
<td>0</td>
<td>-47.5</td>
<td>-50.0 *</td>
</tr>
<tr>
<td>mean nest surface area (Å, cm²)</td>
<td>0</td>
<td>-66.9</td>
<td>-69.4 *</td>
</tr>
<tr>
<td>nest opening surface area (A₂₀̴ₜ, cm²)</td>
<td>0.36</td>
<td>-94.2</td>
<td>-95.1 *</td>
</tr>
<tr>
<td>nest mass (Mᵣ, g)</td>
<td>1.0</td>
<td>7.1</td>
<td>15.2</td>
</tr>
<tr>
<td>nest density (ρ, g cm⁻³)</td>
<td>0.78</td>
<td>-11.3 *</td>
<td>-5.8</td>
</tr>
<tr>
<td>nest volume (Vᵢ, cm³)</td>
<td>0</td>
<td>-2.5</td>
<td>-5.1 *</td>
</tr>
<tr>
<td>nest cup volume (Vᵣ, cm³)</td>
<td>1.0</td>
<td>-46.8</td>
<td>-48.9 *</td>
</tr>
<tr>
<td>total nest conductance (G, mW °C⁻¹)</td>
<td>1.0</td>
<td>-65.4</td>
<td>-64.1 *</td>
</tr>
<tr>
<td>surface-specific nest conductance (Gₜ, W °C⁻¹ m⁻²)</td>
<td>1.0</td>
<td>-39.0</td>
<td>-45.0 *</td>
</tr>
<tr>
<td>thermal conductivity (k, mW °C⁻¹ m⁻¹)</td>
<td>0.16</td>
<td>-33.4</td>
<td>-35.3 *</td>
</tr>
</tbody>
</table>

* Represents the model with the best fit for the data, where the model with the lowest AICc is retained for an AICc difference in excess of four, and the non-phylogenetic model retained for an AICc difference of less than four.
N = 36 for all comparisons except nest mass and density which has N = 27. The replicate for the nest mass and density measurements are lower as some nests were excluded from analysis due to the attachment of supporting branches.

Table S2.4.2. Phylogenetically corrected allometric relationships between parent mass (M, g) and the dimensions of avian cup-shaped nests according to y = aM^b

<table>
<thead>
<tr>
<th>nest parameter</th>
<th>intercept, a</th>
<th>scaling exponent, b</th>
<th>statistics *</th>
</tr>
</thead>
<tbody>
<tr>
<td>nest mass (Mᵣ, g)</td>
<td>0.15 ± 1.77</td>
<td>1.41 ± 0.15</td>
<td>LCL = 1.10</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>UCL = 1.73 *</td>
</tr>
<tr>
<td>nest density (ρ, g cm⁻³)</td>
<td>0.09 ± 1.48</td>
<td>0.03 ± 0.11</td>
<td>LCL = -0.20</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>UCL = 0.25</td>
</tr>
</tbody>
</table>

Statistics include the intercept of the regression mean (a) and scaling exponent (slope, b) according to the allometric relationship y = aM^b. The intercept and scaling exponent values represent the mean ± S.E. for all species.
* Statistics include the lower critical limit and upper critical limit for phylogenetic models.
* Indicates that the regression for the variable of interest is statistically significant (slope ≠ 0).
N = 27.
SUPPLEMENT 2.5: THE INFLUENCE OF SEXUAL SIZE DIMORPHISM ON THE STRUCTURE AND THERMAL PROPERTIES OF AVIAN CUP-SHAPED NESTS

Sexual size dimorphism (morphological differentiation of sexually mature males and females) may correlate with female reproductive effort or the energy invested in a reproductive attempt (Cabana et al. 1982; Fairbaim 1997 and references within). Chapter 3 shows that sexual size dimorphism is indeed important for birds with respect to reproduction by influencing egg size and clutch size. Nest construction can be energetically expensive for birds (Withers 1977), therefore the amount of material used in avian nests and hence the size of nests may represent the energy invested in a reproductive attempt also, thus may be influenced by sexual size dimorphism.

Nest dimensions and thermal properties were measured, as outlined in Chapter 2 and parent mass (M) values for each species were obtained from the Handbook of Australian, New Zealand and Antarctic Birds resource series (Marchant and Higgins 2001; 2002; 2006). Sexual size dimorphism index (SDI) was calculated as described in Chapter 3.

Data were analysed in R (Gentleman and Ihaka (2011), version 2.14.1) using multiple linear regression techniques, whilst also accounting for phylogenetic relatedness, according to the methods of Chapter 3. Logarithmically-transformed data for each of the nest variables were regressed against log parent mass and log SDI. Phylogenetic correlation was determined from the lambda (λ) value that maximised the likelihood of the model (Pagel 1999). The strength of the phylogenetic models was assessed by repeating analyses with λ equal to zero and comparing the second-order Akaike Information Criterion (AICc) values produced from the phylogenetic and non-phylogenetic models (Burnham and Anderson 2002). The need to account for phylogeny in the analysis of these data was supported if the AICc was lowest for the phylogenetic model, and if the AICc difference (ΔAICc) between the phylogenetic and non-phylogenetic models was greater than four; the non-phylogenetic model was retained if the ΔAICc was less than four.

Further statistical analyses on allometric relationships were performed in JMP IN (SAS Institute (2001), version 4.0.4) using linear regression techniques on log-transformed data. Residuals of the data met the assumptions required for parametric linear regression tests of normality (Shapiro-Wilk W Test) and equal variance (constant spread of the residuals) in all but two cases. The residuals for internal nest surface area ($W = 0.90, P < W = 0.003$) and nest cup volume ($W = 0.90, P < W = 0.003$) were not normally distributed due to a potential outlier (*Microeca fascinans*). Removal of the problem species did improve the normality of residuals, however, did not significantly change the allometric relationship and so the author could see no other reason for its removal and retained the data point. A secondary multiple linear regression analysis including incubation care (either by the female only or by both sexes) (Marchant and Higgins 2001; 2002; 2006) as a model variable was carried out to determine if the sex of the bird ultimately incubating and sitting in the nest influenced the nest mass or density, once controlling for parent mass and SDI. The significance value was set at 0.05 for all analyses.
There is no influence of phylogeny on the relationship between the structural and thermal properties of nests and parent mass and SDI (Table S2.5.1). The multiple linear regression models confirmed that parent mass influences nest construction, as reported in Chapter 2 and Supplement 2.3. Sexual size dimorphism does not influence the thermal properties of nests (Table S2.5.2). Sexual size dimorphism does not have an effect on the structural properties of nests either, except for nest mass \((M_N)\) and nest density \((\rho)\), which both decrease as SDI increases (Table S2.5.2). Thus, in species where the female is the larger of the two sexes, nests are heavier and contain more material (on a weight basis) per unit cubic area. Nests are lighter and contain less material (on a weight basis) per unit cubic area for species where the male is the larger of the two sexes.

Nest mass and density are influenced by the ratio of male to female mass, such that nests are heavier and denser in species where the female is the larger of the two sexes and the opposite holds true when the male is the larger sex. Decreases in nest mass with SDI are likely to be due to changes in the mass of the materials used, or through a tighter nest weave, as the size of the nest and its thickness do not change significantly with SDI. One would expect that the bird that predominantly incubates would dictate the structural requirements of the nest and therefore the mass of the nest, such that nests reflect the female mass when the female is the sole incubator or the heavier of the two sexes when both sexes incubate. However, neither the mass of the nest \((F_1 = 0.12, P = 0.73)\) or its density \((F_1 = 0.07, P = 0.80)\) is influenced by incubation care when parent mass and SDI are controlled for. It is of interest to note that the increase in the mass of the nest materials or density of the nest wall does not influence the thermal conductivity of the nest materials. The independence of thermal conductivity and SDI suggest that birds with contrasting SDI are not necessarily using different types of materials in construction. Since the thermal conductivity, surface area and thickness of a nest are not influenced by SDI, nest conductance is also unaffected by SDI. Further studies are required to elucidate the biological significance of changes in nest mass and density with sexual size dimorphism.

Due to the influence of SDI on nest mass and density, we suggest using the multiple regression exponents reported here for use in calculating mass-independent data. However, for the structural and thermal properties of nests that are not influenced by SDI, we recommend using the scaling exponents for parent mass alone that are reported in Chapter 2 and Supplement 2.3.
Table S2.5.1. Phylogenetic analysis of the allometric relationships between parent mass (M, g), sexual size dimorphism (SDI) and the dimensions and thermal properties of avian cup-shaped nests according to $y = aM^\lambda SDI^\beta$

<table>
<thead>
<tr>
<th>nest parameter</th>
<th>lambda ($\lambda$)</th>
<th>second-order Akaike Information Criterion (AICc)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>phylogenetic model</td>
<td>non-phylogenetic model</td>
</tr>
<tr>
<td>internal nest diameter ($d_i$, cm)</td>
<td>0.21</td>
<td>-141.8</td>
</tr>
<tr>
<td>external nest diameter ($d_e$, cm)</td>
<td>0.0</td>
<td>-96.0</td>
</tr>
<tr>
<td>internal nest height ($h_i$, cm)</td>
<td>1.0</td>
<td>-78.5</td>
</tr>
<tr>
<td>external nest height ($h_e$, cm)</td>
<td>0.0</td>
<td>-53.6</td>
</tr>
<tr>
<td>diameter:height ratio ($d:h$)</td>
<td>0.29</td>
<td>-77.2</td>
</tr>
<tr>
<td>nest wall thickness ($X_w$, cm)</td>
<td>0.0</td>
<td>-19.6</td>
</tr>
<tr>
<td>nest base thickness ($X_b$, cm)</td>
<td>0.10</td>
<td>9.6</td>
</tr>
<tr>
<td>mean nest thickness ($X$, cm)</td>
<td>0.07</td>
<td>-15.7</td>
</tr>
<tr>
<td>internal nest surface area ($A_i$, cm$^2$)</td>
<td>1.0</td>
<td>-72.1</td>
</tr>
<tr>
<td>external nest surface area ($A_e$, cm$^2$)</td>
<td>0.0</td>
<td>-44.8</td>
</tr>
<tr>
<td>mean nest surface area ($\bar{A}$, cm$^2$)</td>
<td>0.0</td>
<td>-64.2</td>
</tr>
<tr>
<td>nest opening surface area ($A_{LID}$, cm$^2$)</td>
<td>0.21</td>
<td>-91.9</td>
</tr>
<tr>
<td>nest mass ($M_N$, g)</td>
<td>0.96</td>
<td>9.0</td>
</tr>
<tr>
<td>nest density ($\rho$, g cm$^{-3}$)</td>
<td>0.55</td>
<td>-13.3</td>
</tr>
<tr>
<td>nest volume ($V_N$, cm$^3$)</td>
<td>0.0</td>
<td>0.12</td>
</tr>
<tr>
<td>nest cup volume ($V_{CUP}$, cm$^3$)</td>
<td>1.0</td>
<td>-44.1</td>
</tr>
<tr>
<td>total nest conductance ($G$, mW °C$^{-1}$)</td>
<td>1.0</td>
<td>-62.7</td>
</tr>
<tr>
<td>surface-specific nest conductance ($G_{SA}$, W °C$^{-1}$ m$^{-2}$)</td>
<td>0.0</td>
<td>-39.8</td>
</tr>
<tr>
<td>thermal conductivity ($k$, mW °C$^{-1}$m$^{-1}$)</td>
<td>0.16</td>
<td>-30.7</td>
</tr>
</tbody>
</table>

* Represents the model with the best fit for the data, where the model with the lowest AICc is retained for an AICc difference in excess of four, and the non-phylogenetic model retained for an AICc difference of less than four.

N = 36 for all comparisons except nest mass and density which has N = 27. The replicate for the nest mass and density measurements are lower as some nests were excluded from analysis due to the attachment of supporting branches.
Table S2.5.2. Statistics for the regression of nest dimensions and thermal properties against body mass (M, g) and sexual size dimorphism index (SDI) according to $y = aM^bSDI^b$

<table>
<thead>
<tr>
<th>nest parameter</th>
<th>R²</th>
<th>intercept, a</th>
<th>scaling exponent, b</th>
<th>$F_1$</th>
<th>$F_1$</th>
<th>$F_1$</th>
<th>$F_1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>nest mass</td>
<td>0.77</td>
<td>0.17 ± 3.14</td>
<td>1.43 ± 0.34</td>
<td>75.05</td>
<td>9.84</td>
<td>0.0045*</td>
<td></td>
</tr>
<tr>
<td>nest density</td>
<td>0.36</td>
<td>0.08 ± 2.09</td>
<td>0.10 ± 0.22</td>
<td>0.92</td>
<td>13.20</td>
<td>0.0013*</td>
<td></td>
</tr>
<tr>
<td>nest volume</td>
<td>0.86</td>
<td>3.07 ± 1.87</td>
<td>1.20 ± 0.17</td>
<td>198.05</td>
<td>8.50</td>
<td>0.0003*</td>
<td></td>
</tr>
<tr>
<td>nest cup volume</td>
<td>0.93</td>
<td>3.99 ± 1.41</td>
<td>0.94 ± 0.09</td>
<td>410.34</td>
<td></td>
<td>0.11</td>
<td></td>
</tr>
<tr>
<td>total nest conductance</td>
<td>0.57</td>
<td>44.23 ± 1.32</td>
<td>0.25 ± 0.08</td>
<td>43.87</td>
<td>0.26</td>
<td>0.61</td>
<td></td>
</tr>
<tr>
<td>surface-specific nest conductance</td>
<td>0.71</td>
<td>37.85 ± 1.43</td>
<td>-0.44 ± 0.10</td>
<td>78.63</td>
<td>0.04</td>
<td>0.83</td>
<td></td>
</tr>
<tr>
<td>thermal conductivity</td>
<td>0.04</td>
<td>112.68 ± 1.51</td>
<td>0.06 ± 0.11</td>
<td>1.14</td>
<td>0.32</td>
<td>0.58</td>
<td></td>
</tr>
</tbody>
</table>

Intercepts, scaling exponents and accompanying statistics are those from the best fit model. Functions are represented as intercept/exponent ± 95% C.I.

* Statistics include the F-ratio (degrees of freedom) and the P-value.
* Indicates that the regression for the variable of interest is statistically significant (slope ≠ 0). The alpha value (α) used is 0.05.
N = 36 for all comparisons except nest mass and density which has N = 27. The replicate for the nest mass and density measurements are lower as some nests were excluded from analysis due to the attachment of supporting branches.
SUPPLEMENT 2.6: AVIAN CUP-SHAPED NEST DESIGN CONTAINS A PHYLOGENETIC SIGNAL

Our understanding of animal physiology is often improved through comparative studies; however, such studies can be statistically flawed through non-independence of data when phylogenetic relatedness is not taken into account (Blomberg et al. 2003; Garland and Adolph 1994). Consequently, we seek here to test if the structural and thermal properties of avian nests are influenced by phylogeny. The present study differs from our previous study (see Supplement 2.4), in that here we do not regress nest variables against mass, but rather test for a phylogenetic signal in the nest data itself.

Nest dimensions and thermal properties were measured, as outlined in Chapter 2, 3 and 5. Data were analysed in R (Gentleman and Ihaka 2011, version 2.14.1) according to the methods of Chapter 3. We tested the nest structure and thermal properties against the phylogeny to determine if nest design contains a phylogenetic signal. This involved calculating Blomberg et al.’s K-statistic (the strength of the signal) and determining the significance of the phylogenetic relationship using a generalised least square in comparative phylogenetics (PGLS) code modified from code that accompanies Duncan et al. (2007).

Nest dimensions and thermal properties are influenced by phylogeny (Table S2.6.1). The majority of the nest parameters (dimensions, surface areas, conductance) contain a significant phylogenetic signal, with exception to mean nest thickness and nest base thickness, nest mass, nest density, nest volume and thermal conductivity. In all cases Blomberg et al.’s (2003) K-statistic is less than would be expected based on Brownian motion evolution (i.e. K < 1, Table S2.6.1) (Blomberg et al. 2003). Consequently, nest design and thermal properties may represent homoplasy or adaptation that occurs in some, but not all, species.
### Table S2.6.1. Statistics for the relationship between nest morphology and phylogeny

<table>
<thead>
<tr>
<th>nest parameter</th>
<th>Blomberg’s K</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>internal nest diameter (d&lt;sub&gt;i&lt;/sub&gt;, cm)</td>
<td>0.64</td>
<td>0.005 *</td>
</tr>
<tr>
<td>external nest diameter (d&lt;sub&gt;e&lt;/sub&gt;, cm)</td>
<td>0.50</td>
<td>0.019 *</td>
</tr>
<tr>
<td>internal nest height (h&lt;sub&gt;i&lt;/sub&gt;, cm)</td>
<td>0.61</td>
<td>0.005 *</td>
</tr>
<tr>
<td>external nest height (h&lt;sub&gt;e&lt;/sub&gt;, cm)</td>
<td>0.51</td>
<td>0.015 *</td>
</tr>
<tr>
<td>diameter:height ratio (d:h)</td>
<td>0.49</td>
<td>0.041 *</td>
</tr>
<tr>
<td>nest wall thickness (X&lt;sub&gt;w&lt;/sub&gt;, cm)</td>
<td>0.45</td>
<td>0.029 *</td>
</tr>
<tr>
<td>nest base thickness (X&lt;sub&gt;b&lt;/sub&gt;, cm)</td>
<td>0.42</td>
<td>0.12</td>
</tr>
<tr>
<td>mean nest thickness (X, cm)</td>
<td>0.43</td>
<td>0.069</td>
</tr>
<tr>
<td>internal nest surface area (A&lt;sub&gt;i&lt;/sub&gt;, cm&lt;sup&gt;2&lt;/sup&gt;)</td>
<td>0.68</td>
<td>0.003 *</td>
</tr>
<tr>
<td>external nest surface area (A&lt;sub&gt;e&lt;/sub&gt;, cm&lt;sup&gt;2&lt;/sup&gt;)</td>
<td>0.46</td>
<td>0.037 *</td>
</tr>
<tr>
<td>mean nest surface area (Ā, cm&lt;sup&gt;2&lt;/sup&gt;)</td>
<td>0.55</td>
<td>0.021 *</td>
</tr>
<tr>
<td>nest opening surface area (A&lt;sub&gt;LID&lt;/sub&gt;, cm&lt;sup&gt;2&lt;/sup&gt;)</td>
<td>0.57</td>
<td>0.029 *</td>
</tr>
<tr>
<td>nest mass (M&lt;sub&gt;N&lt;/sub&gt;, g)</td>
<td>0.35</td>
<td>0.53</td>
</tr>
<tr>
<td>nest density (ρ, g cm&lt;sup&gt;-3&lt;/sup&gt;)</td>
<td>0.46</td>
<td>0.081</td>
</tr>
<tr>
<td>nest volume (V&lt;sub&gt;N&lt;/sub&gt;, cm&lt;sup&gt;3&lt;/sup&gt;)</td>
<td>0.38</td>
<td>0.21</td>
</tr>
<tr>
<td>nest cup volume (V&lt;sub&gt;CUP&lt;/sub&gt;, cm&lt;sup&gt;3&lt;/sup&gt;)</td>
<td>0.64</td>
<td>0.006 *</td>
</tr>
<tr>
<td>total nest conductance (G, mW °C&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>0.69</td>
<td>0.002 *</td>
</tr>
<tr>
<td>surface-specific nest conductance (G&lt;sub&gt;A&lt;/sub&gt;, W °C&lt;sup&gt;-1&lt;/sup&gt; m&lt;sup&gt;-2&lt;/sup&gt;)</td>
<td>0.44</td>
<td>0.048 *</td>
</tr>
<tr>
<td>thermal conductivity (k, mW °C&lt;sup&gt;-1&lt;/sup&gt; m&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>0.40</td>
<td>0.17</td>
</tr>
</tbody>
</table>

* Indicates that the nest parameter of interest contains a significant phylogenetic signal.
The structural and thermal properties of avian cup-shaped nests
A COMPARATIVE ANALYSIS OF AVIAN EGG SHAPE, CLUTCH SIZE AND NEST DESIGN

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STATEMENT OF AUTHORSHIP

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Text in manuscript

HEENAN, C. B. (Candidate)

Lead study design, constructed equipment, collected all data and photographs, performed statistical analyses, interpreted data, wrote manuscript and acted as corresponding author

I hereby certify that the statement of contribution is accurate.

Signed Date 27/02/2013

BUCHDAHL, N. P.

Developed macro for oomorphology analysis, helped with data interpretation, assisted with manuscript preparation and evaluation

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis.

Signed Date 27/02/2013

SEYMOUR, R. S.

Supervised development of work, helped in data interpretation and manuscript evaluation

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis.

Signed Date 27/02/2013
ABSTRACT

The size of bird eggs and clutch is linked to many important life-history traits and can influence the reproductive success of individuals. Previous studies have rarely measured egg shape and size accurately. Furthermore, the relationship between nest size and egg size has not been assessed across multiple species at once. This study is the first to use image-based methods to determine egg morphology and assess variables phylogenetically and allometrically against female mass (M_F, g) and the sexual size dimorphism index (SDI), simultaneously. In addition, we assess egg morphology against nest size (depth, surface area, volume, mass) for 36 Australian passerine species. We show that egg size is influenced by phylogeny, increases with female body mass (ranging from 8 to 380 g), and increases with the sexual size dimorphism index (ranging from female-biased to male-biased). Clutch size is negatively influenced by the SDI and we suggest that there is a trade-off between egg size and clutch size. Ultimately, we find that egg size parameters are related to the size of the nest. Furthermore, we reanalyse nest morphology scaling from our previous study, with the contribution of clutch mass, and confirm that nests have the primary role of structural support of the parent and clutch.

Keywords: egg size; egg shape; clutch size; bird nest morphology; scaling; allometry
1. INTRODUCTION

The size of bird eggs is linked to many important life-history traits, including female mass, egg composition, reproductive success, rate of development and hatchling size (reviewed extensively elsewhere - Christians 2002; Deeming 2007a; b; Deeming and Birchard 2007; Deeming et al. 2006; Williams 1994). Larger eggs are known to take longer to incubate, cool and rewarmp at slower rates and the efficiency of brood patch use decreases with the number of eggs in a clutch (henceforth referred to as clutch size) (Barta and Székely 1997; Rahn et al. 1975; Reid et al. 2000a). In addition, the number of eggs in a clutch can influence the amount of energy required by the parent during egg-laying and incubation, which can in turn influence the success of a reproductive event (Biebach 1981; de Heij et al. 2007; Rahn et al. 1985; Reid et al. 2000a).

Egg size and shape is relatively inflexible within individual female birds but variation between individuals is substantial (Christians 2002; Martin et al. 2006). Egg morphology may vary with environmental conditions (Järvinen and Ylimaunu 1986) or clutch size (Barta and Székely 1997; Potti 1993) but contrary to initial suggestions it is unlikely that variation arises from the nutritional state of the female (Christians 2002; Nol et al. 1997). As egg shape is determined by muscular action of the female, variation likely to be explained in part by the physiological systems involved in egg production (Christians 2002; Smart 1991).

Initial studies into the morphology of birds’ eggs used sticky-tape to measure egg surface area (Murray 1925), as well as simple equations to describe egg mass (Bergtold 1929) and volume (Pearl and Surface 1914; cited in Romanoff and Romanoff 1949). Later studies used equations in combination with mechanical equipment to trace the outline of an egg and define egg shape (Preston 1953). Preston (1953) was the first to suggest that photographic methods could be used but advised that it would not be accurate given the technology at the time. Preston (1968) then suggested the use of a spherometer to determine egg curvature and several years later assured that the four parameters of length, breadth, asymmetry and bicone would be sufficient to describe egg shape (Preston 1974). Tatum (1975) expanded on Preston’s (1974) formula by using graphs to determine curvature. However, Paganelli et al. (1974) pointed out that eggs come in a variety of shapes and can rarely be described by simple, analytic functions incorporating only two parameters. Despite this, several papers (Hoyt 1979; Järvinen 1991; 1994; 1996; Narushin 2005) have gone on to use simple functions to describe egg dimensions. The most commonly referenced equation is that of Hoyt (1979) which has been used in a number of studies involving egg size (Galbraith 1988; Mainwaring and Hartley 2008; McCracken et al. 1997; Slagsvold 1982; Turner 1985). Hoyt’s (1979) method was critically analysed in recent years by Bridge et al. (2007) who found that the equation is ineffective for unusually round or pointed eggs. Algebraic equations have been used more recently to generate traces of egg outlines (Baker and Brawn 2002; Todd and Smart 1984) but the focus has been placed on eggs that deviate significantly from ovoid.

Others have used water displacement methods to determine egg volume (Hoyt 1976; Rush et al. 2009; Stonehouse 1965) as well as grids, occasionally in conjunction with equations, to describe egg morphology (Paganelli et al. 1974; Smart 1991). More advanced techniques incorporating modern photography and
trapezoidal integration have been suggested for the calculation of egg size and shape (Bridge et al. 2007; Mänd et al. 1986), however, these techniques have not yet been applied across multiple species.

Of interest here is how egg morphology is influenced by nest morphology, or vice versa. Nest morphology may be adapted to metabolic rates of young, which are products of embryo size and clutch size (McCracken et al. 1997). Wesolowski (2003, cited in Alvarez and Barba 2008) attempted to address this but results were inconclusive. Studies of nesting American kestrels (Falco sparverius), magpies (Pica pica), goldeneyes (Bucephala clangula) and northern flickers (Colaptes auratus) found that nest size has no impact on the size of a clutch (Bortolotti 1994; de Neve and Soler 2002; Eriksson 1979; Wiebe and Swift 2001). Nor does clutch size change with nest diameter for the fieldfare (Turdus pilaris) or nest volume for lesser snow geese (Chen caerulescens caerulescens) and rufous bush robins (Cercotrichas galactotes) (McCracken et al. 1997; Palomino et al. 1998; Slagsvold 1982). On the other hand, for a range of birds, nest material volume (Soler et al. 1998a) and nest size does influence the number of eggs a female will lay in a reproductive attempt (Álvarez and Barba 2008; Karlsson 1977; Korpimäki 1985; Møller 1982; Slagsvold 1989b).

Since nest size is influenced by the body mass of the incubating adult (Chapter 2), and egg size is often found to be related to body mass (Blueweiss et al. 1978; Rahn et al. 1975; Rahn et al. 1985), we seek to understand if nest and egg design are correlated once accounting for allometric relationships. We test the following hypotheses to determine if egg and clutch morphology relate to nest morphology:

**Egg width:** The width of the eggs for a given species is proportional to the internal height of the nest, assuming that eggs lie on their sides in a nest and do not overlap (Drent 1975 suggests the long axis sits at an angle of 20 degrees).

**Profile area:** The two-dimensional area occupied by eggs within a nest is proportional to the surface area of the nest opening, assuming that eggs lie on their sides in a nest and do not overlap.

**Surface area:** The surface area of the clutch is proportional to the surface area of the nest cup, although not all egg shell is in contact with the nest wall.

**Volume:** The combined volume of the eggs in a nest is proportional to the volume of space available within the nest cup. Since the primary factor influencing nest design is structural support (Chapter 2), we suggest that the volume of the clutch (or mass of the clutch) would be proportional to the mass of the nest (the amount of structural material).

To test these hypotheses, we assess egg shape and size across 36 species of Australian passerines (weighing 8 to 380 g) using a combination of direct measurements, photography, computer image analysis and trapezoidal integration. We define the allometric relationships between female body mass and egg size and test the mass-independent data against nest size parameters, accounting for known allometric relationships at both the egg and nest level (Chapter 2). We also analyse egg size and shape with respect to sexual size dimorphism (morphological differentiation of sexually mature males and females), which may correlate with female reproductive effort or the energy invested in a reproductive attempt (Cabana et al. 1982; Fairbaim 1997...
and references within). We assess all relationships while accounting for phylogenetic relatedness between species, as eggs of closely-related species are expected to be more similar than distantly-related species.

Finally, our former study incorporated modelling to test if nest size and thermal properties arise through heat loss, isometric or structural scaling laws (Chapter 2). We hypothesised that if insulation is important to nest design, thermal conductance of the nest would scale with bird mass with an exponent of 0.48, as plumage conductance does (Schleucher and Withers 2001). Secondly, if nest size increases in proportion to bird size (isometrically) then the ratio of surface area ($M^{0.67}$) to thickness ($M^{0.33}$) would give rise to a conductance exponent of 0.33. Finally, if structural support is of primary importance, then thermal conductance would be proportional to mass with an exponent of 0.25, as it would be secondarily related to nest mass ($M^{1.33}$). We found that conductance scales allometrically with an exponent of 0.25 and concluded that structural support is the primary factor influencing nest construction; however, we were unable to account for the mass of the clutch, rather modelled nest morphology on parent mass alone (Chapter 2). Therefore, we use the understanding of the scaling of clutch volume to remodel and test predicted and observed scaling exponents of nest structure and thermal properties.
2. METHODS

(a) Egg measurements

Eggs were used with kind permission from the South Australian Museum ornithology collection. A total of 360 eggs from 36 passerine species (10 eggs per species) and female masses ranging from 8 to 380 g were included in this study (egg images in Appendix 5). The species selected for this study were those that were included in the assessment of bird nest construction (Chapter 2).

Each clutch of eggs was assigned a registration number when the sample was submitted to the South Australian Museum ornithology collection. The database of eggs was then sorted by species and then by the registration number. Each clutch was then provided a new number between 1 and n, where n is the total number of clutches available for a particular species. A random numbers table was then used to select ten clutches (from each of the 36 species) to be included in the study. A random point was selected as the starting point in the table and the first ten two-digit numbers between 1 and n to appear from that point were those that were included. One egg from each clutch was measured, where the egg selected for measurement was based on its position in the clutch – the first egg in the box (top left corner) was measured for the first clutch, the second egg (next egg positioned clockwise) for the second clutch, and so forth.

The length (L, cm) and width (W, cm) of the eggs (Figure 3.1) were measured with dial calipers (± 0.1 mm; Bergeon Typ-5921, Switzerland).

(b) Egg photography

Eggs were photographed using a Panasonic Lumix DMC-FZ35 digital camera with a 27 mm wide-angle 18x zoom Leica DC Vario Elmarit lens. Photos were taken at ISO 400 and aperture of f3.4, with exposure varying from ~ 0.07 to 0.2 seconds. Manual focus was used for all photographs and no flash-photography was used. Samples were not provided with additional illumination but rather subjected to standard room halogen-lighting above the sample.
The camera was mounted directly above the egg sample on a stand and positioned with a clamp such that it faced downwards (Figure 3.2). A wooden platform with a sheet of black cardboard was used to support the eggs and provide a contrasting background. Eggs were positioned so that the long axis was aligned parallel with the platform, so that an even egg profile of the longitudinal section could be viewed by the camera; and were held in place by a small piece of Blu-Tack. Proper positioning was assured by viewing mounted eggs from the side as well as aligning the egg centre with the preview focus zone.

Barrel distortion from the camera was tested by photographing a series of straight and vertical lines, as suggested by Bridge et al. (2007). The photograph was loaded into CorelDraw (Corel Corporation (2002), v. 11.633) and the original set of straight lines was superimposed on the photographed image. The lines from the photographed image closely matched those from the computer image, thus barrel distortion was considered negligible.

![Diagram of camera set-up used to photograph egg samples, as shown in profile. 1. Egg sample held in place with Blu-Tack, 2. Wooden platform and black cardboard background, 3. Camera stand, 4. Clamps to stabilise the camera, 5. Digital camera. Note that the diagram is not to scale.](image)

**Figure 3.2.** Diagram of camera set-up used to photograph egg samples, as shown in profile. 1. Egg sample held in place with Blu-Tack, 2. Wooden platform and black cardboard background, 3. Camera stand, 4. Clamps to stabilise the camera, 5. Digital camera. Note that the diagram is not to scale.

(c) **Egg image processing**

Egg photographs were imported into CorelDraw for initial processing (Figure 3.3.a). A circle was drawn over the egg, which was converted to curves and the Shape Tool was used to adjust the shape to fit the outline of the egg under high zoom. Once the shape outline matched the egg outline, the shape was filled with white and the image exported as a .JPG file (Figure 3.3.b). This was done to prevent any eggshell patterns from affecting the egg measurement process.
The new egg shape image for each egg was then opened with ImageJ (Rasband (2010), v. 1.43u) for further processing. Egg shape images were cropped and scaled down to 50 % (96 dpi) of the original resolution (180 dpi). This was considered a satisfactory resolution to increase the speed of the analysis, yet maintain accuracy of the calculations. The colour channels were then split and the blue and red layers discarded. The minimum brightness and contrast of the green layer was set to 254 so that the egg remained white and the background became entirely black, without blemishes (Figure 3.3.c). The Find Edges function was then used to detect the egg outline (Figure 3.3.d), this was evened out with the Smooth function and the image inverted (Figure 3.3.e). The resulting image was a black outline of the egg with a white background. Images were then rotated clockwise by 90° so that they lay flat with the blunt end of the egg facing left.

The image was then analysed with a custom-written macro (developed by N. Buchdahl; Appendix 6, given in the Electronic Supplementary Material, Appendix 7), the analysis of which is outlined in § 2(d) below.

Figure 3.3. Diagram of the image adjustment steps for egg photographs, where a – original egg photograph, b – egg vector created in CorelDraw, c – egg image with adjusted contrast, d – egg outline following use of the Find Edges tool and e – egg outline following image inversion.

(d) Egg macro

i. Bodies and surfaces of revolution

Consider a curve $C$ in the Euclidean plane $\mathbb{R}^2$. If $C$ is rotated about an axis that it does not cross, it generates a surface of revolution (Figure 3.4). Similarly, if $R$ is a region in the plane that is rotated about an axis that does not pass through that region, this generates a volume of revolution.
The structural and thermal properties of avian cup-shaped nests

Using basic calculus, it is straightforward to construct integral formulae for the areas and volumes of such surfaces and volumes of revolution. If the curve \( C \) is given by Equation 3.1, where \( f \) is a non-negative function and the axis of rotation is the \( x \)-axis, that is, the horizontal axis. The area (\( SA_H \)) of the surface generated by \( C \) is Equation 3.2.

\[
C = \{ y = f(x) | a \leq x \leq b \} \tag{3.1}
\]

\[
SA_H = 2\pi \int_a^b f(x) \sqrt{1 + (f'(x))^2} \, dx \tag{3.2}
\]

The region \( R \) under the graph of \( y = f(x) \) over the interval \([a, b]\) has area (\( A_R \)) according to Equation 3.3 and the volume (\( V_R \)) of the solid generated by rotating \( R \) about the \( x \)-axis is calculated according to Equation 3.4.

\[
A_R = \int_a^b f(x) \, dx \tag{3.3}
\]

\[
V_R = \pi \int_a^b f(x)^2 \, dx \tag{3.4}
\]

For rotations about a vertical axis, assume that \( a \geq 0 \). If the curve \( C \) is rotated about the \( y \)-axis, the area of the surface so generated (\( SA_v \)) is given by Equation 3.5 and the volume of the solid generated by rotating \( R \) about the \( y \)-axis (\( V_v \)) is given by Equation 3.6.

\[
SA_v = 2\pi \int_a^b x \sqrt{1 + (f'(x))^2} \, dx \tag{3.5}
\]

\[
V_v = 2\pi \int_a^b x f(x) \, dx \tag{3.6}
\]
ii. The shape of an egg

The cross-section of an egg is circular so it is legitimate to consider the egg as a surface of revolution, or axisymmetric (Preston 1974; Todd and Smart 1984). A number of terms have been used to describe eggs, including oval, ovate and subspherical (Preston 1968). However, a typical egg has a roughly ellipsoidal shape, with one end more pointed than the other (Barta and Székely 1997).

An equation for an ellipse in the plane is Equation 3.7 \((a, b > 0)\), for which the part lying in the upper half-plane is given by Equation 3.8.

\[
\frac{x^2}{a^2} + \frac{y^2}{b^2} = 1 \quad (3.7)
\]

\[
y = b \sqrt{a^2 - x^2} \quad (3.8)
\]

Rotating this curve (and the region under it) about the \(x\)-axis generates the ellipsoidal surface (solid). When \(a = b\), the ellipse is a circle and the surface of revolution is a sphere; when \(a < b\), the surface of revolution is an \textit{oblate} ellipsoid, whereas when \(a > b\), the surface is \textit{prolate}. Eggs found in nature are all prolate, or at worst, spherical.

As suggested by Barta and Székely (1997), it is reasonable to use a perturbed version of Equation 3.8 to describe the shape of an egg. To this end, we assume that the egg is accurately described by an equation of the form given in Equation 3.9 where the parameters \(c, d, e, \ldots\) tend to 0. For purposes of calculation, it is necessary to truncate the series, and from a number of observations we found that the egg can be described sufficiently accurately by an equation of the form given in Equation 3.10.

\[
y = b \frac{1}{a} \sqrt{a^2 - x^2} \left(1 + cx + dx^2 + ex^3 + \ldots\right) \quad (3.9)
\]

\[
y = b \frac{1}{a} \sqrt{a^2 - x^2} \left(1 + cx + dx^2 + ex^3\right) \quad (3.10)
\]

iii. Interpretation of the parameters

The length of the egg is \(2a\), so if units are chosen so that this is 2 (i.e. \(a = 1\)), then equation 3.10 becomes Equation 3.11.

\[
y = b \sqrt{1 - x^2} \left(1 + cx + dx^2 + ex^3\right) \quad (3.11)
\]
The parameter $b$, which should satisfy $0 < b \leq a$ to ensure prolateness, represents the deviation from spherical (Figure 3.5), with $b = 1$ corresponding to a sphere. As shall be seen later, a more useful measure of deviation from spherical turns out to be the quantity (Equation 3.12); see § 2(d)iv.

$$\sqrt{1 - \left(\frac{b}{a}\right)^2}$$

(3.12)

![Figure 3.5. Plots of the parameter $b$ according to the form $y = b\sqrt{1-x^2}$, where $b$ is equal to 0.5 (blue curve), 0.65 (gold curve), 0.8 (green curve) and 1.0 (red curve).](image)

The parameter $c$ represents deviation from ellipsoidal (Figure 3.6), with $c = 0$ corresponding precisely to an ellipsoid. For $d = 0 = e$, the maximum value of $f(x)$ (Equation 3.13) occurs at $x$ (Equation 3.14) at which the maximum value, representing half the width of the egg, is given by Equation 3.15.

$$f(x) = b \sqrt{1-x^2} \left(1 + cx\right)$$

(3.13)

$$x = \frac{2c}{1 + \sqrt{1 + 8c^2}} = c - 2c^3 + 8c^5 + O(c^7)$$

(3.14)

$$\frac{b}{4} \left[\frac{3 + \sqrt{1 + 8c^2}}{2 + 2\sqrt{1 + 8c^2}}\right]^3 = \frac{b}{2} \left(1 + \frac{c^2}{2} + \frac{5c^4}{8} + O(c^6)\right)$$

(3.15)

If $d = 0 = e$, in order that $f(x)$ (Equation 3.13) be positive for $-1 < x < 1$, $c$ must satisfy $|c| < 1$. In addition, in order that the region under the graph of $f$ be convex (which is a reasonable assumption for eggs), it is necessary and sufficient that $f(x)$ be negative for $|x| < 1$, and basic differential calculus reveals this to be equivalent to Equation 3.16.

$$|c| < \frac{1}{\sqrt{2}} \approx 0.7$$

(3.16)
Replacing $c$ by $-c$ in Equation 3.13 is equivalent to replacing $x$ by $-x$, which has the effect of reflecting the graph in the vertical axis. If $c > 0$, the sharp end of the egg is to the left and the blunt end is to the right; if $c < 0$, the opposite applies.

Figure 3.6. Plots of the parameter $c$ according to the form $y = 0.8 \sqrt{1-x^2 (1+cx)}$, where $c$ is equal to -0.6 (blue curve), -0.4 (gold curve), -0.2 (green curve) and 0 (red curve).

The parameter $d$ can be seen to affect the "squareness" of the egg (Figure 3.7). Because $x^2$ is an even function of $x$, the effect of the perturbation $dx^2$ is the same whether $x$ is positive or negative. Because of the quadratic term, the effect of this term is small near the middle of the egg ($|x| \approx 0$), but becomes significant near the ends ($|x| \approx a$).

Figure 3.7. Plots of the parameter $d$ according to the form $y = 0.9 \sqrt{1-x^2 (1+dx^2)}$, where $d$ is equal to -0.6 (violet curve), -0.3 (gold curve), 0 (red curve), 0.3 (green curve) and 0.6 (blue curve).

The parameter $e$ is somewhat harder to interpret. Because of the cubic factor $ex^3$, the effect of this term will be very small near the middle of the egg, but will become more pronounced towards each end. Because $x^3$ is an odd function, its effect will be to sharpen the egg towards one end and flatten the egg towards the other (Figure 3.8). As for $c$, the sign of $e$ determines which will be the pointy end.
Figure 3.8. Plots of the parameter $e$ according to the form $y = 0.9\sqrt{1 - x^2(t + ex^3)}$, where $e$ is equal to -0.6 (blue curve), -0.4 (gold curve), -0.2 (green curve) and 0 (red curve).

If image analysis is not possible for the reader, the egg shape parameters can also be approximated mathematically using a few simple measurements, as outlined in Supplement 3.1.

iv. **The area and volume of an egg**

As in §2(d)ii, in order to specify the shape of an egg, and also for purposes of calculating the integrals of §2(d)i, it is better to use units of measurement in which the length of the egg is always 2 exactly, giving size-independent parameters. To this end, we begin with Equation 3.17, where $t := x/a$, $b_0 := b/a$, $c_0 := ac$, $d_0 := a^2d$ and $e_0 := a^2e$. Then with $z := y/a$, $y$ is given by Equation 3.18. The latter being the equation describing the egg in units of measurement for which the length is exactly 2. The size-independent parameters $b_0$, $c_0$, $d_0$, $e_0$ correspond to the parameters $b$, $c$, $d$, $e$ of §2(d)ii. For chicken eggs, their values were all of the order $b_0 = 0.76 \pm 0.03$, $c_0 = -0.07 \pm 0.01$, $d_0 = -0.04 \pm 0.02$, $e_0 = 0.05 \pm 0.02$.

$$b/a \sqrt{a^2 - x^2 \left(1 + cx + dx^2 + ex^3\right)} = ab_0 \sqrt{1 - t^2 \left(1 + c_0 t + d_0 t^2 + e_0 t^3\right)}$$ (3.17)

$$y = b/a \sqrt{a^2 - x^2 \left(1 + cx + dx^2 + ex^3\right)} \Leftrightarrow z = b_0 \sqrt{1 - t^2 \left(1 + c_0 t + d_0 t^2 + e_0 t^3\right)}$$ (3.18)

For $f(x)$ (Equation 3.19), the easiest of the integrals of §2(d)i to calculate is Equation 3.4. This corresponds to the volume of the egg ($V_E$) given by Equation 3.20.

$$f(x) = b/a \sqrt{a^2 - x^2 \left(1 + cx + dx^2 + ex^3\right)}$$ (3.19)
\[ V_e = \pi \frac{b^2}{a^2} \int_0^a \left( a^2 - x^2 \right) \left( 1 + cx + dx^2 + ex^3 \right)^2 \, dx \] 

(3.20)

\[ = \pi ab^2 \int_1^0 \left( 1 - t^2 \right) \left( 1 + c_0 t + d_0 t^2 + e_0 t^3 \right)^2 \, dt \]

\[ = \frac{4\pi a^3 b_0^2}{3} \left( 1 + \frac{2}{5} d_0 + \frac{1}{5} c_0^2 + \frac{6}{35} c_0 e_0 + \frac{3}{35} d_0^2 + \frac{1}{21} e_0^2 \right) \]

\[ \approx \frac{4\pi a^3 b_0^2}{3} \left( 1 + \frac{2}{5} d_0 \right) \]

The next simplest integral to calculate is the area of the egg profile (PAE), corresponding to (Equation (3.3)) (or rather, twice that integral because of the symmetry about the x-axis). This is given by Equation 3.21.

\[ PA_e = 2 \frac{b}{a} \int_0^a \sqrt{a^2 - x^2} \left( 1 + cx + dx^2 + ex^3 \right) \, dx \]

(3.21)

\[ = 2ab \int_1^0 \left( 1 - t^2 \right) \left( 1 + c_0 t + d_0 t^2 + e_0 t^3 \right) \, dt \]

\[ = \pi a^2 b_0 \left( 1 + \frac{1}{4} d_0 \right) \]

The most challenging integral of § 2(d) is that for the surface area (SAE) of the egg, integral (Equation 3.2). In this case, with \( f(x) \) (Equation 3.19), the integrand in Equation 3.22 simplifies to Equation 3.23.

\[ f(x) \sqrt{1 + f'(x)^2} \]

(3.22)

\[ = \frac{b}{a} \left( 1 + cx + dx^2 + ex^3 \right) \sqrt{a^2 - x^2 + \frac{b^2}{a^2} \left( 2a^2 c + (2a^2 d - 1)x + (3a^2 e - 2c)x^2 - 3dx^3 - 4ex^4 \right)^2} \]

(3.23)

\[ = ab_0 \left( 1 + c_0 t + d_0 t^2 + e_0 t^3 \right) \sqrt{1 - t^2 + b_0^2 \left( - t + \left( c_0 + 2d_0 t + (3e_0 - 2c_0) t^2 - 3d_0 t^3 - 4e_0 t^4 \right) \right)^2} \]

Using a Taylor expansion to second order in \( c_0, d_0, e_0 \) and integrating with respect to \( t \) from -1 to 1 gives egg surface area (SAE) in Equation 3.24 (after also multiplying by \( 2\pi a \)), with \( w \) given by Equation 3.25.
\[
\frac{S_{A_e}}{2\pi a^2} = \frac{b_0}{w} \left( \arcsin (w) + b_0 w \right) + d_0 \frac{b_0}{4w^6} \left( \arcsin (w) \left( 9 - 16w^2 + 8w^4 \right) - b_0 w \left( 9 - 10w^2 \right) \right) + \frac{b_0^3}{2w^2} \left( \arcsin (w) \left( 15 - 21w^2 + 8w^4 \right) - b_0 w \left( 15 - 11w^2 + 2w^4 \right) \right) + c_0 e_0 \frac{b_0^3}{12w^9} \left( 3 \arcsin (w) \left( 140 - 255w^2 + 144w^4 - 24w^6 \right) - b_0 w \left( 420 - 485w^2 + 146w^4 \right) \right) + d_0^2 \frac{b_0^3}{16w^{11}} \left( \arcsin (w) \left( 315 - 600w^2 + 360w^4 - 64w^6 \right) - b_0 w \left( 315 - 390w^2 + 128w^4 \right) \right) + e_0^2 \frac{b_0^3}{16w^{15}} \left( 3 \arcsin (w) \left( 210 - 455w^2 + 320w^4 - 72w^6 \right) - b_0 w \left( 630 - 945w^2 + 386w^4 - 16w^6 \right) \right)
\]

\( w := \sqrt{1 - \left( \frac{b}{a} \right)^2} \)  
\[ (3.25) \]

Note that the apparently singular nature of the terms on the right hand side of the formula as \( w \) becomes small are not actual singularities. This can be checked by Taylor expansion of arcsin \( w \). Indeed, direct calculation gives Equation 3.26.

\[
\frac{S_{A_e}}{2\pi a^2} = 2 + b_0 \left( 1 + b_0 + \frac{w^2}{6} \right) + d_0 \left( \frac{7}{105} - \frac{4w^2}{105} \right) + c_0^2 \frac{52w^2}{105} + c_0 e_0 \left( \frac{88}{315} - \frac{64w^2}{231} \right) + d_0^2 \left( \frac{4}{21} - \frac{32w^2}{165} \right) + e_0^2 \left( \frac{124}{1155} - \frac{128w^2}{1365} \right) + O(w^4)
\]

This approximation is only valid for small values of \( w \), i.e., eggs that are close to spherical. However, for any value of \( w \) between 0 and 1, a detailed study of the terms in Equation 3.24 reveals that the maximum value of any of the coefficients of \( d_0, c_0^2, c_0 e_0, d_0^2, e_0^2 \) in that formula is less than 0.5.
The egg shape macro

The macro (Appendix 6, given in the Electronic Supplementary Material, Appendix 7) was developed by N. Buchdahl in collaboration with the primary author for use in ImageJ (Rasband (2010), v. 1.43u). The macro processes the outline of an egg that is given in a .JPG file. Initially, the macro does some pre-processing on the file: it first converts the image to 1-bit (i.e. a black-and-white image), and determines the height and width of the entire image as measured in pixels. The macro assumes that the outline of the egg has been appropriately cropped so that there is not too much white space around the outside. If necessary, it then rotates the image by 90° so that the egg appears to be lying on its side.

The macro then determines the bounding box for the egg: this is the rectangle (with horizontal and vertical sides) that exactly surrounds the egg. Because of photographic constraints, the axis of the egg might not be exactly horizontal, so the macro determines where the middle of each of the two sides is and compares these. If it is greater than a specified amount (currently set to 2 pixels), the macro rotates the image appropriately.

Having straightened the image of the egg, the macro then determines the length of the egg in pixels, and this determines the scale factor to be used later in the macro, the actual length of the egg (L) having been entered by the user earlier. The measured width (W) was not used in the egg function directly, but rather is utilized largely to confirm the accuracy of the macro to detect the outline of the egg.

The process for measuring lengths is not completely straightforward: because of errant pixels, gaps, and blurred outlines (Figure 3.9), it is not sufficient to subtract the x-coordinate of the first non-zero pixel from that of the last or to take simple averages. Instead, for any column (or row) of pixels, the macro computes the “centre of mass” of that column (or row). Using this as the middle, it then calculates the centre of mass of the pixels above this centre, and the centre of mass of the pixels below it; these two values are then used to specify the pixel values for the upper edge and lower edges of the egg in that column.

Figure 3.9. Close-up of an egg outline showing blurred outlines and errant pixels.
The macro proceeds to determine the location of the maximum width of the egg, and the maximum width itself, all measured in pixels.

The next part of the macro simply performs three different numerical integrations to determine the volume, surface area, and profile area of the image. These numerical integrations are very basic, being essentially the trapezoidal method (Figure 3.10), as described in (Mänd et al. 1986). It is not hard to implement (the generally significantly more accurate) Simpson's Rule, but simple experiments suggested that there was little to be gained from doing this, at least using the relatively low-resolution images used for doing the tests.

![Figure 3.10. Diagram showing the direction of slicing for egg images in the trapezoidal integration process.](image)

A critical issue in the use of numerical integration methods is the step size; (this is the variable $h$ that appears in the macro). In theory, the smaller the step size, the more accurate are the results, but for discrete information that is modeling a continuous function, the accuracy in fact decreases if the step size is too small. This is particularly true of the formula for the surface area of the egg, as it involves the derivative of the modeling function. Another problem with setting $h$ too small is that the computation time is inversely proportional to $h$. The value for $h$ used in the macro was set at about four pixels, which was chosen on the basis of experiments with images of perfect spheres for which the relevant numbers can all be calculated to arbitrary precision. The fewest slices made on any egg were 113 (on an egg sample of Zosterops lateralis) and the most slices made were 849 (on an egg sample of Strepera versicolor).

Having computed the various quantities of interest and converting dimensions from pixels to metric units, the macro then prints these out in a log file, along with estimates of the extent to which the egg is deviating from spherical and ellipsoidal. These were then be copied for further use in Microsoft Excel (2007).

The macro then goes on to calculate the values of the parameters $a$, $b_0$, $c_0$, $d_0$, $e_0$ based on the measurements that have been made and the assumption that the egg is accurately described by Equation 3.10. It sets $a$ to be the length of the egg divided by 2, where the length is that which the macro measured rather than the value entered by the user. The values of $b_0$ and $c_0$ are determined using Equations A15.4,
A15.5 and A15.6 (see Supplement 3.1), since both \( t_m \) and \( z_m \) have been determined in the earlier calculations of the macro. The values for \( d_0 \) and \( e_0 \) are calculated by determining the width of the egg halfway to the left and halfway to the right of where the maximum width occurs. These choices were made somewhat arbitrarily, and it might be that they could be improved by choosing points closer to the two ends, as the effect of these parameters becomes more significant in these regions.

Using the value of the parameters \( a, b_0, c_0, d_0, e_0 \) and the overall scale factor, the macro then computes the three integrals using the formulas given in § 2(d)iv. These numbers can be compared with the numbers determined earlier by “direct measurement”, and the results of a number of experiments showed good agreement between the two sets. In fact, in experiments on idealised perfectly spherical eggs, the numbers calculated by the second method were more accurate than those of the direct measurement.

Finally, the macro attempts to give the users some idea of how accurately it has made its approximations, by plotting the graphs of \( y = f_i(x) \) for \( i = 0, 1, 2 \), where \( f_0(x) \) (corresponding to the red curve) is the function determined by measurements on the image – the “true” shape, \( f_1(x) \) is Equation 3.27 determined by computing the values of the shape parameters (corresponding to the blue curve), and \( f_2(x) \) (Equation 3.28) gives a curve (the green curve) that would be the result of computations arising from measurements of just the length, width and where the maximum width occurs.

\[
f_1(x) = \frac{b}{a} \sqrt{1-x^2} \left( 1 + cx + dx^2 + ex^3 \right)
\]

(3.27)

\[
f_2(x) = \frac{b}{a} \sqrt{1-x^2} \left( 1 + cx \right)
\]

(3.28)

\[\text{vi. Macro testing}\]

The accuracy of the macro was tested on 10 eggs from free-range chickens (\textit{Gallus gallus domesticus}). The length and width of the ten eggs was measured with callipers, photographed and analysed with the macro (as outlined above). Egg volume was then measured by water displacement in a cylinder of water. While this method of validation may not be optimal as it is unlikely to exceed the accuracy of the macro (Bridge et al. 2007), it did prove a useful system to compare the approximate volume of eggs with the two methods. The mean volume of the chicken eggs according to the macro (51 ± 4 cm\(^3\)) was very close to the mean volume as measured from water displacement (50 ± 4 cm\(^3\)). The mean width of the chicken eggs as determined by the macro (4.2 ± 0.1 cm) was indistinguishable from the value obtained with calliper measurements (4.2 ± 0.1 cm).
(e) **Clutch size**

Clutch size (the number of eggs in each individual clutch) was obtained from the South Australian Museum ornithology collection egg database. Individual egg measurements were then multiplied by the number of eggs for their respective clutch to obtain total clutch surface area ($P_A$ and $S_A$) and volume ($V_C$).

(f) **Nest dimensions**

The methods used to determine the nest dimensions are those described in Chapter 2. In brief, nest internal diameter ($d_I$) and height ($h_I$) was measured, and nest cup surface area ($A_I$) and nest opening surface area ($A_{LID}$, Figure 3.11) calculated. Values of nest mass ($M_N$) were obtained for nests without supporting branches. In addition, nest cup volume ($V_{CUP}$) was calculated as half of the volume for a spheroid based on internal nest dimensions (Equation 3.29).

\[
V_{CUP} = \frac{\pi d_I^2 h_I}{6} \quad \text{for a deep nest } \left( \frac{d_I}{2} < h_I \right) \text{ i.e. prolate spheroid}
\]

\[
V_{CUP} = \frac{\pi h_I^2 d_I}{3} \quad \text{for an open bowl nest } \left( \frac{d_I}{2} > h_I \right) \text{ i.e. oblate spheroid}
\]

where the symbols are:
- $V_{CUP}$ = Nest cup volume (cm$^3$)
- $h_I$ = Internal nest height (cm)
- $d_I$ = Internal nest diameter (cm)

![Figure 3.11](image.png)

**Figure 3.11.** Diagram showing the aerial diagrammatic representation of a nest, where the clutch profile area ($P_A$, cm$^2$) is equal to that of the white surfaces and the nest opening surface area ($A_{LID}$, cm$^2$) is equal to the surface area of the light grey circle. Note that specific arrangement of eggs does not represent actual arrangement in a nest, rather is for graphical purposes only.
(g) **Parent mass**

Parent mass values were obtained from the Handbook of Australian, New Zealand and Antarctic Birds resource series (Marchant and Higgins 2001; 2002; 2006). Egg size and morphology was assessed against female body mass ($M_F$, g), where values are those of adults in museum collections, as well as the sexual size dimorphism index (SDI, Equation (3.30)), introduced by Cabana et al. (1982).

\[
SDI = \frac{M_M}{M_F} \tag{3.30}
\]

where the new symbols are:

- $SDI$ = Sexual size dimorphism index
- $M_M$ = Male body mass (g)
- $M_F$ = Female body mass (g)

Since nest design is influenced by adult body mass and both sexes contribute to nest construction (Chapter 2), nest data were transformed to be mass-independent based on the mean of the male and female mass values ($M$, g). For those where a mean value was not reported, the median of the minimum and maximum mass values was used. Mass-independent nest data were calculated as the untransformed value divided by $M^b$, where values of $b$ for nest parameters were obtained from Chapter 2 and Supplement 2.3, while mass-independent egg data were calculated as the untransformed value divided by $M_F^b$.

(h) **Links to previous studies**

i. **Simple linear equations**

To test the accuracy of simple equations for egg volume, such as that of Hoyt (1979), egg lengths and widths were collected for additional eggs in the South Australian Museum ornithology collection. Eggs that were included in the digital image analysis method were not re-used here. Egg volume was then calculated as per the equation of Hoyt (1979) and the resulting regression compared to the data from the macro (digital image analysis method).

ii. **Nest morphology and thermal properties remodelled**

Initial studies into the morphology of birds’ nests suggested that nest surface area was largely determined by the size of the incubating parent and nest thickness was largely driven by the need for structural support of the incubating parent’s mass (Chapter 2). The analyses tested predicted modelling exponents for heat loss, isometric and structural scaling against known nest dimensions and thermal properties. However, it was unable to account for the mass of the clutch. In order to validate the findings of our previous paper, the combined mass of the incubating parent ($M$, g) and clutch ($M_C$, g) was substituted throughout the model of Chapter 2. Values for nest dimensions were calculated as before; however, the modelled internal nest
dimensions and subsequent model outcomes for external dimensions, thickness, surface area and mass incorporated internal nest volume changes to account for additional volume and mass of the clutch (M_C). The model was run under three scenarios: a typical clutch of eggs (M + M_C), a clutch with one chick just prior to fledging (M + M) and a clutch with five chicks just prior to fledging (M + 5M). Here, we assumed that the mass of the clutch is equivalent with the volume of the clutch (M_C = V_C), the mass of a chick prior to fledging would be equivalent with that of the adult (M = parent mass or fledgling mass), and clutch sizes represent those of the species in this study (one to five eggs).

(i) Statistical analyses

An informal supertree (a reconstruction of multiple trees [Bininda-Emonds 2004], Figure 3.12) was derived following trees provided by http://www.tolweb.org, Loynes et al. (2009), Jønsson et al. (2010), Nyári and Joseph (2011) and Driskell and Christidis (2004). The supertree was constructed in Mesquite (Maddison and Maddison 2007), version 2.75 and formatted in FigTree (Rambaut 2007), version 1.3.1). Branch lengths of the tree were adjusted to be punctuated (representing the punctuated evolution theory where long periods of stasis are punctuated by rapid periods of development) and equal to one.

Data were analysed in R (Gentleman and Ihaka 2011, version 2.14.1) using multiple linear regression techniques, whilst also accounting for phylogenetic relatedness. The analyses utilised the packages: ape (Analysis of phylogenetics and evolution, Paradis et al. 2004), version 3.0), gee (Generalised estimation equation solver, Carey 2011), version 4.13-17), nlme (Linear and non-linear mixed effects models, Pinheiro et al. 2011), version 3.1-103) and lattice (Multivariate data visualization, Sarkar 2008), version 0.20-0), as well as a generalised least square in comparative phylogenetics (PGLS) code modified from code that accompanies Duncan et al. (2007).

We tested the egg shape parameters (b_0, c_0, d_0, e_0) against the phylogeny to determine if egg shape contains a phylogenetic signal. This involved using the packages Picante (Phylocom integration, community analyses, null-models, traits and evolution, Kembel et al. 2010), version 1.3-0), Vegan (Community ecology package, Oksanen et al. 2011), version 2.0-3) and Permute (Functions for generating restricted permutations of data, Simpson 2011), version 0.6-3) to calculate Blomberg et al.’s (2003) K-statistic (the strength of the signal) and determine the significance of the phylogenetic relationship.

Phylogenetic correlation was determined from the lambda (λ) value that maximised the likelihood of the model (Pagel 1999). The strength of the phylogenetic models was assessed by repeating analyses with λ equal to zero and comparing the second-order Akaike Information Criterion (AICc) values produced from the phylogenetic and non-phylogenetic models (Burnham and Anderson 2002). The need to account for phylogeny in the analysis of these data was supported if the AICc was lowest for the phylogenetic model, and if the AICc difference (ΔAICc) between the phylogenetic and non-phylogenetic models was greater than four; the non-phylogenetic model was retained if the ΔAICc was less than four. PGLS estimates were accepted as
significant when the lower and upper 95% confidence limits (Phy-CL) of a given parameter estimate (slope) excluded zero.

Further statistical analyses were performed in JMP IN (SAS Institute, 2001, version 4.0.4), employing multiple linear regression techniques. Residuals of the data met the assumptions required for parametric linear regression tests of normality (Shapiro–Wilk W test) and equal variance (constant spread of the residuals), except where stated in the results. Analysis of co-variance (ANCOVA) techniques were used to test if regression slopes differed from expected scaling laws for linear dimensions ($M^{0.33}$), surface areas ($M^{0.67}$) and volumes ($M^1$) (Schmidt-Nielsen, 1984); as well as to test if the regression of egg volume against female mass differed between our results and results based on the equation of Hoyt (1979). As in our previous paper, the model predictions for nest dimensions and thermal properties were tested against the data from Chapter 2 with ANCOVA techniques.

Statistical analyses on allometric relationships were assessed using logarithmically-transformed values. Multiple linear regression models incorporated $M_F$ and SDI as explanatory variables simultaneously. While there is generally a strong association between sexual size dimorphism and body size (termed Rensch’s rule, (Fairbairn, 1997; Székely et al., 2007)), we found no such relationship with the species in this study, as the slope of male mass ($M_M$) to female mass ($M_F$) is not significantly different to 1 ($AICc (Phy) = -98.0$, $AICc (Non-Phy) = -102.5$, $M_M = 0.02 M_F^{-1.01}$, LCL = 0.97, UCL = 1.06). Consequently, we did not include an interaction term ($M_F^*SDI$) in statistical analyses of egg size. Explanatory (nest) and response (egg) variables were transformed to be mass-independent ($\Sigma^2 (g)$) for simple linear regression analyses of egg morphology against nest morphology, to account for the known allometric relationships with nest structure (Chapter 2 and Supplement 2.3). For variables that are influenced by SDI (nest mass, $M_N$ (Supplement 2.5), and egg width, $W$ (Table 3.3), the residuals of the multiple linear regression model (including both $M_F$ and SDI) were used. Egg to nest relationships were repeated for logarithmically-transformed variables (rather than mass-independent) to test if the slopes differed significantly from 1. The significance value was set at 0.05 for all analyses. Data are expressed as mean ± 95% confidence interval (C.I.).
The structural and thermal properties of avian cup-shaped nests

Figure 3.12. Informal supertree showing the phylogenetic relationships between bird species. Phylogenetic relationships were derived following trees provided by www.tolweb.org, Loynes et al. (2009), Jansson et al. (2010), Nyári and Joseph (2011) and Driskell and Christidis (2004). Replicate nest values (N) separated by commas indicate the replicate for the nest dimensions, followed by the replicate for the nest mass and density measurements. * Multiple nests and species could not be included in nest mass analysis due to the attachment of supporting branches.
3. RESULTS

(a) The shape of an egg

There is considerable variation in egg shape within some species (*e.g.* *Manorina flavigula*, Figure 3.13) and very little in others (*e.g.* *Pachycephala rufogularis* Figure 3.13). When the mean rescaled shape parameters for a species (Appendix 8) are used to plot the egg outline function (*f*(z), Equation 3.18), the variation in egg shape between species becomes clear (Figure 3.14). Egg shape parameters are influenced by phylogeny, where *b*₀ and *d*₀ contain a significant phylogenetic signal, though in all cases Blomberg *et al.*’s (2003) K-statistic is less than would be expected based on Brownian motion evolution (*i.e.* K < 1) (Table 3.1).

Circular distortion, but not elliptical distortion, is significantly influenced by the phylogenetic relationships of the adults (Table 3.2). While circular distortion increases with female body mass, elliptical distortion is independent of the mass of the female (Table 3.3 and Figure 3.15.a). Both circular and elliptical distortion are independent of the sexual size dimorphism index (Table 3.3).
The structural and thermal properties of avian cup-shaped nests

<table>
<thead>
<tr>
<th>Species</th>
<th>Egg Profile</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acan tenu</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Anth coru</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Anth chry</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Coll harm</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Coro mela</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Croc forq</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Daph chry</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Eops aust</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Gral cyan</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Lich chry</td>
<td>![Egg Profile]</td>
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<tr>
<td>Lich crat</td>
<td>![Egg Profile]</td>
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<tr>
<td>Lich indl</td>
<td>![Egg Profile]</td>
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<tr>
<td>Lich leuc</td>
<td>![Egg Profile]</td>
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<tr>
<td>Lich orna</td>
<td>![Egg Profile]</td>
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<tr>
<td>Lich penl</td>
<td>![Egg Profile]</td>
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<tr>
<td>Lich plum</td>
<td>![Egg Profile]</td>
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<tr>
<td>Lich vire</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Mano flav</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Mela cucu</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Mela vitt</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Micr fasc</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Orlo sagi</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Pach inor</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Pach oliv</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Pach pect</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Pach rufi</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Pach rulo</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Petr good</td>
<td>![Egg Profile]</td>
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<tr>
<td>Petr mult</td>
<td>![Egg Profile]</td>
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<tr>
<td>Psop nigtr</td>
<td>![Egg Profile]</td>
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<tr>
<td>Rhip albi</td>
<td>![Egg Profile]</td>
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<tr>
<td>Rhip leuc</td>
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<td>Stre vers</td>
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<tr>
<td>Stru cine</td>
<td>![Egg Profile]</td>
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<tr>
<td>Turd meru</td>
<td>![Egg Profile]</td>
</tr>
<tr>
<td>Zost late</td>
<td>![Egg Profile]</td>
</tr>
</tbody>
</table>

**Figure 3.13.** Diagram showing replicate egg profiles for individual species (N = 10), where egg height has been standardised. Black profile lines represent the egg shape for a given egg. Dark grey surfaces show the minimum extent of egg shape, while the light grey surfaces show the maximum extent of egg shape. Species names have been abbreviated, but can be found in full in Figure 3.12.
Figure 3.14. Plotted curves of egg outlines for the function $z = b_0 \sqrt{1 - t^2} \left(1 + c_0 t^2 + d_0 t^4 + e_0 t^6\right)$, based on rescaled shape parameters ($a, b_0, c_0, d_0, e_0$). Black dashed lines represent the minimum and maximum extent of shape for all species. Individual coloured lines represent mean egg shape for individual species based on mean values for $a, b_0, c_0, d_0, e_0$.

Table 3.1. Statistics for the relationship between egg shape and phylogeny

<table>
<thead>
<tr>
<th>egg shape parameter</th>
<th>minimum</th>
<th>maximum</th>
<th>Blomberg’s K</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$b_0$</td>
<td>0.59</td>
<td>0.87</td>
<td>0.50</td>
<td>0.012 *</td>
</tr>
<tr>
<td>$c_0$</td>
<td>-0.28</td>
<td>-0.0026</td>
<td>0.52</td>
<td>0.38</td>
</tr>
<tr>
<td>$d_0$</td>
<td>-0.18</td>
<td>0.12</td>
<td>0.58</td>
<td>0.028 *</td>
</tr>
<tr>
<td>$e_0$</td>
<td>-0.11</td>
<td>0.19</td>
<td>0.34</td>
<td>0.63</td>
</tr>
</tbody>
</table>

* Indicates that the egg shape parameter of interest contains a significant phylogenetic signal.
The area and volume of an egg

Species-specific values for egg size are given in Appendix 9. Egg size is significantly influenced by phylogeny when regressed against mass, however, whole clutch measurements are not (Table 3.2), and egg size alone contains a significant phylogenetic signal (Supplement 3.2). Egg size increases with female body mass (Table 3.3), including egg length (Figure 3.15.b), width (Figure 3.15.b), profile area (Figure 3.15.c), surface area (Figure 3.15.d) and volume (Figure 3.15.e). Whole clutch egg measurements increase with female mass because egg size does (Table 3.3).

Egg length ($F_{1,113} = 163.0, P < 0.001$) and width ($F_{1,113} = 435.7, P < 0.001$) increase with female body mass with an exponent lower than would be expected for a linear dimension ($M^{0.33}$). Egg surface area ($F_{1,113} = 309.6, P < 0.001$), clutch surface area ($F_{1,113} = 58.4, P < 0.001$), egg profile area ($F_{1,113} = 283.7, P < 0.001$) and clutch profile area ($F_{1,113} = 52.1, P < 0.001$) also increase with an exponent that is lower than what would be expected for a typical surface area ($M^{0.67}$). In addition, egg volume ($F_{1,113} = 334.0, P < 0.001$) and clutch volume ($F_{1,113} = 139.8, P < 0.001$) increase with an exponent lower than expected for a volume ($M^{1.0}$).

Egg length, width, profile area, surface area and volume (Figure 3.16) increase with the sexual size dimorphism index (Table 3.3). However, whole clutch measurements of egg size are independent of sexual size dimorphism. Smaller eggs are laid by species where the female is the larger of the two sexes.

Egg surface area increases in proportion to egg volume ($R^2 = 1.0, F_{1,69} = 17.68, P < 0.001$) according to the relationship $SA_E = 5.05 \pm 1.01 V_E^{0.67 \pm 0.01}$, though it should be noted that the residuals are not normally distributed ($W = 0.76, P < W < 0.0001$) due to some variation for eggs of small species.

### Table 3.2. Comparative phylogenetics statistics for the regression of egg morphology against female body mass ($M_F, g$) and sexual size dimorphism index (SDI) according to $y = aM_F^b SDI^b$

<table>
<thead>
<tr>
<th>egg parameter</th>
<th>lambda ($\lambda$)</th>
<th>second-order Akaike Information Criterion (AICc)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>phylogenetic model</td>
</tr>
<tr>
<td>individual eggs</td>
<td></td>
<td>non-phylogenetic model</td>
</tr>
<tr>
<td>egg length ($L$, cm)</td>
<td>1.0</td>
<td>$-169.6^*$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$-160.5$</td>
</tr>
<tr>
<td>egg width ($W$, cm)</td>
<td>1.0</td>
<td>$-186.2^*$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$-176.5$</td>
</tr>
<tr>
<td>profile area ($PA_E$, cm$^2$)</td>
<td>1.0</td>
<td>$-129.4^*$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$-120.3$</td>
</tr>
<tr>
<td>surface area ($SA_E$, cm$^2$)</td>
<td>1.0</td>
<td>$-127.7^*$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$-119.9$</td>
</tr>
<tr>
<td>volume ($V_E$, cm$^3$)</td>
<td>1.0</td>
<td>$-102.8^*$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$-93.7$</td>
</tr>
<tr>
<td>circular distortion ($D_C$)</td>
<td>1.0</td>
<td>$-214.8^*$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$-208.8$</td>
</tr>
<tr>
<td>elliptical distortion ($D_E$)</td>
<td>0.0</td>
<td>$-174.3$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$-177.1^*$</td>
</tr>
<tr>
<td>whole clutch</td>
<td></td>
<td></td>
</tr>
<tr>
<td>profile area ($PA_C$, cm$^2$)</td>
<td>0.21</td>
<td>$-80.9$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$-83.1^*$</td>
</tr>
<tr>
<td>surface area ($SA_C$, cm$^2$)</td>
<td>0.22</td>
<td>$-80.1$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$-82.2^*$</td>
</tr>
<tr>
<td>volume ($V_C$, cm$^3$)</td>
<td>0.31</td>
<td>$-73.4$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$-74.9^*$</td>
</tr>
<tr>
<td>clutch size (E)</td>
<td>0.31</td>
<td>$-79.8$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$-82.5^*$</td>
</tr>
</tbody>
</table>

Lambda ($\lambda$) indicates the strength of the phylogenetic relationship, where values lie between 0 and 1.

* Represents the model with the best fit for the data, where the model with the lowest AICc is retained for an AICc difference in excess of four, and the non-phylogenetic model retained for an AICc difference of less than four.
Table 3.3. Statistics for the regression of egg morphology against female body mass (\(M_F\), g) and sexual size dimorphism index (SDI) according to \(y = aM_F^bSDI^b\)

<table>
<thead>
<tr>
<th>egg parameter</th>
<th>intercept, (a)</th>
<th>scaling</th>
<th>(M_F) statistics #</th>
<th>scaling</th>
<th>(SDI) statistics #</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>exponent, (b)</td>
<td>LCL = 0.23 UCL = 0.27 *</td>
<td>LCL = 0.01 UCL = 0.28 *</td>
<td></td>
</tr>
<tr>
<td>individual eggs</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>egg length (L, cm)</td>
<td>0.96 ± 1.04</td>
<td>0.25 ± 0.01</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>egg width (W, cm)</td>
<td>0.76 ± 1.03</td>
<td>0.23 ± 0.01</td>
<td>LCL = 0.21 UCL = 0.24 *</td>
<td>0.17 ± 0.05</td>
<td>LCL = 0.06 UCL = 0.27 *</td>
</tr>
<tr>
<td>profile area ((PA_E), cm(^2))</td>
<td>0.57 ± 1.07</td>
<td>0.48 ± 0.02</td>
<td>LCL = 0.44 UCL = 0.51 *</td>
<td>0.31 ± 0.11</td>
<td>LCL = 0.08 UCL = 0.54 *</td>
</tr>
<tr>
<td>surface area ((SA_E), cm(^2))</td>
<td>0.34 ± 0.03</td>
<td>0.47 ± 0.02</td>
<td>LCL = 0.43 UCL = 0.50 *</td>
<td>0.32 ± 0.12</td>
<td>LCL = 0.08 UCL = 0.56 *</td>
</tr>
<tr>
<td>volume ((V_E), cm(^3))</td>
<td>0.29 ± 1.10</td>
<td>0.70 ± 0.02</td>
<td>LCL = 0.66 UCL = 0.75 *</td>
<td>0.47 ± 0.16</td>
<td>LCL = 0.13 UCL = 0.81 *</td>
</tr>
<tr>
<td>circular distortion ((D_C))</td>
<td>1.25 ± 1.02</td>
<td>0.02 ± 0.01</td>
<td>LCL = 0.01 UCL = 0.03 *</td>
<td>-0.01 ± 0.03</td>
<td>LCL = -0.08 UCL = 0.06</td>
</tr>
<tr>
<td>elliptical distortion ((D_E))</td>
<td>1.26 ± 1.06</td>
<td>0.002 ± 0.02</td>
<td>R(^2) = 0.08 F(_1) = 0.07 P = 0.80</td>
<td>0.10 ± 0.11</td>
<td>R(^2) = 0.08 F(_1) = 2.90 P = 0.10</td>
</tr>
<tr>
<td>whole clutch</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>profile area ((PA_C), cm(^2))</td>
<td>1.13 ± 1.23</td>
<td>0.54 ± 0.06</td>
<td>R(^2) = 0.92 F(_1) = 371.9 P &lt; 0.0001 *</td>
<td>-0.22 ± 0.42</td>
<td>R(^2) = 0.92 F(_1) = 1.19 P = 0.28</td>
</tr>
<tr>
<td>surface area ((SA_C), cm(^2))</td>
<td>4.40 ± 1.23</td>
<td>0.53 ± 0.06</td>
<td>R(^2) = 0.91 F(_1) = 350.8 P &lt; 0.0001 *</td>
<td>-0.22 ± 0.43</td>
<td>R(^2) = 0.91 F(_1) = 1.16 P = 0.29</td>
</tr>
<tr>
<td>volume ((V_C), cm(^3))</td>
<td>0.57 ± 1.26</td>
<td>0.77 ± 0.06</td>
<td>R(^2) = 0.95 F(_1) = 601.0 P &lt; 0.0001 *</td>
<td>-0.13 ± 0.47</td>
<td>R(^2) = 0.95 F(_1) = 0.32 P = 0.58</td>
</tr>
<tr>
<td>clutch size (E)</td>
<td>2.02 ± 1.23</td>
<td>0.06 ± 0.06</td>
<td>R(^2) = 0.21 F(_1) = 3.83 P = 0.059</td>
<td>-0.45 ± 0.42</td>
<td>R(^2) = 0.21 F(_1) = 4.64 P = 0.039 *</td>
</tr>
</tbody>
</table>

Intercepts, scaling exponents and accompanying statistics are those from the best fit model. Functions are represented as intercept/exponent ± 95 % C.I. in the case of non-phylogenetic models and intercept/exponent ± S.E. in the case of phylogenetic models.

\(^\#\) Statistics for non-phylogenetic models include the R\(^2\) for the model regression, the F-ratio (degrees of freedom) and the P-value; while the lower critical limit and upper critical limit are reported for phylogenetic models.

\(^*\) Indicates that the regression for the variable of interest is statistically significant (slope ≠ 0). For non-phylogenetic models the alpha value (α) used is 0.05.
Figure 3.15. Relationship between female body mass ($M_F$, g) and a – circular distortion ($D_C$, $b = 0.02$, solid circles) and elliptical distortion ($D_E$, $b = 0.002$, open circles); b – egg length (cm, $L$, $b = 0.25$, solid circles) and width (cm, $W$, $b = 0.76$, open circles); c – profile area of the egg (cm$^2$, $PA_E$, $b = 0.48$, circles) and clutch (cm$^2$, $PA_C$, $b = 0.54$ squares); d – surface area of the egg (cm$^2$, $SA_E$, $b = 0.47$, circles) and clutch (cm$^2$, $SA_C$, $b = 0.53$, squares) and e – volume of the egg (cm$^3$, $V_E$, $b = 0.70$, circles) and clutch (cm$^3$, $V_C$, $b = 0.77$, squares). Each point represents the mean ± 95 % C.I. for a species of bird (N = 36). Regression lines and confidence bands are not shown as statistical analyses employ phylogenetically-informed multiple linear regression techniques with sexual size dimorphism in the model.
Figure 3.16. Relationship between female mass (M feminism, g, black circles) and sexual size dimorphism (SDI, grey circles) and egg volume (\( V = 0.29 \times M^{0.70} \times SDI^{0.47} \)). Each point represents the mean for a species of bird (N = 36). Regression lines and confidence bands are not shown as statistical analyses employed phylogenetically-informed multiple linear regression techniques.

(c) Clutch size

Clutch size is not significantly influenced by phylogeny (Table 3.2) or the size of the female (Table 3.3 and Figure 3.17.a) but decreases significantly with the sexual size dimorphism index (Table 3.3 and Figure 3.17.b). More eggs are laid in a clutch for species where the female is the larger of the two sexes. Species-specific values for clutch size are given in Appendix 9.

Clutch size also influences egg morphology (Supplement 3.3) and secondarily influences nest conductance through changes to nest surface area (Supplement 3.4).

Figure 3.17. Relationship between a – female mass (M feminism, g) and clutch size (M feminism 0.06) and b – sexual size dimorphism (SDI) and clutch size (SDI 0.45). Each point represents the mean ± 95 % C.I. for a species of bird (N = 36). The solid line for b represents the regression mean for an individually run regression, for graphical purposes, where the line represented is E = 2.02 SDI 0.45. Black dashed lines represent the 95 % confidence bands for the regression mean. Regression lines and confidence bands are not shown for a as actual statistical analyses employed multiple linear regression techniques, and graphical representation of the line E = 2.02 M feminism 0.06 does not prove insightful or representative in this case.
(d) **Egg morphology and nest morphology**

Egg width is not influenced by the internal height of the nest (Figure 3.18.a). Clutch profile area is significantly influenced by the nest opening area (Figure 3.18.b). In addition, clutch surface area is significantly influenced by the internal surface area of the nest (Figure 3.18.c). While clutch volume is influenced by the volume of the nest cup (Figure 3.18.d), it is not influenced by nest mass (Figure 3.18.e). Accompanying statistics can be found in (Table 3.4).

Clutch profile area increases at a slower rate than the nest opening surface area \( \left( PA_C = 0.47 \, A_W^{0.75} \pm 0.07 \right) \), \( F_{1,34} = 437.8, P < 0.0001 \), clutch surface area at a slower rate than the internal nest surface area \( \left( SA_C = 0.74 \, A_I^{0.81} \pm 0.10 \right) \), \( F_{1,34} = 290.7, P < 0.0001 \) and clutch volume at a slower rate than nest cup volume \( \left( V_C = 0.22 \, V_{CUP}^{0.77} \pm 0.08 \right) \), \( F_{1,34} = 379.9, P < 0.0001 \), as shown by the slopes that are significantly shallower than 1.

**Table 3.4. Statistics for the relationship between egg morphology and nest morphology**

<table>
<thead>
<tr>
<th>response variable *</th>
<th>experimental variable *</th>
<th>intercept, a</th>
<th>slope, b</th>
<th>statistics *</th>
<th>lambda (λ)</th>
<th>Akaike Information Criterion (AICc)</th>
<th>second-order Akaike Information Criterion (AICc)</th>
</tr>
</thead>
<tbody>
<tr>
<td>log egg width residuals (W, cm)</td>
<td>internal nest height (h, cm g -0.26)</td>
<td>-0.003 ± 0.02</td>
<td>0.0004 ± 0.01</td>
<td>LCL = -0.02 UCL = 0.02</td>
<td>1.0</td>
<td>-187.0 *</td>
<td>-179.4</td>
</tr>
<tr>
<td>clutch profile area (PA_C, cm² g -0.54)</td>
<td>nest opening surface area (A_O, cm² g -0.71)</td>
<td>0.58 ± 0.42</td>
<td>0.18 ± 0.13</td>
<td>( R^2 = 0.19 ) ( F_{1,34} = 8.17 ) ( P = 0.007 * )</td>
<td>0.17</td>
<td>-20.7</td>
<td>-22.7 *</td>
</tr>
<tr>
<td>clutch surface area * (SA_C, cm² g -0.53)</td>
<td>internal nest surface area (A_I, cm² g -0.62)</td>
<td>2.80 ± 1.43</td>
<td>0.17 ± 0.14</td>
<td>( R^2 = 0.15 ) ( F_{1,34} = 6.16 ) ( P = 0.018 * )</td>
<td>0.25</td>
<td>78.7</td>
<td>78.4 *</td>
</tr>
<tr>
<td>clutch volume (V_C, cm³ g -0.77)</td>
<td>nest cup volume (V_CUP, cm³ g -0.84)</td>
<td>0.44 ± 0.15</td>
<td>0.04 ± 0.03</td>
<td>( R^2 = 0.12 ) ( F_{1,34} = 4.44 ) ( P = 0.043 * )</td>
<td>0.24</td>
<td>-60.7</td>
<td>-61.5 *</td>
</tr>
<tr>
<td>clutch volume (V_C, cm³ g -0.77)</td>
<td>log nest mass residuals (M_N, g)</td>
<td>0.59 ± 0.04</td>
<td>0.13 ± 0.16</td>
<td>( R^2 = 0.10 ) ( F_{1,25} = 2.84 ) ( P = 0.10 )</td>
<td>0.09</td>
<td>-44.0</td>
<td>-46.7 *</td>
</tr>
</tbody>
</table>

* Represents the model with the best fit for the data, where the model with the lowest AICc is retained for an AICc difference in excess of four, and the non-phylogenetic model retained for an AICc difference of less than four.

\( \lambda \) indicates the strength of the phylogenetic relationship, where values lie between 0 and 1.

* Statistics for non-phylogenetic models include the \( R^2 \) for the model regression, the \( F \)-ratio (degrees of freedom) and the \( P \)-value.

* Indicates that the regression is statistically significant \((slope \neq 0)\) at the specified alpha value \((\alpha = 0.05)\).

\( N = 36 \) for all comparisons, except nest mass which has \( N = 27 \). The replicate for nest mass measurements is lower as some nests were excluded from analysis owing to the attachment of supporting branches.

* Response variables have been rendered mass-independent (see §2(g)) for the purpose of this analysis to account for allometric relationships with female mass \((M_F, g)\), with exception to egg width. Egg width is represented by the logged residuals of the phylogenetic multiple regression model including female mass \((M_F, g)\) and sexual size dimorphism index (SDI). Experimental variables have been rendered mass-independent (see §2(g)) for the purpose of this analysis to account for allometric relationships with mean parent mass \((M, g)\), with exception to nest mass. Nest mass is represented by the logged residuals of the non-phylogenetic multiple regression model including mean parent mass \((M, g)\) and sexual size dimorphism index (SDI).

* Statistics for the surface area of a clutch are represented by those for the whole egg, followed by those for half the egg \((i.e.\ the surface in contact with nest material)\).
Figure 3.18. Relationship between a – nest height (h, cm g$^{-0.20}$) and log egg width residuals (W, cm, W = -0.003 + 0.0004 h); b – nest opening surface area (A_{lid}, cm$^2$ g$^{-0.71}$) and clutch profile area (PA_{c}, cm$^2$ g$^{-0.54}$, PA_{c} = 0.58 + 0.18 A_{lid}); c – internal nest surface area (A_{i}, cm$^2$ g$^{-0.62}$) and clutch surface area (SA_{c}, cm$^2$ g$^{-0.53}$, SA_{c} = 2.80 + 0.17 A_{i}); d – nest cup volume (V_{cup}, cm$^3$ g$^{-0.77}$) and clutch volume (V_{c}, cm$^3$ g$^{-0.77}$, V_{c} = 0.44 + 0.04 V_{cup}) and e – log nest mass residuals (M_{n}, g) and clutch volume (V_{c}, cm$^3$ g$^{-0.77}$, V_{c} = 0.59 + 0.13 M_{n}). Each point represents the mean for a species of bird (N = 36). Solid lines represent the regression mean. Dashed lines represent the 95% confidence bands for the regression mean. Response variables have been rendered mass-independent (see § 2(g)) for the purpose of this analysis to account for allometric relationships with female mass (M_{f}, g), with exception to egg width in a. Egg width is represented by the logged residuals of the phylogenetic multiple regression model including female mass (M_{f}, g) and sexual size dimorphism index (SDI). Experimental variables have been rendered mass-independent (see § 2(g)) for the purpose of this analysis to account for allometric relationships with mean parent mass (M, g), with exception to nest mass in e. Nest mass is represented by the logged residuals of the non-phylogenetic multiple regression model including mean parent mass (M, g) and sexual size dimorphism index (SDI). Confidence bands are not shown in a as statistical analyses employ phylogenetically-informed multiple linear regression techniques.
(e) **Links to previous studies**

**i. Simple linear equations**

The allometric relationship between female body mass and egg volume can be approximated to an extent by Hoyt’s (1979) equation. Simple equations provide rough estimates of egg volume, and the scaling exponent derived does not differ significantly from the present study \(b_{\text{Hoyt}} = 0.70, F_{1,68} = 0.11, P = 0.74\), however the elevation (intercept) of the regression line is slightly overestimated for Hoyt’s (1979) equation \(a_{\text{Hoyt}} = 0.33, F_{1,69} = 7.76, P = 0.007\) – 0.04 cm\(^3\) greater than our regression intercept.

**ii. Nest morphology and thermal properties remodelled**

The model predictions and statistical analyses are shown in Table 3.5. The model outcomes match those of Chapter 2, with exception to internal diameter of the nest and the surface area of the nest. When accounting for parent mass only, the exponent for internal diameter \(M^{0.35}\) is significantly different to heat loss, isometric and structural scaling exponents (Chapter 2). When including the mass of a typical clutch of eggs, the exponents are still significantly different on all accounts. However, when including the mass of fledglings (either one chick or five), the internal diameter scaling exponent is in line with all three scaling hypotheses. For mean nest surface area, the observed scaling exponent \(M^{0.68}\) was significantly different to that of heat loss scaling and structural scaling but no different to isometric scaling when considering the mass of the parent alone (Chapter 2). However, when including the clutch mass, the structural scaling exponent does not become significantly different. When the nest contents increase to one chick or five, the predicted scaling exponents again become significantly different to the observed data. The opposite holds true for heat loss scaling. The predicted exponent for a clutch of eggs is significantly different to the observed data, as is the exponent when considering parent mass alone, but the predicted exponent for one chick or five is not different to the observed value.
Table 3.5. Model predictions for the allometric relationship between parent mass (M, g) and the dimensions and thermal properties of a hemispherical object according to y = aM^b for heat loss, isometric and structural scaling, and tests for significant differences between actual scaling exponents and predictions.

<table>
<thead>
<tr>
<th>Nest parameter</th>
<th>Heat loss scaling</th>
<th>Isometric scaling</th>
<th>Structural scaling</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>eggs 1-5 chicks</td>
<td>eggs 1-5 chicks</td>
<td>eggs 1 chick</td>
</tr>
<tr>
<td>Internal diameter (di, cm)</td>
<td>F = 11.31,</td>
<td>F = 11.31,</td>
<td>M^0.32</td>
</tr>
<tr>
<td></td>
<td>P = 0.0013 *</td>
<td>P = 0.061</td>
<td>P = 0.0013 *</td>
</tr>
<tr>
<td>External diameter (de, cm)</td>
<td>F = 45.4,</td>
<td>F = 24.1,</td>
<td>M^0.32</td>
</tr>
<tr>
<td></td>
<td>P &lt; 0.001 *</td>
<td>P &lt; 0.001 *</td>
<td>P = 0.001 *</td>
</tr>
<tr>
<td>Internal height (hi, cm)</td>
<td>F = 5.08,</td>
<td>F = 5.08,</td>
<td>M^0.32</td>
</tr>
<tr>
<td></td>
<td>P = 0.027 *</td>
<td>P = 0.0056 *</td>
<td>P = 0.027 *</td>
</tr>
<tr>
<td>Thickness (X, cm)</td>
<td>M^0.12</td>
<td>M^0.15</td>
<td>M^0.32</td>
</tr>
<tr>
<td></td>
<td>F = 37.9, F = 31.6</td>
<td>F = 8.25,</td>
<td>F = 0.016,</td>
</tr>
<tr>
<td></td>
<td>P &lt; 0.001 *</td>
<td>P = 0.90</td>
<td>P = 0.098,</td>
</tr>
<tr>
<td>Surface area (Å, cm²)</td>
<td>M^0.80</td>
<td>M^0.83</td>
<td>M^0.67</td>
</tr>
<tr>
<td></td>
<td>F = 7.55, F = 2.87</td>
<td>F = 2.41,</td>
<td>F = 0.028,</td>
</tr>
<tr>
<td></td>
<td>P = 0.0076 *</td>
<td>P = 0.13</td>
<td>P = 0.060,</td>
</tr>
<tr>
<td>Nest mass (Mn, g)</td>
<td>M^0.71</td>
<td>M^0.77</td>
<td>M^1.0</td>
</tr>
<tr>
<td></td>
<td>F = 22.7, F = 18.4</td>
<td>F = 8.93,</td>
<td>F = 0.47,</td>
</tr>
<tr>
<td></td>
<td>P &lt; 0.001 *</td>
<td>P &lt; 0.001 *</td>
<td>P = 0.011 *</td>
</tr>
<tr>
<td>Total nest conductance (G, mW °C⁻¹)</td>
<td>M^0.48</td>
<td>M^0.48</td>
<td>M^0.33</td>
</tr>
<tr>
<td></td>
<td>F = 48.6, F = 48.6</td>
<td>F = 4.34,</td>
<td>F = 0.12,</td>
</tr>
<tr>
<td></td>
<td>P &lt; 0.001 *</td>
<td>P &lt; 0.001 *</td>
<td>P = 0.013 *</td>
</tr>
</tbody>
</table>

Nest thermal properties model output values represent the predicted exponent (slope, b) of the regression mean according to the allometric relationship y = aM^b. Heat loss and isometric scaling for one and five chicks produces identical scaling exponents and statistics, thus columns have been merged for simplicity. Accompanying statistics include the F-ratio and P-value for the ANCOVA comparisons between the model predictions and real nest data.

* Indicates that the predicted scaling exponent for the model output (above) and real nest data (see Chapter 2) are statistically different at the specified alpha value (α = 0.05) following Bonferroni adjustment.

N = 73 and DF = 1,69 for all comparisons, except nest mass, which has N = 64 and DF = 1,60. The replicate for the nest mass measurements is lower as some nests were excluded from analysis due to the attachment of supporting branches.
4. DISCUSSION

(a) The shape of an egg

Egg shape has been discussed in the literature for several decades now; however, the development of technology and understanding has meant that techniques to measure and define egg shape have improved and as such, egg shape continues to be of interest to avian biologists. There are conflicting ideas regarding the functional significance of variation in egg shape. Differences in egg morphology may reflect adaptations to different environmental conditions according to Hoyt (1976). However, Smart (1991) believes that variation in egg shape is unrelated to physiological exchanges with the environment, but rather shape arises from maximising egg strength from a minimum amount of material.

Egg shape is presumed to be the result of natural selection (Hoyt 1976) with a moderate heritable component (Galbraith 1988; Nol et al. 1997). Here, we confirm that egg shape is influenced by the phylogenetic relationships of individuals; however, the evolution of egg shape is occurring at a rate slower than expected for Brownian motion evolution and hence may represent homoplasy or adaptation that occurs in some, but not all, species (Blomberg et al. 2003). It is of interest to note that the deviation from circular ($b_0$) and the squareness of the egg ($d_0$), the two shape parameters that act on modifying the shape of the egg at both poles of the egg symmetrically, are those that contain a phylogenetic signal. Research on eggshells has shown that phenotypic variation in eggs can be confined to specific poles of the egg (Polačiková et al. 2011), but that doesn’t hold true for egg shape. There is considerable variation in egg shape between species and since egg morphology is influenced by phylogenetic relationships, further studies should be conducted to develop order-specific allometric equations (Deeming et al. 2006).

(b) The area and volume of an egg

Egg surface area is proportional to egg volume with an exponent of 0.67, as has been found in previous studies (Hoyt 1976; Paganelli et al. 1974). However, the elevation (intercept) of the relationship was underestimated in the foregoing studies (4.9 compared to 5.1 here). While the elevations are statistically significant, the difference is small and therefore unlikely to be of biological significance. Egg size can be determined quite accurately once species-specific values for the shape parameters ($b_0$, $c_0$, $d_0$, $e_0$) have been obtained via the methods outlined in § 2 and Supplement 3.1. Such calculations can be made with ease using a spreadsheet incorporating the equations used here, provided in the Electronic Supplementary Material (Appendix 7). The macro accuracy could be improved in several ways (see Supplement 3.5); however, it provides values of surface area and volume that are accurate to two or three significant figures.

The scaling exponent for egg volume as a function of female body mass (0.70) is within the range of exponents for egg mass found in other studies (0.67 to 0.77) (Blueweiss et al. 1978; Brody 1945; Cabana et al. 1982; Martin et al. 2006; Peters 1983; Rahn et al. 1975; Saether 1985), if we assume egg volume is proportional to egg weight (i.e. density equal to one – egg density is approximately 1.04 and is relatively independent of egg mass ($M_E^{0.006}$) (Paganelli et al. 1974; Romanoff and Romanoff 1949)). However, several
of these studies did not distinguish between passerines and non-passerines. Therefore, it would be of interest to repeat the study with eggs of non-passerines, as the two avian groups are known to differ allometrically for some variables (Peters 1983; Schmidt-Nielsen 1984). For example, egg mass for passerines scales with adult mass with an exponent of 0.73 (Ricklefs 1974), while for non-passerines the exponent is 0.68 (Cabana et al. 1982). Therefore, it is probable that the scaling exponents for egg surface area and volume are also different for non-passerines but this requires further study, where the clutch as a whole is also taken into consideration.

While scaling rules state that linear dimensions should increase with mass to the power of 0.33, surface area with an exponent of 0.67 and volume with an exponent of 1, egg dimensions increase with exponents that are significantly lower than expected on all accounts. Thus egg size becomes a smaller proportion of female mass for larger birds than we would expect and hence a smaller proportion of the female’s energetic reserves are allocated to a reproductive attempt, as proposed by Blueweiss et al. (1978). This is also true considering clutch size does not change with mass of the female.

Small eggs and clutches have slower rates of heat loss but decrease temperature quicker due to the surface area to volume relationships (McCracken et al. 1997; Reid et al. 2000a; Turner 1985). Eggs of large birds are relatively smaller but absolutely larger than eggs of small birds. When a large bird takes leave from the nest to forage, the temperature of the clutch should be maintained for longer. Nest conductance increases for larger birds, but increases with an exponent that is lower than that of the heat loss from the parent and therefore nests of large birds are better insulated than expected for their size (Chapter 2). For small birds, clutch temperature will decrease quickly when the parent takes an incubation recess, but the low absolute thermal conductance of the nest may help to retain heat within the nest. Furthermore, birds are known to moderate heat loss from eggs through appropriate microhabitat selection and patterns of incubation or nest attendance (D'Alba et al. 2009; White and Kinney 1974). For example, egg size influences incubation attendance patterns for a number of avian species according to a comparative study by Deeming (2002a).

We also show that egg size is influenced by morphological differentiation of the parents. Once accounting for absolute body size of the female, eggs are small for species where the female is the heavier of the two sexes and large when the male is the largest of the pair (discussed in § 4(d)).

(c) Clutch size

Clutch size is independent of phylogenetic relationships and the absolute body mass of the female, but is negatively influenced by the sexual size dimorphism index (discussed in § 4(d)). Clutch size can be influenced by a number of variables, such as local climate conditions (Cooper et al. 2005; Järvinen and Väisänen 1984; Lack 1947), latitude (Briskie 1995; Järvinen and Väisänen 1983; Kulesza 1990; Ojanen et al. 1978), altitude (Carey et al. 1982; Lee et al. 2011), nest concealment (Ost et al. 2008; Saether 1985), the cost of nest cavity excavation (Martin and Li 1992), mortality (Lack 1954) and laying date (Dawson et al. 2011; Järvinen and Väisänen 1983; 1984; Wiebe and Swift 2001) (factors reviewed by Kulesza 1990; and Lack 1947). Factors that may influence clutch size and relate to sexual size dimorphism include female condition (Järvinen and
The structural and thermal properties of avian cup-shaped nests (Väisänen 1983; Nol et al. 1997) and parental care (Durant et al. 2010; Szentirmai et al. 2005), though further studies would need to be conducted to identify direct causes of SDI-driven clutch size changes.

It is unlikely that clutch size is limited by the size of the brood patch of the incubating parent, as suggested by Lack (1954). If the area of the brood patch is proportional to female area and clutch profile area is relatively smaller in larger females, the clutch profile area will therefore be a smaller proportion of the brood patch as birds increase in size. As clutch size is independent of female body mass, and clutch volume ($M^{0.77}$) increases with body mass at a slower rate than nest cup volume ($M^{0.94}$, Supplement 2.3), it is unlikely that clutch size is limited by space restrictions within the nest, as suggested by Slagsvold (1982). But rather, extra space is provided within the nest and increases disproportionately as birds increase in size. Furthermore, in most cases actual clutch sizes are below the potential limit of egg production (Lack 1947). The variability in clutch size within and between species and independence of clutch size to absolute parent mass suggests that the number of eggs laid by a female is somewhat flexible and that the number of eggs laid can possibly be adjusted according to the energy reserves available for a breeding attempt or food availability, as has been found in other studies (Durant et al. 2010; Järvinen and Väisänen 1983; Nol et al. 1997).

(d) **The absolute and relative size of the female**

The absolute mass of the incubating female influences egg morphology at a number of levels; however, sexual size dimorphism (the relative size of the female compared to the male) influences the size and number, but not the shape, of eggs. The female is the larger of the sexes in only 10 out of 36 of the species included in this study and the range in the dimorphism index across these species is narrow compared with the range exhibited by those where the male is the larger of the two sexes. This is not surprising, as male-biased size dimorphism is more common than female-biased size dimorphism in birds (Blanckenhorn 2005; Fairbairn 1997; Szekely et al. 2007). The singing honeyeater (*Lichenostomus virescens*) is at the upper extreme of the dimorphism index, where the male is 37% heavier than the female. The red wattlebird (*Anthochaera carunculata*) male is only 12% heavier than the female. With a paucity of species filling in the gap between these two species, the slightly higher clutch size for *L. virescens* may be having an inflated effect on pushing the slope of the relationship between dimorphism and clutch size towards zero and hence the relationship may prove to be more extreme than reported here.

Sexual size dimorphism can have important implications for the life-history of a species, through modifications to reproductive output (such as fertilisation ability (Fairbairn 1997) and copulation time (Blanckenhorn 2005)), time-energy budgets of adults (Blanckenhorn 2005), growth rates of young (Teather and Weatherhead 1994), fledging success (through sex-biased mortality) (Kalmbach and Benito 2007) and the reproductive investment of the female (Badyaev 2002; Blanco et al. 2003). In turn, sexual size dimorphism is influenced by these factors and hence it can be difficult to disentangle cause and effect (Blanckenhorn 2005). In the present study, species of birds with relatively large females, compared to the male, increase reproductive effort by increasing the number of eggs in a clutch, but reduce egg size (lower $PA_E$, $SA_E$ and $V_E$).
These results contradict findings of Cabana et al. (1982), who found the opposite is true, though do confirm their predictions that laying more eggs in a clutch is the primary method of increasing reproductive output. Parents of different sizes are able to exploit different food resources, reducing intra-pair and inter-sexual food competition (Blanckenhorn 2005). Thus, there is the potential that sexual size dimorphism effects on clutch size and egg size may reflect differences in the ability of parents to provide food to young – more hatchlings will require more food for growth and development, as will larger hatchlings. The behaviour of the incubating parents should be considered when looking at the effect of SDI on egg size and the number of eggs in a clutch, as the mass of the male may only be of importance for biparental incubators. However, additional analyses (see Supplement 3.6) show that the mode of incubation (single-sex incubation by the female or biparental incubation) does not influence the size of eggs or the clutch as a whole for the species included in the present study.

The opposing effect of sexual size dimorphism on egg size (e.g. volume, \( b = 0.47 \)) and clutch size (\( b = -0.45 \)) balance such that size parameters for the whole clutch (\( P_{AC}, S_{AC}, V_{C} \)) are independent of sexual size dimorphism. Therefore it appears that there may be a trade-off between the number and size of eggs in a clutch that is driven by morphological differentiation between a breeding pair, rather than their absolute size. Since bigger clutch sizes result in increased incubation costs (Biebach 1984; Haftorn and Reinertsen 1985; Thomson et al. 1998) and egg size is related to the size of the hatchling (Deeming and Birchard 2007), which influences the cost of brooding (Hails and Bryant 1979) and nest attendance (Deeming 2002a), the question remains: Is the potential increase in the cost of reproduction arising through greater clutch sizes for females with female-biased dimorphism, negated by the smaller size of individual eggs? Further studies should investigate the importance of egg and clutch size trade-offs in relation to sexual size dimorphism, incorporating understanding of allometric relationships.

(e) Egg morphology and nest morphology

Like eggs, birds’ nests are thought to be adapted to local conditions (Briskie 1995; Britt and Deeming 2011; Hoyt 1976; Kern 1984; Mainwaring and Hartley 2008; Mainwaring et al. 2012; Rohwer and Law 2010; Schaefer 1976; 1980). Our research shows that egg and nest morphology are largely linked. While nest thickness and mass for the species in this study are largely determined by requirement for structural support of the incubating parent (Chapter 2) and material use is influenced by local climate conditions (Chapter 4), the internal cup dimensions are influenced by the space requirements of the clutch. Whether a nest is constructed to suit a clutch of eggs in the making, or the clutch is modified to suit the pre-constructed nest is unclear. The female may be able to gauge the space requirements needed for her clutch of eggs and construct a nest accordingly, since clutch size is determined more than five days before laying begins for some cavity-nesting species (Durant et al. 2010), though the timing of reproductive events (such as nest construction and clutch size determination) across the species in the present study is unknown. The weak egg and clutch to nest relationships expressed in these data may, at least in part, be due to variability in clutch size.
The male assists with nest construction for 27 of the 36 of the species included in the present study and 13 of those involved in construction also go on to assist with incubation (Marchant and Higgins 2001; 2002; 2006). The males of an additional four species are not involved with nest construction but contribute to incubation of the clutch. The mode of incubation (and therefore the role of the male) does not influence nest morphology or egg morphology (see Supplements 2.5 and 3.6). It is unlikely that the male is capable of gauging the ability of the female to produce a certain egg or clutch size, unless he can do so due to shared genetics at the species-level or through instinct, so may be incapable of modifying nest size in response to the forthcoming clutch. Since nest design is in part influenced by the male and egg morphology is controlled by muscles in the pelvis of the female (Smart 1991), it is likely that one does not control the other. However, nest (Chapter 2) and egg morphology are influenced by body size and contain a significant phylogenetic signal (see Supplement 2.6 and 3.2). Therefore, we propose that the nest and clutch are in fact independent, yet matched secondarily due to the shared influence of allometric and phylogenetic relationships on nest and egg size.

(f) Links to previous studies
The new model results suggest that the internal nest opening diameter is constructed to account for the space that the chicks will occupy. The surface area of the nest is consistently isometric for parents, eggs and chicks, but conforms to heat loss and structural scaling under various scenarios of nest contents. Most importantly, the re-evaluation of the scaling exponents against modelled predictions once accounting for the clutch shows that nest mass, thickness and conductance are influenced primarily by the need for structural support of the parent, the eggs and chicks, which supports the findings of our previous study (Chapter 2).

There is considerable variation in egg shape within and between species and so using standard linear equations to determine egg size, such as Hoyt’s (1979), will overestimate egg volume. However this overestimation is only 0.04 cm³ – which is statistically significant but perhaps not biologically significant for the birds involved. Therefore, considering the simplicity of Hoyt’s (1979) equation, it remains a reasonable method to predict approximate egg volume. Hoyt (1979) assessed egg size for birds ranging in mass from around 77 g to 1.3 Kg, a range that extends beyond the mass range of birds in this study. The use of an interpolation spreadsheet (Electronic Supplementary Material, Appendix 7) with basic egg dimensions can be used as an alternative to Hoyt’s (1979) equation to obtain an accurate calculation of egg volume, but also provides estimations of profile area and surface area. Alternatively, the macro employed here (Appendix 6) can be used to gather accurate information regarding egg size (profile area, surface area and volume) as well as egg shape.

(g) Summary
Egg size and shape show considerable intraspecific variation, which is largely attributable to the size of the female and sexual size dimorphism. Interspecific variation in egg morphology is also considerable and hence complex polynomials should be used that take into account shape specifiers. The number of eggs in a clutch is more flexible and may be related to the energetic reserves of the female, as well as the relative size of the
male, where there is a trade-off between clutch size and egg size in relation to sexual size dimorphism. Nest morphology and clutch volume/area are likely to be matched secondarily due to the shared influence of allometric and phylogenetic relationships on nest and egg size. The mass of the eggs and chicks contributes to the need for structural support within the nest, though this acts at an interspecific level as nest mass is not adjusted according to an individual clutch.
ACKNOWLEDGEMENTS

We thank the South Australian Museum (in particular, Dr Philippa Horton) for use of their egg collection, Dr Craig White for his assistance with phylogenetic analyses and Georgina Allan for her help with egg measurements.
SUPPLEMENT 3.1: CALCULATION OF THE EGG SHAPE PARAMETERS

In order to use the formulas given in Chapter 3 § 2(d)iv to calculate volumes and areas of eggs, the parameters $a$, $b$, $c$, $d$, $e$ must be determined. Equivalently, the parameters $a$, $b_0 = b/a$, $c_0 = ac$, $d_0 = a^2d$ and $e_0 = a^3e$ must be determined. One of these is immediately available, namely the parameter $a$: this is always half the length ($L$, Equation S3.1.1).

$$a = \frac{L}{2} \quad (S3.1.1)$$

If the researcher uses a photograph of an egg, after inputting the measured length of the egg, the egg shape macro will calculate all the other parameters from this image as well as the volume, surface area and profile area.

If the researcher does not have access to a photograph or a computer with the macro installed, he or she must use other methods to compute the parameters. A pair of calipers will enable the researcher to accurately determine the length ($L$) of a given egg, as well as its width ($W$). A first approximation to the parameter $b_0$ is then given by Equation S3.1.2, which assumes an ellipsoidal shape.

$$b_0 = \frac{W}{L} \quad (S3.1.2)$$

If the egg is not close to ellipsoidal but is assumed to be reasonably described by Equation 3.10 with $d_0 = 0 = e_0$, the shape is that of the curve, given by $z(t)$ in Equation S3.1.3 where, as before, $t = x/a$ and $z = y/a$. Using the same calculations as in Chapter 3 § 2(d)ii, it is found that the maximum value of $z$ for $|t| \leq 1$ is given by $z_m$ (Equation S3.1.4) occurring at $t_m$ (Equation S3.1.5).

$$z = b_0 \sqrt{1 - t^2 \left(1 + c_0 t \right)} \quad (S3.1.3)$$

$$z_m = \frac{b_0}{4} \sqrt{\frac{3 + \sqrt{1 + 8c_0^2}}{2 + 2 \sqrt{1 + 8c_0^2}}} \quad (S3.1.4)$$

$$t_m = \frac{c_0}{1 + \sqrt{1 + 8c_0^2}} \quad (S3.1.5)$$

Thus the width ($W$) of the egg is then $W = 2az_m$, and the widest part of the egg, as measured along the axis of symmetry, is at the position $x_m = at_m$ (as in Figure S3.1.1).
The structural and thermal properties of avian cup-shaped nests

94

Figure S3.1.1. Diagram of the egg outline function, where: \(-a\) and \(a\) represent the tip of the egg at the blunt end and pointy end, respectively, and \(2a\) is equal to the length of the egg; \(az_m\) is half of the width of the egg at the widest point and equal to \(W/2\); \(b\) is half of the width of the egg taken from the point of origin (or mid-point of the long axis of the egg); \(x_m\) is the distance of the centre of mass from the point of origin, representing the deviation from an ellipse.

Inverting the formula in Equation S3.1.4 and taking scale into account gives Equation S3.1.6, which is only useful once a value for \(c_0\) has been established.

\[
b_0 = 2W \frac{2 + 2 \left( 1 + \frac{8c_0^2}{3} \right)}{\sqrt{3 + \sqrt{1 + 8c_0^2}}} \]

\[
= \frac{W}{L} \left( 1 + \frac{c_0^2}{2} + \frac{7c_0^4}{8} + O(c_0^6) \right)
\]

If the location \(x_m\) of the maximum width of the egg can be determined accurately, then \(t_m = x_m/a = 2x_m/L\) and inversion of Equation S3.1.5 gives \(c_0\) (Equation S3.1.7).

\[
c_0 = \frac{2t_m}{1 - 2t_m^2}
\]

If \(x_m\) cannot be measured (or accurately estimated) for a given egg, an average value of \(c_0\) for the given species can be used. Once a value for \(c_0\) has been fixed, the parameter \(c\) is then given by \(c = c_0/a = 2c_0/L\).

Given only basic measuring tools such as calipers, values for the other two parameters \(d_0\) and \(e_0\) will be difficult to determine. Using Equation 3.21, it follows that if the egg profile area (\(PA_E\)) can be determined accurately, then \(d_0\) can be calculated according to Equation S3.1.8, but finding this area is likely to involve a photograph. Using Equation 3.20 for the volume (\(V\)), dropping all quadratic terms in \(c_0\), \(d_0\), \(e_0\) gives the approximation of \(d_0\) according to Equation S3.1.9. If it is possible to immerse the egg in a volumetric flask, determining the volume can be achieved with some accuracy.
\[ d_{o} = \left( \frac{4PA_{E}}{\pi ab} \right) - 1 \]  

(S3.1.8)

\[ d_{o} = \frac{5}{2} \left( \frac{3V}{4\pi ab^2} - 1 \right) \]  

(S3.1.9)

\[ = \frac{5}{2} \left( \frac{3V}{4\pi a^2 b_{o}^2} - 1 \right) \]

If the values of the parameters \( a, b_{o}, c_{o}, d_{o}, e_{o} \) can be accurately determined for a given egg, the formulas in the accompanying spreadsheet (Electronic Supplementary Material, Appendix 7) will give accurate estimates for the areas and the volume for that egg.

A very simple device used in conjunction with calipers should yield quite accurate measurements. The device itself consists simply of a plate of metal or wood with several circular holes of varying widths bored through it. The radii of these holes should be measured accurately. The given egg should be placed on a hole in vertical position, \( i.e. \), so that its axis is perpendicular to the plate, and the calipers used to measure the distance from the egg of the egg to a point at which the egg touches the plate. That is, the calipers are used to measure the lengths of either (or both) of the dotted lines in Figure S3.1.2. Given that the radius \( r \) of the hole is known, the length along the axis from the end of the egg to the plate can be calculated from Pythagoras’ theorem (Equation S3.1.10).

\[ \text{dashed} = \sqrt{\text{dotted}^2 - r^2} \]  

(S3.1.10)

The same hole can be used twice by turning the egg over. Once four such lengths have been determined, these can be inserted into the spreadsheet (Electronic Supplementary Material, Appendix 7), and this will then return accurate estimates of the volume and areas.

An alternative to using a plate like this is simply to use calipers or a compass to draw circles on the egg in the plane perpendicular to the axis of rotation, and to use them again to measure the straight line distance from the end of the egg to the circle. Apart from requiring less equipment, this would have the advantage that the circle sizes can be tailored to the egg, ensuring that there are two reasonable close to the ends and two reasonably central ones. However, it may be difficult to ensure that the planes of the circles are truly perpendicular to the axis of rotation.
Figure S3.1.2. Diagram of a potential set-up to measure egg tip to plate distances.
SUPPLEMENT 3.2: AVIAN EGG SIZE CONTAINS A PHYLOGENETIC SIGNAL

Our understanding of animal physiology is often improved through comparative studies; however, such studies can be statistically flawed through non-independence of data when phylogenetic relatedness is not taken into account (Blomberg et al. 2003; Garland and Adolph 1994). Consequently, we seek here to test if avian egg size is influenced by phylogeny. The present study differs from our previous study (see Chapter 3), in that here we do not regress egg size variables against mass, but rather test for a phylogenetic signal in the egg data itself.

A total of 360 eggs (from 36 species) were included in the study. Egg size was measured according to Chapter 3. Data were analysed in R (Gentleman and Ihaka (2011), version 2.14.1) according to the methods of Chapter 3. We tested the egg size parameters against the phylogeny to determine if egg size contains a phylogenetic signal. This involved calculating Blomberg et al.’s K-statistic (the strength of the signal) and determining the significance of the phylogenetic relationship.

Egg size is influenced by phylogeny (Table S3.2.1). In all cases Blomberg et al.’s (2003) K-statistic is less than would be expected based on Brownian motion evolution (i.e. K < 1) (Blomberg et al. 2003). Consequently, egg size may represent homoplasy or adaptation that occurs in some, but not all, species.

Table S3.2.1. Statistics for the relationship between egg morphology and phylogeny

<table>
<thead>
<tr>
<th>egg parameter</th>
<th>Blomberg’s K</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>individual eggs</td>
<td></td>
<td></td>
</tr>
<tr>
<td>egg length (L, cm)</td>
<td>0.52</td>
<td>0.013 *</td>
</tr>
<tr>
<td>egg width (W, cm)</td>
<td>0.55</td>
<td>0.007 *</td>
</tr>
<tr>
<td>profile area (PA_e, cm²)</td>
<td>0.52</td>
<td>0.025 *</td>
</tr>
<tr>
<td>surface area (SA_e, cm²)</td>
<td>0.52</td>
<td>0.020 *</td>
</tr>
<tr>
<td>volume (V_e, cm³)</td>
<td>0.49</td>
<td>0.032 *</td>
</tr>
<tr>
<td>whole clutch</td>
<td></td>
<td></td>
</tr>
<tr>
<td>profile area (PA_C, cm²)</td>
<td>0.62</td>
<td>0.005 *</td>
</tr>
<tr>
<td>surface area (SA_C, cm²)</td>
<td>0.63</td>
<td>0.003 *</td>
</tr>
<tr>
<td>volume (V_C, cm³)</td>
<td>0.56</td>
<td>0.016 *</td>
</tr>
<tr>
<td>clutch size (E)</td>
<td>0.64</td>
<td>0.003 *</td>
</tr>
</tbody>
</table>

* Indicates that the nest parameter of interest contains a significant phylogenetic signal.
SUPPLEMENT 3.3: THE EFFECT OF CLUTCH SIZE ON THE MORPHOLOGY OF AUSTRALIAN PASSERINE EGGS

Aristotle (384 – 322 B.C.) believed that the shape of the chicken egg was defined by the sex that hatched from it – males from pointed eggs and females from round eggs (cited in Romanoff and Romanoff 1949). Egg morphology continues to be of interest to avian biologists but our understanding of factors influencing egg morphology has increased significantly in recent decades. Egg shape is thought to be controlled by the muscles in the female pelvis (Smart 1991), contains a significant heritable component (Supplement 3.2) and may be influenced by stability of the egg in the nest site, appropriate gas exchange via the air cell, or positioning of the ‘thermal centre’ (Smart 1991).

Chapter 3 looked at how the nest can influence egg size, or vice versa. We concluded that nest size and egg size are matched but likely arise through independent means and therefore do not influence each other directly. Clutch size in the species studied is variable and hence we next seek to understand if the size and shape of eggs is influenced by the number of eggs in a clutch (henceforth referred to as clutch size). Based on algorithms egg shape should be influenced by clutch size, where eggs would optimally be spherical in clutches of one egg, biconical in clutches of two to three eggs and pointed in clutches of four eggs (Barta and Székely 1997). Egg shape is indeed influenced by clutch size for a number of species where eggs in small clutches are longer and greater in volume than in big clutches (Ojanen et al. 1978). However, such studies have only been conducted on a few species and results vary. In addition, egg size is largely driven by female body mass and sexual size dimorphism (Chapter 3) and so actual trends may be hidden by variation in body size. Here, we report the effect of clutch size on the morphology of avian eggs across 36 species of passerines ranging in body size from 8 to 380 g, accounting for both female body mass and morphological differentiation of the sexes in the analysis.

A total of 360 eggs from 36 passerine species (10 eggs per species) were included in this study and methods followed those outlined in Chapter 3. Egg size, egg shape and clutch size were determined and assessed against parent mass and the sexual size dimorphism index (SDI).

Data were analysed in R (Gentleman and Ihaka (2011), version 2.14.1) using multiple linear regression techniques, whilst also accounting for phylogenetic relatedness. Egg shape parameters ($b_0$, $c_0$, $d_0$, $e_0$, $t_0$) cannot be universally logarithmically-transformed. Therefore, shape parameters were assessed against clutch size (E) with linear regression techniques, according to the relationship $y = a + bE$. The remaining egg shape and size parameters were logarithmically-transformed and assessed with multiple linear regression techniques against log female body mass ($M_F$), log sexual size dimorphism index (SDI) and log clutch size (E). Circular distortion ($D_C$) is not influenced by SDI (Chapter 3 REF) and as such SDI was not included in the model for $D_C$. The relationship in this case is $y = aM_F^{b_1}E^{b_2}$. Elliptical distortion ($D_E$) is not influenced by SDI or MF and so only clutch size was assessed here according to $y = aE^{b_3}$. Egg size parameters of length (L), width (W), profile area ($PA_E$), surface area ($SA_E$) and volume ($V_E$) were assessed with the full model according to the relationship $y =$
Phylogenetic correlation was determined from the lambda (λ) value that maximised the likelihood of the model (Pagel 1999). The strength of the phylogenetic models was assessed by repeating analyses with λ equal to zero and comparing the second-order Akaike Information Criterion (AICc) values produced from the phylogenetic and non-phylogenetic models (Burnham and Anderson 2002). The need to account for phylogeny in the analysis of these data was supported if the AICc was lowest for the phylogenetic model, and if the AICc difference (ΔAICc) between the phylogenetic and non-phylogenetic models was greater than four; the non-phylogenetic model was retained if the ΔAICc was less than four.

Further statistical analyses on allometric relationships were performed in JMP IN (SAS Institute 2001, version 4.0.4) using multiple linear regression techniques on log-transformed data. Residuals of the data met the assumptions required for parametric linear regression tests of normality (Shapiro-Wilk W Test) and equal variance (constant spread of the residuals). The significance value was set at 0.05 for all analyses. Data are expressed as mean ± 95% confidence interval.

The effect of clutch size on egg shape is not influenced by phylogenetic relationships (Table S3.3.1) but egg size is influenced by phylogenetic relationships (Table S3.3.1). Once accounting for phylogeny, egg morphology is not influenced by clutch size, except for $d_0$, which decreases significantly with increasing clutch size (Table S3.3.1).

Once accounting for the effect of female mass and sexual size dimorphism, only $d_0$ is negatively influenced by clutch size. The egg shape parameter $d_0$ represents the squareness of the egg (see Chapter 3 § 2(d)iii for a full description and Figure 3.7 for diagrammatic representation). Positive values of $d_0$ produce ‘square’ eggs, values of $d_0$ close to zero produce round eggs and negative values of $d_0$ produce ‘square’ eggs as well (i.e. the effect of $d_0$ is the same regardless of whether it is positive or negative but the area of flattening changes in each case). While values of $d_0$ for eggs of the species studied range from -0.18 to 0.12, species means (which are analysed here) only range from -0.11 to -0.02. Therefore small clutches have eggs that are rounded, while eggs of large clutches are more square-shaped. The length to width ratio is the same since $d_0$ (deviation from spherical), or $D_C$ (deviation from circular), is not influenced by clutch size. But rather the surface of the egg between the poles and egg waist become increasingly flattened in larger clutches. Rather, the egg shape approaches a diamond, as opposed to a square. This may be important in large clutches as the eggs may fit close together with less space between the eggs, as suggested by Barta and Székely (1997). But unlike the modelling of Barta and Székely (1997), we did not find a relationship between clutch size and the pointedness of the egg poles ($c_0$) or deviation from ellipsoid ($b_0$ and $D_E$).

Laying rounded eggs with small surface area to volume ratios in large clutches may save the female calcium and require less space than elliptical eggs, are better covered by the incubating female, in turn increasing the efficiency of incubation (Ojanen et al. 1978). However, the surface area and volume of eggs are not influenced by the number of eggs in a clutch, once accounting for female mass, sexual size dimorphism and phylogenetic relationships.
Table S3.3.1. Relationship between clutch size (E) and the morphology of avian eggs

<table>
<thead>
<tr>
<th>egg parameter</th>
<th>slope, b</th>
<th>statistics *</th>
<th>lambda (λ)</th>
<th>second-order Akaike Information Criterion (AICc)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>phylogenetic model</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$b_0$</td>
<td>0.001 ± 0.01</td>
<td>LCL = -0.02</td>
<td>1.0</td>
<td>-156.8 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>UCL = 0.02</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$c_0$</td>
<td>0.01 ± 0.02</td>
<td>$R^2 = 0.04$</td>
<td>0.0</td>
<td>-159.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$F_1 = 1.60$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P = 0.22$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$d_0$</td>
<td>-0.02 ± 0.01</td>
<td>$R^2 = 0.15$</td>
<td>0.57</td>
<td>-171.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$F_1 = 6.17$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P = 0.018$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$e_0$</td>
<td>0.002 ± 0.01</td>
<td>$R^2 = 0.00$</td>
<td>0.07</td>
<td>-180.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$F_1 = 0.06$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P = 0.81$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$t_m$</td>
<td>0.01 ± 0.02</td>
<td>$R^2 = 0.04$</td>
<td>0.0</td>
<td>-166.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$F_1 = 1.60$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P = 0.21$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>circular distortion ($D_C$)</td>
<td>-0.05 ± 0.06</td>
<td>$R^2 = 0.49$</td>
<td>0.96</td>
<td>-215.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$F_1 = 3.16$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P = 0.085$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>elliptical distortion ($D_E$)</td>
<td>-0.05 ± 0.10</td>
<td>$R^2 = 0.11$</td>
<td>1.0</td>
<td>-174.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$F_1 = 0.93$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P = 0.34$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>egg length (L, cm)</td>
<td>-0.06 ± 0.05</td>
<td>LCL = -0.16</td>
<td>0.93</td>
<td>-168.2 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>UCL = 0.04</td>
<td></td>
<td></td>
</tr>
<tr>
<td>egg width (W, cm)</td>
<td>-0.02 ± 0.04</td>
<td>LCL = -0.10</td>
<td>1.0</td>
<td>-183.6 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>UCL = 0.06</td>
<td></td>
<td></td>
</tr>
<tr>
<td>egg profile area (PA_E, cm²)</td>
<td>-0.08 ± 0.08</td>
<td>LCL = -0.25</td>
<td>1.0</td>
<td>-127.4 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>UCL = 0.09</td>
<td></td>
<td></td>
</tr>
<tr>
<td>egg surface area (SA_E, cm²)</td>
<td>-0.07 ± 0.09</td>
<td>LCL = -0.24</td>
<td>1.0</td>
<td>-125.5 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>UCL = 0.11</td>
<td></td>
<td></td>
</tr>
<tr>
<td>egg volume (VE, cm³)</td>
<td>-0.10 ± 0.12</td>
<td>LCL = -0.35</td>
<td>1.0</td>
<td>-100.7 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>UCL = 0.15</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Statistics represent the influence of clutch size on egg morphology only. Statistics for the effect of female mass (M_F) and sexual size dimorphism (SDI) on egg morphology are reported in Chapter 3.

Statistics include the slope (b): according to the relationship $y = a + bE$ for egg shape parameters $b_0$, $c_0$, $d_0$, $e_0$ and $t_m$ as these parameters cannot be logarithmically-transformed; according to $y = aM_F^b E^c$ for circular distortion as SDI does not influence $D_C$; according to $y = aE^c$ for elliptical distortion as neither $M_F$ or SDI influence $D_E$; and according to the relationship $y = aM_F^b SDI^c E^d$ for the remaining egg dimensions.

Slopes and accompanying statistics are those from the best fit model, represented as the slope ± 95 % C.I. in the case of non-phylogenetic models and slope ± S.E. in the case of phylogenetic models.

* Statistics for non-phylogenetic models include the $R^2$ for the model regression, the F-ratio (degrees of freedom) and the $P$-value; while the lower critical limit and upper critical limit are reported for phylogenetic models.

* Indicates that the regression for the variable of interest is statistically significant (slope ≠ 0). For non-phylogenetic models the alpha value (α) used is 0.05. N = 36.

Lambda (λ) indicates the strength of the phylogenetic relationship, where values lie between 0 and 1.

* Represents the model with the best fit for the data, where the model with the lowest AICc is retained for an AICc difference in excess of four, and the non-phylogenetic model retained for an AICc difference of less than four.
SUPPLEMENT 3.4: CLUTCH SIZE INCREASES WITH CONDUCTANCE OF AVIAN CUP-SHAPED NESTS

It has been suggested that clutch size may be influenced by the thermal properties of a nest, as warmer nests might provide energy savings to the parent (Reid et al. 2000b). Following on from a detailed analysis on the effect of a clutch on nest morphology (Chapter 3), we test if the number of eggs in a clutch influences the thermal properties of a nest.

Nest conductance was determined from the methods of Chapter 2. Average clutch size values from Chapter 3 were assessed against sexual size dimorphism index (SDI) and conductance simultaneously. Data were analysed in R (Gentleman and Ihaka (2011), version 2.14.1) using multiple linear regression techniques on logarithmically-transformed data, whilst also accounting for phylogenetic relatedness, according to the methods of Chapter 3. Phylogenetic correlation was determined from the lambda (λ) value that maximised the likelihood of the model (Pagel 1999). The strength of the phylogenetic models was assessed by repeating analyses with λ equal to zero and comparing the second-order Akaike Information Criterion (AICc) values produced from the phylogenetic and non-phylogenetic models (Burnham and Anderson 2002). The need to account for phylogeny in the analysis of these data was supported if the AICc was lowest for the phylogenetic model, and if the ΔAICc difference (ΔAICc) between the phylogenetic and non-phylogenetic models was greater than four; the non-phylogenetic model was retained if the ΔAICc was less than four. PGLS estimates were accepted as significant when the lower and upper 95% confidence limits (Phy-CL) of a given parameter estimate (slope) excluded zero. Further statistical analyses were performed in JMP IN (SAS Institute (2001), version 4.0.4) using multiple linear regression techniques. Residuals of the data met the assumptions required for parametric linear regression tests of normality (Shapiro-Wilk W Test) and equal variance (constant spread of the residuals). The significance value was set at 0.05 for all analyses.

The relationship between nest conductance, sexual size dimorphism and clutch size is not influenced by phylogeny (ΔAICc < 4; AICc-Phy = -83.1, AICc-Non-Phy = -85.9; lambda (λ) = 0). The mean number of eggs in a clutch increases with increasing nest conductance (Estimate = 0.22 ± 0.17, $F_1 = 7.45$, $P = 0.010$), once accounting for the effect of sexual size dimorphism (Estimate = -0.45 ± 0.40, $F_1 = 5.03$, $P = 0.032$). The full model is significant ($R^2 = 0.28$, $F_{2,33} = 6.32$, $P = 0.0048$) and represented as $E = 0.87$ SDI$^{-0.45} G^{0.22}$.

The thermal properties of a nest and the number of eggs in a clutch are significantly related and likely arise through the greater nest surface area provided for large clutches (Chapter 3), which in turn increases the thermal conductance of the nest.
SUPPLEMENT 3.5: ACCURACY AND MODIFICATIONS TO THE OOMORPHOLOGY MACRO

There are a number of factors that affect the accuracy of the macro, for some of which it is possible to compensate and improve the performance.

1. One of the most important factors is the resolution of the image. As the resolution increases, so does the accuracy in the calculation of all quantities calculated by the macro, but the trade-off is in the time that it takes the macro to run. Reducing the resolution of the images causes the macro to run much faster (the speed is roughly inversely proportional to the square of the resolution), but this also makes it less accurate. An experiment on an 8000 × 8000 pixel image of a circle to calculate the volume and area of a sphere of radius 1 took several minutes to run, but calculated π accurately to two or three decimal places.

2. The macro calculates the areas and volume in two different ways. The first is effectively to count pixels and use these counts in simple numerical integration formulae to compute the unknown quantities. The second is to determine the width of the egg at four different points along the axis of symmetry of the egg, and use these to determine the four unknown constants in Equation S3.5.1 by solving the appropriate system of linear equations. These are then used in the formulae of Chapter 3 § 2(d)iv.

\[
y = b \sqrt{1 - \left( \frac{x}{a} \right)^2 \left( 1 + cx + dx^2 + ex^3 \right)}
\]  

(S3.5.1)

The numerical integration technique is quite basic, being only the trapezoidal method. It could be improved by using Simpson’s Rule, but experiments suggest that this is only worthwhile for higher-resolution images.

As the resolution increases, the determination of the shape parameters will become more accurate, and the second method for computing the unknown quantities is likely to become more accurate. For lower-resolution images, the fact that the widths are calculated at only four points can create inaccuracies that can’t be predicted, whereas the “pixel-count” approach is more likely to average out the inaccuracies involved in making measurements from the image.

3. The macro could be modified to divide the egg into three separate parts, being the two ends and the middle. The integrals for the middle can be calculated as described above, but the volume and surface areas of the ends will be determined far more accurately using the equations in 3.5 and 3.6, rather than 3.2 and 3.4.

4. A higher degree of accuracy will be obtained if the equation describing the egg is assumed to be of the form in Equation S3.5.2 where \( p(x) \) is a polynomial of degree five or higher, rather than a quartic polynomial as has been assumed here.
If $p(x)$ is taken to be quintic for example, there will be one more parameter to determine, and this can be done by making one more measurement of the width of the egg at some point along its axis, either by a physical method as described in Supplement 3.1 or using a modified version of the macro (Appendix 6 and 7) on a photograph. The calculations themselves will be more complicated but certainly achievable. However, for the basic purposes that motivated the work here, there is not much to be gained by going to such a degree of detail given the variability of egg shapes even within a species.
SUPPLEMENT 3.6: PARENTAL CARE AND THE MORPHOLOGY OF AUSTRALIAN PASSERINE EGGS

Lack (1954) proposed that the number of eggs in a clutch reflects the largest number of young for which the parents can provide food. This suggests that biparental incubators would be able to raise more young than single-sex incubators, as the quantity of food that can be obtained when foraging is increased in biparental incubators. A comparative study by Martin et al. (2006), found that birds with biparental incubation produced larger eggs than species with uniparental (female-only) incubation but not larger clutches. Incubation attentiveness did not follow the same pattern and so the authors suggested that biparental incubation increased parental investment (larger eggs) but not reproductive effort (clutch mass and incubation effort). On the other hand, a study by Deeming (2002a) on a host of avian species found that incubation attentiveness is influenced by egg size.

Martin et al. (2006) included body mass of the incubating parent in their model, which we have shown to influence egg size and clutch volume/surface area (Chapter 3). However, our previous study also found that egg size and clutch size are influenced by sexual size dimorphism. Here, we wish to test Martin et al.’s (2006) theory, accounting for body size and sexual size dimorphism. In addition, the behaviour of the incubating parents should be considered when looking at the effect of SDI on egg size and the number of eggs in a clutch, as the mass of the male may only be of importance for biparental incubators.

A total of 360 eggs from 36 Passerine species (10 eggs per species) and female masses ranging from 8 to 380 g were included in this study. The species selected for this study were those that were included in Chapter 3. Incubation tactic or parental care and parent mass values for each species was obtained from the Handbook of Australian, New Zealand and Antarctic Birds resource series (Marchant and Higgins 2001; 2002; 2006). There was no parental care information available for three species included in the earlier study (Lichenostomus cratitius, L. ornatus and L. plumulus). For these species, the female was assumed to be the sole incubator, as the remaining three Lichenostomus species in the study were also had female-only incubation as a tactic. Results of analyses that exclude these three species are not significantly different to those reported in the present study and hence the species were retained in the analysis. Egg size, egg shape, clutch size and the sexual size dimorphism index (SDI) was calculated as described in Chapter 3.

Data were analysed in R (Gentleman and Ihaka (2011), version 2.14.1) using multiple linear regression techniques, whilst also accounting for phylogenetic relatedness, according to the methods of Chapter 3. Egg size parameters of length (L), width (W), profile area (PA\textsubscript{E}), surface area (SA\textsubscript{E}) and volume (VE) were assessed against female body mass (MF), sexual size dimorphism (SDI) and parental care (C) with the full model according to the relationship $y = aM_F^b SDI^b C^b$. Clutch profile area (PA\textsubscript{C}), surface area (SA\textsubscript{C}) and volume (VC) were assessed with a shorter model according to the relationship $y = aM_F^b C^b$, since sexual size dimorphism does not influence these parameters (Chapter 3). Clutch size (E) was assessed according to the relationship $y = aSDI^b C^b$, since female mass does not influence clutch size (Chapter 3).
Phylogenetic correlation was determined from the lambda (λ) value that maximised the likelihood of the model (Pagel 1999). The strength of the phylogenetic models was assessed by repeating analyses with λ equal to zero and comparing the second-order Akaike Information Criterion (AICc) values produced from the phylogenetic and non-phylogenetic models (Burnham and Anderson 2002). The need to account for phylogeny in the analysis of these data was supported if the AICc was lowest for the phylogenetic model, and if the AICc difference (ΔAICc) between the phylogenetic and non-phylogenetic models was greater than four; the non-phylogenetic model was retained if the ΔAICc was less than four. PGLS estimates were accepted as significant when the lower and upper 95% confidence limits (Phy-CL) of a given parameter estimate (slope) excluded zero.

Further statistical analyses on allometric relationships were performed in JMP IN (SAS Institute (2001), version 4.0.4) using multiple linear regression techniques on log-transformed data. Residuals of the data met the assumptions required for parametric linear regression tests of normality (Shapiro-Wilk W Test) and equal variance. The significance value was set at 0.05 for all analyses. Data are expressed as mean ± 95% confidence interval.

Egg morphology is not influenced by the incubation tactic (parental care) once accounting for phylogeny, female mass and sexual size dimorphism (Table S.3.6.1).

Results of this study do not support the findings of Martin et al. (2006). The incubation tactic adopted by the species in this study does not result in bigger eggs, bigger clutches or more eggs. However the biological significance of the mode of parental care may be related to the energetic cost of incubation experienced by each parent or some other ecological factor and warrants further study.
Table S3.6.1. Relationship between parental care (C) and the size and shape of avian eggs

<table>
<thead>
<tr>
<th></th>
<th>estimate</th>
<th>statistics *</th>
<th>lambda (λ)</th>
<th>second-order Akaike Information Criterion (AICc)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>phylogenetic model</td>
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<tr>
<td><strong>individual eggs</strong></td>
<td></td>
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<tr>
<td>egg length (L, cm)</td>
<td>0.003 ± 0.009</td>
<td>LCL = -0.014</td>
<td>1.0</td>
<td>-166.9 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>UCL = 0.021</td>
<td></td>
<td></td>
</tr>
<tr>
<td>egg width (W, cm)</td>
<td>0.007 ± 0.007</td>
<td>LCL = -0.006</td>
<td>1.0</td>
<td>-184.6 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>UCL = 0.021</td>
<td></td>
<td></td>
</tr>
<tr>
<td>profile area (PA_E, cm²)</td>
<td>0.012 ± 0.015</td>
<td>LCL = -0.018</td>
<td>1.0</td>
<td>-127.2 *</td>
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<tr>
<td></td>
<td></td>
<td>UCL = 0.042</td>
<td></td>
<td></td>
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<tr>
<td>surface area (SA_E, cm²)</td>
<td>0.013 ± 0.015</td>
<td>LCL = -0.018</td>
<td>1.0</td>
<td>-125.6 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>UCL = 0.044</td>
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<td></td>
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<tr>
<td>volume (V_E, cm³)</td>
<td>0.019 ± 0.021</td>
<td>LCL = -0.025</td>
<td>1.0</td>
<td>-100.8 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>UCL = 0.063</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>whole clutch</strong></td>
<td></td>
<td></td>
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<tr>
<td>profile area (PA_C, cm²)</td>
<td>0.027 ± 0.027</td>
<td>R² = 0.92</td>
<td>0.42</td>
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<td></td>
<td></td>
<td>F₁ = 0.01</td>
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<td></td>
<td></td>
<td>P = 0.92</td>
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<tr>
<td>surface area (SA_C, cm²)</td>
<td>0.026 ± 0.027</td>
<td>R² = 0.91</td>
<td>0.41</td>
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</tr>
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<td></td>
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<td>F₁ = 0.02</td>
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<td></td>
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<td>P = 0.88</td>
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<tr>
<td>volume (V_C, cm³)</td>
<td>0.035 ± 0.029</td>
<td>R² = 0.95</td>
<td>0.41</td>
<td>-74.4</td>
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<td></td>
<td>F₁ = 0.002</td>
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<tr>
<td></td>
<td></td>
<td>P = 0.96</td>
<td></td>
<td></td>
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<tr>
<td>clutch size (E)</td>
<td>0.021 ± 0.028</td>
<td>R² = 0.12</td>
<td>0.69</td>
<td>-78.7</td>
</tr>
<tr>
<td></td>
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<td>F₁ = 0.10</td>
<td></td>
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</tr>
<tr>
<td></td>
<td></td>
<td>P = 0.75</td>
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</tr>
</tbody>
</table>

Statistics represent the influence of parental care on egg morphology only. Statistics for the effect of female mass (M_f) and sexual size dimorphism (SDI) on egg morphology are reported in Chapter 3. Statistics include the regression model estimate for parental care (C); according to the relationship \( y = aM_f^{b_1} SDI^{b_2} C^{b_3} \) for individual egg dimensions. Clutch dimensions were assessed with a shorter model according to the relationship \( y = aM_f^{b_1} C^{b_2} \), since sexual size dimorphism does not influence these parameters (Chapter 3). Clutch size (E) was assessed according to the relationship \( y = aSDI^{b_1} C^{b_2} \), since female mass does not influence clutch size (Chapter 3). Estimates and accompanying statistics are those from the best fit model, represented as the estimate ± 95% CI in the case of non-phylogenetic models and estimate ± SE in the case of phylogenetic models. * Statistics for non-phylogenetic models include the R² for the model regression, the F-ratio (degrees of freedom) and the P-value; while the lower critical limit and upper critical limit are reported for phylogenetic models. * Indicates that the regression for the variable of interest is statistically significant (slope > 0). For non-phylogenetic models the alpha value (α) used is 0.05. N = 36. Lambda (λ) indicates the strength of the phylogenetic relationship, where values lie between 0 and 1. * Represents the model with the best fit for the data, where the model with the lowest AICc is retained for an AICc difference in excess of four, and the non-phylogenetic model retained for an AICc difference of less than four.
CHAPTER 4

KEEPING DRY IN A WARMING CLIMATE:
THE IMPORTANCE OF MATERIAL CHOICE IN AVIAN NEST CONSTRUCTION

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KEEPING DRY IN A WARMING CLIMATE: THE IMPORTANCE OF MATERIAL CHOICE IN AVIAN NEST CONSTRUCTION

Text in manuscript

HEENAN, C. B. (Candidate)

Lead study design, constructed equipment, collected all data and performed statistical analyses, interpreted data, wrote manuscript and acted as corresponding author

I hereby certify that the statement of contribution is accurate.

Signed Date 27/02/2013

WHITE, C. R.

Assisted with statistical analysis of phylogenetic relationships and multiple regression interactions, helped with manuscript evaluation

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis.

Signed Date 27/02/2013
GOODMAN, B. A.

Assisted with statistical analysis, helped with manuscript evaluation

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis.

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Date 27/02/2013

SEYMOUR, R. S.

Provided feedback on study design, supervised development of work, helped with manuscript evaluation

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis.

Signed  

Date 27/02/2013
The structural and thermal properties of avian cup-shaped nests
ABSTRACT

The nest microclimate is critical for the successful development of avian offspring and therefore should impose a strong selective force on nest design and the choice of nest materials. Despite its importance, the contribution of climate to nest insulation has not been adequately addressed. Climate variables, such as temperature and precipitation, may vary with altitude and geographical context; but previous studies have failed to separate the effects of these variables. We measured the structural and thermal properties of 201 cup-shaped nests, from 36 Australian passerine species, and related these to climate variables (altitude and 19 bioclimatic variables) for the collection locality. The data show that altitude, temperature and precipitation all influence the construction of avian nests, via the use of different materials that alter the rate of heat loss from the nest as a whole. Birds that construct nests in cool climates use well-insulating materials irrespective of precipitation, while birds in warm climates use poorly-insulating materials – but only when exposed to high rainfall. Anthropogenic nest materials (such as plastic and nylon) are used in warm and wet climates to provide a structurally sound nest with a low water-holding capacity, thus preventing nest saturation and heat loss from clutches following rain events.

Keywords: bird nest design; insulation; thermal conductance; reproductive energetics; climate; altitude
1. INTRODUCTION

Oviparity, the exclusive method of reproduction used in birds, requires the developmental conditions experienced by offspring to be modulated externally (Reid et al. 2002a). Successful egg development requires the clutch to have a suitable substrate, camouflage and defence from predators, appropriate egg turning, as well as an appropriate microclimate (Ar and Sidis 2002). The latter of these – the nest microclimate – is one of the most widely studied aspects of avian reproduction (Cooper 1999; Lundy 1969; McComb and Noble 1981; Rauter and Reyer 2000; Rhodes et al. 2009; Vleck et al. 1983; Wagner and Seymour 2001; Walsberg 1981; 1986; With and Webb 1993). The critical properties of the nest microclimate include: air temperature, wind, solar radiation, gas composition and humidity (Ar and Sidis 2002; Colllias and Colllias 1984; Deeming 2011; Pinowski et al. 2006; Walsberg 1985). Precipitation influences humidity, as well as the thermal properties of nests and is therefore undoubtedly important (Hilton et al. 2004).

The nest microclimate can have important consequences on avian reproduction as it can influence embryo survival and chick growth (Lombardo et al. 1995; Lundy 1969; Møller 1991; Perez et al. 2008; Reid et al. 2000b; Webb 1987). The amount of solar radiation, air temperature and wind to which the clutch is exposed will determine the equilibrium egg temperature when an incubating parent leaves the nest (Carey 2002; Webb and King 1983a). During inclement weather the parent may leave the nest for extended periods to forage, in order to meet their own energy demands (Gates and Gysel 1978; Haftorn 1988; Morton et al. 1993), and this may in turn put the clutch at risk by lengthening the incubation period, exposing the clutch to increased predation rates, or embryo death (Cresswell 1997; Grant 1982; Lundy 1969; Olson et al. 2006). Some species increase nest attendance during rain events at their own risk (Johnson and Best 1982), but in some cases the incubating bird may have difficulty maintaining nest temperature at appropriate levels, regardless of consistent nest attendance (Haftorn 1978a). Rain events can influence the hatching success of clutches through food- and predator-mediated processes (Boulton et al. 2011). In some species, rainfall is of no concern so long as air temperatures remain high (Haftorn 1978b). However, clutches are equally at risk of embryo death in hot or dry weather (Grant 1982; Lundy 1969). The local climate can also influence the lifetime reproductive success of adults through changes to the energetic cost of incubation (Calder III and King 1974; Grant 1982; Haftorn and Reinertsen 1985; Hilton et al. 2004; McNab 2009; Reid et al. 2000b; Turner 2002; Webster and Weathers 1988) and the intensity of a reproductive event (Aslan and Yavuz 2010; Tinbergen and Williams 2002; Zann et al. 1995).

The nest microclimate can be influenced by chick behaviour (Ricklefs and Hainsworth 1969), parental behaviour (Ar and Sidis 2002; Carey 2002; Prokop and Trnka 2011), the nest itself and a host of biotic (evolution, adaptation, parasites, egg/egg interactions) and abiotic (habitat, time of day, season, climate) factors (Ar and Sidis 2002; Hansell and Deeming 2002). While behaviour is responsive to changes in ambient temperature, nest structure may be less flexible (Chapter 2). Therefore, nest site selection (Colllias and Colllias 1984; Horvath 1964; Sidis et al. 1994; Slagsvold 1989a; Tieleman et al. 2008) and orientation (Austin 1976;
Grant 1982; Ricklefs and Hainsworth 1969) may be important factors in the temperature regulation of the clutch and may vary with the environmental conditions experienced by parents to provide shelter from wind (Austin 1976; Ricklefs and Hainsworth 1969), rain (Conner 1975) and sun (Haggerty 1995; Orr 1970). In addition, nest material composition (Britt and Deeming 2011; Mainwaring and Hartley 2008; Møller 1984), material quantity (Colllias and Colllias 1971; McGowan et al. 2004; Møller 1987; Soler et al. 1998a) and structure (Franklin 1995; Herranz et al. 2004) can change with the prevailing weather as the breeding season progresses. Most commonly, nests are bigger and more insulated at high altitudes (Kern and Van Riper 1984), latitudes away from the equator (Crossman et al. 2011; Kern et al. 1993; Mainwaring et al. 2012; Soler et al. 1998b; Tiainen et al. 1983) or in cold environments (Briskie 1995; Deeming et al. 2012; Kern 1984; Rohwer and Law 2010; Schaefer 1976; 1980), suggesting that geographic variation in bird nests is adaptive (McCracken et al. 1997; Rohwer 2010).

By building a thermally favourable nest, an incubating parent is able to help ameliorate the effects of climate by moderating the heat loss from the clutch and therefore reducing their own energy demands (Hilton et al. 2004; Møller 1984; Reid et al. 2002a; Walsberg 1978). Certain materials may be preferred as they may help to reduce heat loss under certain environmental conditions, or absorb less water during rain events (Rohwer and Law 2010). Lichen flakes are commonly used in bird nest construction, with suggestions that lichen prevents water penetration into nests (Hansell 1996; Hilton et al. 2004). There is a decline in the use of mosses and lichens as the breeding season progresses for some passerine birds, though the use of these materials early in the season may also help to increase nest elasticity to cope with large clutches in the first breeding attempt (Slagsvold 1989b).

Nesting pairs must be able to gauge the thermal environment within their nest and adjust their nest-building behaviour accordingly (Colllias and Colllias 1984; McGowan et al. 2004). Nest site selection and adjustments in the orientation or construction of nests can combine to determine the nest microclimate, provide substantial energy savings and alter the success of the reproductive event (Britt and Deeming 2011; Butler et al. 2009; Calder III 2002; D’Alba et al. 2009; Merola-Zwartjes 1998). While a well-insulated nest may require more energy to construct, the energy invested to provide a suitable microclimate may be paid back by reducing the energetic cost of incubation over the breeding period (Britt and Deeming 2011; Calder III 2002).

Our earlier study on the thermal properties of nests across 36 species of birds weighing 8 to 360 g demonstrated that cup-shaped nests were constructed primarily for support rather than insulation (Chapter 2). Insulation was evaluated by measuring its inverse, the thermal conductance. This is the rate of heat flux (watts) moving across the nest wall, per degree of temperature difference between the inside and outside of the nest, based on Newton’s Law of Cooling (Calder III and King 1974; Tracy 1972). Well-insulated nests have a low conductance and vice versa. However we found considerable variation in total conductance within a species (Chapter 2). It is possible that the variation in nest conductance could be attributable to modifications in nest design in response to factors such as climate.
While nest design and location have been shown to vary in response to climatic conditions, these responses are usually only qualitatively addressed or consider only surface-specific conductance – an inadequate descriptor of the total energy required to maintain the nest temperature (Kern and Van Riper 1984; Reid et al. 2002a). Furthermore, previous studies have focused on variation in nest design using a single variable; based on comparisons among races, within a single species (Schaefer 1980). Therefore it is unclear whether observed relationships between nest size or thickness and ambient conditions translate to changes in the total conductance of the nest. It is also not known if such relationships are independent of other unmeasured variables, or if such trends are common among multiple species. The present study is the first to assess the thermal properties of cup-shaped nests across a wide geographical area (spanning 22° latitude and 20° longitude) and altitudinal (667 m) gradient simultaneously, whilst also accounting for the scaling of nest size with adult body mass (Chapter 2). Here we re-evaluate the conductance of cup-shaped nests across a range of Australian birds and relate this to ambient temperature, precipitation and altitude.

A well-insulated nest can be achieved by selecting strongly insulating material or large quantities of insulating material (Hilton et al. 2004). If climate is important in determining nest design, we would expect that there would be differences in nest conductance, resulting from variations in nest wall thickness or the insulative properties of the materials used in nest construction; and that these differences would be associated with variations in local climatic conditions. We test the following predictions:

**Temperature:** If ambient temperature is an important factor for the design and insulation of avian nests, then we would expect that nest conductance would increase with concurrent increases in temperature in order to facilitate heat loss. This would potentially occur via three processes in response to increasing ambient temperature:
1. Nest wall thickness would decrease.
2. Nest surface area would increase, independently of changes in wall thickness.
3. The insulative value of the materials used in construction would decrease (material conductivity would increase).

**Precipitation:** If precipitation is a significant determinant of avian nest insulation, then it could be expected that there would be an increase in nest conductance with greater exposure to precipitation in order to facilitate nest drying following rain events. This would potentially occur as follows:
1. Nest wall thickness would decrease to facilitate nest ventilation.
2. Nest surface area would decrease to enable the incubating bird to cover the nest and prevent saturation.
3. The insulative value of the materials used in construction would decrease, as less insulative materials will dry more rapidly.

**Climate:** We assessed the interaction between temperature and precipitation (henceforth referred to as climate), as both temperature and precipitation influence habitat productivity (White et al. 2007). The presence of an interaction indicates that the response of birds to one variable depends upon the level of the other.
Finally, since previous studies have found associations between altitude and nest construction (Kern and Van Riper 1984), we also test for an association between altitude and nest thickness, surface area, and conductance. We do so while accounting for temperature, precipitation, and climate, to determine if any association between altitude and nest construction is independent of, for example, the negative association between altitude and temperature (Campbell 1977; Lee et al. 2011).

A nest that is thermally favourable in one season may not be as beneficial in the next; therefore we assess the nest thermal properties at a scale that is specific to the breeding season of each species (Zann and Rossetto 1991). At the annual scale, we assess the importance of a multitude of bioclimatic variables on the thermal properties of nests.
2. METHODS

Nests used in this study were borrowed from the South Australian Museum and Queensland Museum ornithology collections. A total of 201 cup-shaped nests (from 36 species) were included in the study (Figure 4.1), of which 180 nests (across 36 species) were from the South Australian Museum ornithological collection and 21 nests (across 8 species) were from the Queensland Museum ornithological collection. Details regarding the inclusion or omission of individual nests, as well as the analysis of nest age and condition, can be found in Chapter 2. Only nests for which there was information on the collection location were included in the data set.

![Informal supertree showing the phylogenetic relationships between bird species.](image)

*Multiple nests and species could not be included in nest mass analysis due to the attachment of supporting branches.*
(a) Nest dimensions and thermal properties

The methods used to determine the nest dimensions and thermal properties are those described in Chapter 2. Briefly, the physical dimensions of the nests were measured, including the nest thickness (X) and internal / external diameter (d) and height (h), to enable calculations of the geometric mean nest surface area (\(\bar{A}\)).

The total thermal conductance (G, mW °C\(^{-1}\)) of the nests was measured by placing an artificial heat source inside the nest and measuring the heat flow out through the wall (\(\Phi\)), in relation to the temperature difference across the wall (\(\Delta T\)).

The thermal conductivity (k, mW °C\(^{-1}\) m\(^{-1}\)) of the materials used in each nest was calculated using the surface area and thickness (X) of the nest, according to Equation 2.8 (Chapter 2).

To ascertain if material use differed between species breeding in different regions, the types of materials present in each nest were recorded and allocated to either plant, animal, silk, anthropogenic or other derivation (see Appendix 10 to 12). Plant materials include: sticks, twigs, vines, rootlets, tendrils, bark, grass, runners, sedges, leaves, flowers, seed pods, plant-down, cotton, moss and lichen. Animal derived materials include: fur, hair, wool and feathers. Silk products include: spider silk, egg sacks and cocoons. Anthropogenic materials include: processed cottons, cloth, paper, plastic and nylon. Other materials include: faeces, mud and unidentified / nondescript organic material.

(b) Altitude and climate data

Nest collection location, in the form of latitude and longitude points, as well as collection dates for individual nests, were obtained from the South Australian Museum nest collection database. These points were converted to digital reference points (spreadsheet developed by Steve Dutch, 2005, University of Wisconsin, Green Bay, http://www.uwgb.edu/dutchs/UsefulData/ UTMFormulas.HTM) and mapped using DIVA-GIS (Hijmans et al. (2009), version 7.0.2.1).

Altitude and climate grids (WorldClim generic grids, http://www.worldclim.org/) were obtained for Australia, where data layers are generated through interpolation of observed data from weather stations, representative of the climate between 1950 and 2000 (Hijmans et al. 2005). The layers used were from a 2.5 arc-minute (1 km\(^2\)) resolution grid. The climate and altitude layers were overlaid on the nest location map in DIVA-GIS to align collection location with the variables of interest (see Figure 4.2). Climate and altitude point-data relating to each nest collection location were then exported for further analysis (see § 2(d)).
Figure 4.2. Maps showing the altitude (m), mean annual temperature (°C) and annual precipitation (mm) with respect to nest collection location. Nest collection locations are identified with red, green and black points for altitude, temperature and precipitation, respectively. Note that the scale does not increase in equal increments in all cases. Data are sourced from WorldClim generic grids (http://www.worldclim.org/), where data layers (2.5 arc-minute (1 km²) resolution grid) are generated through interpolation of observed data from weather stations, representative of the climate between 1950 and 2000 (Hijmans et al. 2005).

NOTE:
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Mean breeding season temperature (°C) and mean monthly precipitation (mm) values were obtained by taking the mean of each variable at each nest location across the months that were specific to the breeding season of each species. Breeding seasons were obtained from the Handbook of Australian, New Zealand and Antarctic Birds resource series (Marchant and Higgins 2001; 2002; 2006). Annual mean temperature (°C) and total precipitation values (mm) were also obtained for each nest location, in addition to 17 bioclimatic variables that were not available at the breeding season level, listed in Table 4.1.

Table 4.1. Bioclimatic variables for temperature and precipitation with associated eigenvalues

<table>
<thead>
<tr>
<th>climate category</th>
<th>bioclimatic variable</th>
<th>eigenvalue</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>annual mean temperature</td>
<td>5.43</td>
</tr>
<tr>
<td></td>
<td>mean monthly temperature range</td>
<td>3.55</td>
</tr>
<tr>
<td></td>
<td>isothermality *</td>
<td>1.11</td>
</tr>
<tr>
<td></td>
<td>temperature seasonality Α</td>
<td>0.85</td>
</tr>
<tr>
<td></td>
<td>maximum temperature of the warmest month</td>
<td>0.031</td>
</tr>
<tr>
<td></td>
<td>maximum temperature of the coldest month</td>
<td>0.021</td>
</tr>
<tr>
<td></td>
<td>temperature annual range</td>
<td>0.012</td>
</tr>
<tr>
<td></td>
<td>mean temperature of the wettest quarter</td>
<td>0.0007</td>
</tr>
<tr>
<td></td>
<td>mean temperature of the driest quarter</td>
<td>0.0003</td>
</tr>
<tr>
<td></td>
<td>mean temperature of the warmest quarter</td>
<td>0.0000</td>
</tr>
<tr>
<td></td>
<td>mean temperature of the coldest quarter</td>
<td>0.0000</td>
</tr>
<tr>
<td></td>
<td>annual precipitation</td>
<td>5.76</td>
</tr>
<tr>
<td></td>
<td>precipitation of wettest month</td>
<td>1.60</td>
</tr>
<tr>
<td></td>
<td>precipitation of driest month</td>
<td>0.57</td>
</tr>
<tr>
<td></td>
<td>precipitation seasonality Α</td>
<td>0.055</td>
</tr>
<tr>
<td></td>
<td>precipitation of wettest quarter</td>
<td>0.013</td>
</tr>
<tr>
<td></td>
<td>precipitation of driest quarter</td>
<td>0.0027</td>
</tr>
<tr>
<td></td>
<td>precipitation of warmest quarter</td>
<td>0.0012</td>
</tr>
<tr>
<td></td>
<td>precipitation of coldest quarter</td>
<td>0.0003</td>
</tr>
</tbody>
</table>

Statistics include the eigenvalue, representative of the variance explained by each component, where eigenvalues greater than 1 signify that a variable is the most important for nest construction.

Bioclimatic variables from WorldClim generic grids outlined online at http://www.worldclim.org/bioclim

* Isothermality is the mean monthly temperature range divided by the temperature annual range, multiplied by 100.

* Temperature seasonality is the standard deviation multiplied by 100.

* Precipitation seasonality is the coefficient of variation.

(c) Parent mass

Parent mass (g) values for each species were obtained from the Handbook of Australian, New Zealand and Antarctic Birds resource series (Marchant and Higgins 2001; 2002; 2006) to account for the known influence of parent mass on nest design (Chapter 2 and Supplement 2.3). The mean of the male and female mass values was used for each species where reported. For those where a mean value was not reported, the mean of the minimum and maximum mass values was used.
(d) **Statistical analyses**

**i. Nest material use**

An indicator species analysis was performed in PC-Ord (McCune and Mefford (1999), version 5.0) to test if the materials used in nest construction differed between climates and altitudes. An indicator species is the characteristic species of a group; thus a species with a high indicator value occurs frequently in one group and not in other groups (Dufrêne and Legendre 1997). In this test, the materials used in construction are the indicator species and the climate and altitude categories are groups. The analysis was based on indicator values (percent of perfect indication, based on combining relative abundance values and relative frequency) calculated with the methods of Dufrêne and Legendre (1997) and a Monte Carlo one-sided test of significance of the observed maximum indicator value for materials found in nests. The Monte Carlo test yields a *P*-value, which is the proportion of randomised trials with an indicator value equal to or exceeding the observed indicator value, based on 1000 permutations.

The indicator species analysis enabled us to assess material type against four climate groups (low temperature / low precipitation, low temperature / high precipitation, high temperature / low precipitation and high temperature / high precipitation) and two altitude groups (low altitude and high altitude). The temperature, precipitation and altitude groups are determined from the residuals in the lower third and upper third percentile, thus nests from the 2/3 percentile were excluded from the indicator species analysis. Here, the bird species that constructed the nest was not considered.

**ii. Principal component analyses**

We used a the initial stages of a principal component analysis (PCA) in JMP IN (SAS Institute (2001), version 4.0.4) to assess the importance of the 19 annual-level bioclimatic variables (Table 4.1) for nest structural and thermal characteristics. The analysis was performed on the eleven temperature-related and eight precipitation-related bioclimatic variables separately. Bioclimatic variables of the greatest importance for nest construction were determined from the eigenvalues (*i.e.* eigenvalues > 1, Table 4.1). Many of the bioclimatic variables were found to be non-independent when assessed with a correlation matrix and therefore were not rotated to achieve principal components for further linear regression analysis.

**iii. Phylogenetic analyses**

An informal supertree (a reconstruction of multiple trees (Bininda-Emonds 2004), Figure 4.1) was derived following trees provided by http://www.tolweb.org, Loynes *et al.* (2009), Jønsson *et al.* (2010), Nyári and Joseph (2011) and Driskell and Christidis (2004). The supertree was constructed in Mesquite (Maddison and Maddison (2007), version 2.75) and formatted in FigTree (Rambaut (2007), version 1.3.1). Branch lengths of the tree to the level of species were adjusted to be punctuated (representing the punctuated evolution theory where long periods of stasis are punctuated by rapid periods of development) and equal to one. Branch length
transformations of Grafen (1989), Nee (described in Purvis 1995) and Pagel (1992) were applied with the PDAP:TREE (Midford et al. 2005) module of Mesquite to check the suitability of the standard transformation.

The effect of climate on nest structural and thermal properties was analysed in R (Gentleman and Ihaka (2011), version 2.14.1), whilst also accounting for phylogenetic relatedness. The analyses utilised the packages: ape (Analysis of phylogenetics and evolution, Paradis et al. (2004), version 3.0), gee (Generalised estimation equation solver, Carey (2011), version 4.13-17), nlme (linear and non-linear mixed effects models, Pinheiro et al. (2011), version 3.1-103) and lattice (Multivariate data visualization, Sarkar (2008), version 0.20-0), as well as a generalised least square in comparative phylogenetics (PGLS) code modified from code that accompanies Duncan et al. (2007).

Models included altitude, temperature, precipitation, and interaction between temperature and precipitation, as well as parent mass (logarithmically-transformed) to account for the known allometric relationships with nest structure and conductance (Chapter 2). The interactions between altitude and temperature (Phylogenetically informed 95 % confidence limit (Phy-CL): -0.0000076, 0.0000084) and between altitude and precipitation (Phy-CL: -0.0000083, 0.0000016) were non-significant and therefore excluded from the final model. Analyses were performed on individual nest structural and thermal characteristics at the breeding season climate mean scale by including the variables of mean temperature and mean precipitation for the breeding season of the respective species.

Phylogenetic correlation was determined from the lambda (λ) value that maximised the likelihood of the model (Pagel 1999). The strength of the phylogenetic models was assessed by repeating analyses with λ equal to zero and comparing the Akaike Information Criterion (AIC) values produced from the phylogenetic and non-phylogenetic models (Burnham and Anderson 2002). The need to account for phylogeny in the analysis of these data was supported if the AIC was lowest for the phylogenetic model, and if the AIC difference (ΔAIC) between the phylogenetic and non-phylogenetic models was greater than four; the non-phylogenetic model was retained if the ΔAIC was less than four. PGLS estimates were accepted as significant when the lower and upper 95 % confidence limits (Phy-CL) of a given parameter estimate (slope) excluded zero.

iv. Multiple linear regression analyses

To enable interpretation of the phylogenetic analyses, further statistical analyses were performed in JMP IN (SAS Institute (2001), version 4.0.4), employing multiple linear regression techniques. All models included parent mass, as well as species (as a random factor), since nests within a species may be more similar than between species. Data represented in the Figures and Tables are therefore independent of parent mass and represent relationships both within and between species.

As in the phylogenetic analyses, altitude, temperature, precipitation and an interaction term consisting of temperature and precipitation was included in the regression models. Again, neither the interaction between altitude and temperature or the interaction between altitude and precipitation were included in the multiple
linear regression model, as neither interaction proved significant in the phylogenetic analyses (§ 2(d)iii). Where an interaction is significant, the associations between the Y-variable and temperature or precipitation cannot be interpreted independently, because the effect of each depends on the level of the other. To facilitate interpretation of significant interactions between temperature and precipitation, a residual-residual plot was produced by splitting the precipitation residual data into thirds: low, medium and high precipitation; removing the medium range and plotting the low and high precipitation residuals as two series of residual temperature against residual Y-variable. This allowed the interaction to be interpreted by examining the association between the Y-variable and temperature for high and low levels of precipitation.

v. Model assumptions and data transformation

Nest conductance, surface area and thickness are known to scale with adult body mass to an exponent of less than one ($M^{0.25}$, $M^{0.68}$ and $M^{0.49}$, respectively, Chapter 2), consequently parent mass values were logarithmically transformed for analyses to produce linear relationships that conform to the regression assumption of normality of the residuals. Climate and altitude data were not transformed, while nest structural and thermal data were log-transformed for analyses.

The data were tested for outliers using a residual by predicted plot. Points that were significantly different to the rest of the data for one or more structural or thermal variables were removed from the data set to achieve equal variance in the data and a more reliable interpretation of the findings. Following outlier removal, residuals of the data met the assumption of equal variance required for parametric linear regression tests. However the residuals did not meet the assumption of normality (Shapiro-Wilk $W$ test) in all cases. Non-normal nest conductance data were both logarithmically transformed and then subjected to an inverse transformation, resulting in a normal distribution. For ease of understanding and further interpretation, the untransformed nest conductance data are presented in Figures, with the accompanying statistics referring to the inverse-logarithm transformation. While the distribution of surface area residuals appeared normal, there were a few potential outliers resulting in a $P < W < 0.0001$ for the Shapiro-Wilk $W$ test. Transformation of the surface area data did not improve the distribution of the residuals. Due to the high nest replication ($n = 201$), this was considered to be of no great concern as the data should approximate a normal distribution according to the Central Limit Theorem (Anderson 2010).

The significance value was set at 0.05 for all analyses. Species averages for the structural and thermal properties of nests are reported in Appendix 2, 3 and 4.
3. RESULTS

Phylogenetically informed analyses reveal that the regression models for nest conductance, thermal conductivity, surface area and thickness are influenced by phylogeny, as indicated by the lambda value and the lower AIC for the phylogenetic model compared to the non-phylogenetic counterpart (Table 4.2). Consequently, the model term for species as a random variable in the non-phylogenetic multiple regression analysis is significant for nest conductance at the breeding season level ($F_{35,160} = 2.40, P = 0.0001$). As reported in Chapter 2 and supported by the phylogenetic models, total nest conductance (Phy-CL: -0.06, -0.03; $F_{1,160} = 42.82, P < 0.0001$), surface area (Phy-CL: 0.59, 0.72; $F_{1,160} = 344.58, P < 0.0001$) and nest thickness (Phy-CL: 0.37, 0.58; $F_{1,160} = 69.56, P < 0.0001$) increase with parent mass; but thermal conductivity is independent of parent mass (Phy-CL: -0.09, 0.09; $F_{1,160} = 0.10, P = 0.75$).

Table 4.2. Comparative phylogenetics statistics for the relationship between nest structural and thermal properties and model variables

<table>
<thead>
<tr>
<th>nest parameter</th>
<th>lambda ($\lambda$)</th>
<th>Akaike Information Criterion (AIC)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>phylogenetic model</td>
</tr>
<tr>
<td>nest conductance $^a$</td>
<td>0.69</td>
<td>-952.9 *</td>
</tr>
<tr>
<td>(G, mW °C$^{-1}$)</td>
<td></td>
<td>-934.1</td>
</tr>
<tr>
<td>thermal conductivity</td>
<td>0.54</td>
<td>-160.4 *</td>
</tr>
<tr>
<td>(k, mW °C$^{-1}$ m$^{-1}$)</td>
<td></td>
<td>-150.8</td>
</tr>
<tr>
<td>surface area</td>
<td>0.71</td>
<td>-348.6 *</td>
</tr>
<tr>
<td>(Ā, cm$^2$)</td>
<td></td>
<td>-313.8</td>
</tr>
<tr>
<td>thickness</td>
<td>0.62</td>
<td>-136.5 *</td>
</tr>
<tr>
<td>(X, cm)</td>
<td></td>
<td>-112.0</td>
</tr>
</tbody>
</table>

* Represents the model with the best fit for the data, where the model with the lowest AIC is retained for an AIC difference in excess of four, and the non-phylogenetic model retained for an AIC difference of less than four.
Lambda ($\lambda$) indicates the strength of the phylogenetic relationship, where values lie between 0 and 1.
$^a$ Conductance values used in the analysis were the inverse-logarithm transformed values for total conductance (G, mW °C$^{-1}$).

Nest conductance is significantly influenced by the breeding season climate variables when accounting for phylogenetic relatedness (Table 4.3, individual estimates in Table 4.4). Non-phylogenetic multiple regression analysis confirmed the patterns ($R^2 = 0.64$, $F_{40,160} = 8.51, P < 0.0001$). Following adjustment in the non-phylogenetic model, 62.9% of the variance in nest conductance can be predicted by measures of species, parent mass, altitude, temperature and precipitation (Table 4.5). The species model term from the non-phylogenetic analysis of conductance is split into individual species estimates and accompanying statistics in Table 4.5.
The structural and thermal properties of avian cup-shaped nests

Table 4.3. Statistics for the regression of the dimensions and thermal properties of nests against altitude and breeding season climate

<table>
<thead>
<tr>
<th>nest parameter</th>
<th>altitude</th>
<th>climate ^</th>
</tr>
</thead>
<tbody>
<tr>
<td>nest conductance (G, mW °C⁻¹)</td>
<td>F = 8.71, P = 0.0036 *</td>
<td>F = 7.57, P = 0.0086 *</td>
</tr>
<tr>
<td></td>
<td>Phy-CL: -0.00005, -0.00001 *</td>
<td>Phy-CL: -0.00001, -0.000001 *</td>
</tr>
<tr>
<td>thermal conductivity (k, mW °C⁻¹ m⁻¹)</td>
<td>F = 3.09, P = 0.08</td>
<td>F = 5.36, P = 0.022 *</td>
</tr>
<tr>
<td></td>
<td>Phy-CL: -0.00001, 0.0003</td>
<td>Phy-CL: -0.055, 0.007</td>
</tr>
<tr>
<td>surface area (Ā, cm²)</td>
<td>F = 0.15, P = 0.70</td>
<td>F = 0.12, P = 0.73</td>
</tr>
<tr>
<td></td>
<td>Phy-CL: -0.0001, 0.0001</td>
<td>Phy-CL: -0.011, 0.026</td>
</tr>
<tr>
<td>thickness (X, cm)</td>
<td>F = 1.49, P = 0.22</td>
<td>F = 0.55, P = 0.46</td>
</tr>
<tr>
<td></td>
<td>Phy-CL: -0.0002, 0.0002</td>
<td>Phy-CL: -0.048, 0.017</td>
</tr>
</tbody>
</table>

Statistics include the F-ratio and P-value for the non-phylogenetic multiple regression analyses and the 95% confidence limits (Phy-CL) for the slope in the phylogenetic analyses (lower CL, upper CL).

* Indicates that the non-phylogenetic regression for the variable of interest is statistically significant (slope ≠ 0) at the specified alpha value (α = 0.05).

+ Indicates that the phylogenetically-informed regression for the variable of interest is statistically significant (slope ≠ 0).

^ The climate statistics are represented as the interaction between temperature and precipitation as a single statistic, or temperature and precipitation as separate statistics where the interaction is not significant.

N = 201 and DF = 1,160 for all comparisons.

Table 4.4. Comparative phylogenetics estimate and supporting statistics for the relationship between nest conductance (inverse-logarithm) and model variables at the breeding season level

<table>
<thead>
<tr>
<th>model variable</th>
<th>estimate ± S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>intercept</td>
<td>0.57 ± 0.04 *</td>
</tr>
<tr>
<td>parent mass</td>
<td>-0.042 ± 0.007 *</td>
</tr>
<tr>
<td>altitude</td>
<td>-0.000028 ± 0.000011 *</td>
</tr>
<tr>
<td>temperature</td>
<td>-0.00015 ± 0.0021</td>
</tr>
<tr>
<td>precipitation</td>
<td>0.0012 ± 0.0006</td>
</tr>
<tr>
<td>interaction term [temperature × precipitation]</td>
<td>-0.000077 ± 0.000033 *</td>
</tr>
</tbody>
</table>

Statistics include the estimate ± S.E. for the model variables.

* Note that the intercept here is represented in the inverse-logarithm format to retain accuracy. Transformed intercept equates to 58.33 mW °C⁻¹.

* Indicates that the regression for the variable of interest is statistically significant (slope ≠ 0) based on lower and upper critical limits for regression estimates.

^ Indicates values that were logged prior to analysis. Conductance values used in the analysis were the inverse-logarithm transformed values for total conductance (G, mW °C⁻¹). Note that due to the transformation, variables with a positive estimate actually have a negative relationship with conductance and vice versa.

# Note that the variables of temperature and precipitation alone lose meaning in the context of a significant interaction.

Lambda (λ) is 0.69 and the Akaike Information Criterion (AIC, Table 4.2) is -952.9 at the breeding season level for the phylogenetic model (non-phylogenetic AIC = -934.1).
Table 4.5. Non-phylogenetic regression estimates and supporting statistics for the relationship between nest conductance (inverse-logarithm) and model variables at the breeding season level

<table>
<thead>
<tr>
<th>model variable</th>
<th>estimate ± S.E.</th>
<th>t ratio</th>
<th>probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>intercept *</td>
<td>0.64 ± 0.020</td>
<td>31.43</td>
<td>&lt; 0.0001 *</td>
</tr>
<tr>
<td>Acanthorhynchus tenuirostris</td>
<td>0.0059 ± 0.0081</td>
<td>0.73</td>
<td>0.47</td>
</tr>
<tr>
<td>Anthochaera carunculata</td>
<td>-0.0089 ± 0.0072</td>
<td>-1.23</td>
<td>0.22</td>
</tr>
<tr>
<td>Anthochaera chrysoptera</td>
<td>0.0091 ± 0.0070</td>
<td>1.29</td>
<td>0.20</td>
</tr>
<tr>
<td>Colluricincla harmonica</td>
<td>0.0013 ± 0.0091</td>
<td>0.14</td>
<td>0.89</td>
</tr>
<tr>
<td>Corcorax melanorhamphos</td>
<td>-0.0011 ± 0.010</td>
<td>-0.11</td>
<td>0.91</td>
</tr>
<tr>
<td>Cisticolor torquatus</td>
<td>-0.015 ± 0.010</td>
<td>-1.51</td>
<td>0.13</td>
</tr>
<tr>
<td>Daphoenositta chrysoptera</td>
<td>0.00089 ± 0.0091</td>
<td>0.10</td>
<td>0.92</td>
</tr>
<tr>
<td>Eopsalthe australis</td>
<td>0.023 ± 0.0074</td>
<td>3.11</td>
<td>0.0023 *</td>
</tr>
<tr>
<td>Grallina cyanoleuca</td>
<td>-0.0066 ± 0.0074</td>
<td>-0.90</td>
<td>0.37</td>
</tr>
<tr>
<td>Lichenostomus chrysops</td>
<td>-0.00092 ± 0.0074</td>
<td>-0.12</td>
<td>0.90</td>
</tr>
<tr>
<td>Lichenostomus cratitius</td>
<td>0.0026 ± 0.0075</td>
<td>0.34</td>
<td>0.73</td>
</tr>
<tr>
<td>Lichenostomus leucotis</td>
<td>-0.013 ± 0.0084</td>
<td>-1.54</td>
<td>0.13</td>
</tr>
<tr>
<td>Lichenostomus ornatus</td>
<td>0.0046 ± 0.011</td>
<td>0.40</td>
<td>0.69</td>
</tr>
<tr>
<td>Lichenostomus penicillatus</td>
<td>-0.0033 ± 0.0079</td>
<td>-0.42</td>
<td>0.68</td>
</tr>
<tr>
<td>Lichenostomus plumulus</td>
<td>0.0076 ± 0.012</td>
<td>0.66</td>
<td>0.51</td>
</tr>
<tr>
<td>Lichenostomus virescens</td>
<td>0.0017 ± 0.0073</td>
<td>0.24</td>
<td>0.81</td>
</tr>
<tr>
<td>Lichmera indistincta</td>
<td>-0.0027 ± 0.0089</td>
<td>-0.31</td>
<td>0.76</td>
</tr>
<tr>
<td>Manorina flavigula</td>
<td>-0.0028 ± 0.0083</td>
<td>-0.34</td>
<td>0.73</td>
</tr>
<tr>
<td>Melanodryas cucullata</td>
<td>0.024 ± 0.0078</td>
<td>3.04</td>
<td>0.0027 *</td>
</tr>
<tr>
<td>Melanodryas vittata</td>
<td>0.0015 ± 0.012</td>
<td>0.12</td>
<td>0.90</td>
</tr>
<tr>
<td>Microeca fascinans</td>
<td>-0.0024 ± 0.010</td>
<td>-0.24</td>
<td>0.81</td>
</tr>
<tr>
<td>Oriolus sagittatus</td>
<td>-0.0080 ± 0.010</td>
<td>-0.79</td>
<td>0.43</td>
</tr>
<tr>
<td>Pachycephala inornata</td>
<td>0.0032 ± 0.0074</td>
<td>0.44</td>
<td>0.66</td>
</tr>
<tr>
<td>Pachycephala olivacea</td>
<td>0.0088 ± 0.011</td>
<td>0.77</td>
<td>0.44</td>
</tr>
<tr>
<td>Pachycephala pectoralis</td>
<td>0.011 ± 0.0050</td>
<td>2.19</td>
<td>0.030 *</td>
</tr>
<tr>
<td>Pachycephala ruifrons</td>
<td>-0.0065 ± 0.0069</td>
<td>-0.94</td>
<td>0.35</td>
</tr>
<tr>
<td>Pachycephala rufogularis</td>
<td>-0.0039 ± 0.0076</td>
<td>-0.51</td>
<td>0.61</td>
</tr>
<tr>
<td>Petroica goodenovii</td>
<td>-0.030 ± 0.010</td>
<td>-2.96</td>
<td>0.0036 *</td>
</tr>
<tr>
<td>Petroica multicolor</td>
<td>-0.0089 ± 0.0092</td>
<td>-0.97</td>
<td>0.33</td>
</tr>
<tr>
<td>Psophodes nigrogarulis</td>
<td>-0.0068 ± 0.0082</td>
<td>-0.82</td>
<td>0.41</td>
</tr>
<tr>
<td>Rhipidura fuliginosa</td>
<td>0.00073 ± 0.0068</td>
<td>0.11</td>
<td>0.91</td>
</tr>
<tr>
<td>Rhipidura leucophrys</td>
<td>0.0091 ± 0.0067</td>
<td>1.37</td>
<td>0.17</td>
</tr>
<tr>
<td>Strepera versicolor</td>
<td>-0.011 ± 0.012</td>
<td>-0.91</td>
<td>0.37</td>
</tr>
<tr>
<td>Struthidea cinerea</td>
<td>0.0047 ± 0.011</td>
<td>0.44</td>
<td>0.66</td>
</tr>
<tr>
<td>Turdus merula</td>
<td>0.026 ± 0.0072</td>
<td>3.63</td>
<td>0.0004 *</td>
</tr>
<tr>
<td>Zosterops lateralis</td>
<td>-0.013 ± 0.0061</td>
<td>-2.18</td>
<td>0.031 *</td>
</tr>
<tr>
<td>*parent mass</td>
<td>-0.047 ± 0.0072</td>
<td>-6.54</td>
<td>&lt; 0.0001 *</td>
</tr>
<tr>
<td>*altitude</td>
<td>-0.000033 ± 0.0001</td>
<td>-2.95</td>
<td>0.0036 *</td>
</tr>
<tr>
<td>*temperature</td>
<td>-0.0039 ± 0.0009</td>
<td>-4.23</td>
<td>&lt; 0.0001 *</td>
</tr>
<tr>
<td>*precipitation</td>
<td>0.000028 ± 0.0001</td>
<td>0.24</td>
<td>0.81</td>
</tr>
<tr>
<td>interaction term *</td>
<td>-0.000098 ± 0.0001</td>
<td>-2.75</td>
<td>0.0066 *</td>
</tr>
</tbody>
</table>

Statistics include the estimate of the relationship (± standard error), the t-ratio and P-value.

* The intercept here is represented in the inverse-logarithm format to retain accuracy. Transformed intercept equates to 36.86 mW °C⁻¹.

* Indicates that the regression for the variable of interest is statistically significant (slope ≠ 0) at the specified alpha value (α = 0.05). The model term for common name as a random variable is subdivided into the individual species estimates, but is significant as a whole (F_{35,160} = 2.40, P = 0.0001).

* Indicates values that were logged prior to analysis. Conductance values used in the analysis were the inverse-logarithm transformed values for total conductance (G, mW °C⁻¹). Note that due to the transformation, variables with a positive estimate actually have a negative relationship with conductance, and vice versa.

* Note that the variables of temperature and precipitation alone lose meaning in the context of a significant interaction.

* The interaction term consists of (Temperature – 16.20) × (Precipitation – 49.92) at the breeding season level.
There is an interaction between temperature and precipitation on the conductance of nests (Table 4.4 and Table 4.5, phylogenetic and non-phylogenetic analyses, respectively). Birds build nests that have a greater nest conductance in warm climates compared to cold climates, with the trend being more pronounced for wet climates compared to dry climates (Figure 4.3.a). Nest conductance increases with altitude (Figure 4.4) when breeding season climate is accounted for (Table 4.3).

Figure 4.3. Residual-residual (interaction) plots for temperature and precipitation and the relationship with a – nest conductance (G, mW °C⁻¹) and b – material conductivity (k, mW °C⁻¹ m⁻¹). Low precipitation values are denoted by grey triangles, while high precipitation values are denoted by black triangles. Each point represents an individual nest, with no distinction between species. Solid lines represent the regression mean for low precipitation (grey line) and high precipitation (black line) in the untransformed data model. Grey dashed lines represent the zero axes for the residuals.
Figure 4.4. The relationship between altitude (m) and nest conductance (G, mW °C⁻¹) for cup-shaped birds’ nests. Values of nest conductance have been corrected according to the phylogenetically-corrected estimate for parent mass, temperature, precipitation and climate interaction in the untransformed data model, to eliminate the influence of each parameter. Therefore, data represented are effectively mass-independent and climate-independent. Each point represents the mean ± 95 % C.I. for each 50 m altitude range (N for each point in grey text above the horizontal axis).

When accounting for phylogeny, breeding season climate does not significantly influence the thermal conductivity of nests (Table 4.3). Branch length conversions of Grafen (Grafen 1989), Nee (Purvis 1995) and Pagel (Pagel 1992) failed to improve the model AIC. However, the AIC increases from -160.4 to -158.5 when the climate interaction term is removed from the thermal conductivity model. In addition, there is an interaction between temperature and precipitation on the thermal conductivity of nests (Table 4.3) in the non-phylogenetic model. This indicates that birds build nests that have a greater thermal conductivity in warm climates compared to cold climates, but only when built in locations with high rainfall (Figure 4.3.b). Altitude does not influence the thermal conductivity of nests when climate is accounted for (Table 4.3).

Neither altitude nor climate influences the structural properties (surface area and thickness) of the nests in this study (Table 4.3). Unlike the thermal conductivity model, removing the climate interaction term did not increase the AIC for surface area or thickness models and no relationship was found in the non-phylogenetic analyses. There is considerable variation in the proportion of nests containing materials from the categories of plant, animal, silk, anthropogenic and other derivation for each site (Table 4.6). The indicator species analysis revealed that birds breeding in climates with high temperature and high precipitation use anthropogenic materials more often than birds breeding in other climates. Within the high temperature and high precipitation group two Zosterops lateralis nests contained white cotton, one Z. lateralis nest contained nylon and one Z. lateralis nest contained tissue paper; two Rhipidura leucophrys nests contained woven cloth and one Grallina cyanoleuca nest contained nylon, woven cloth and women’s stocking. There is no significant relationship between the use of the other material types and climate categories. In addition, birds breeding at low and high altitudes do not use significantly different materials.
The structural and thermal properties of avian cup-shaped nests

Table 4.6. Indicator species analysis output for materials found in nests from climate and altitude categories ^

<table>
<thead>
<tr>
<th>material #</th>
<th>observed indicator value</th>
<th>indicator value from randomised groups</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>low T low P</td>
<td>low T high P</td>
<td>high T low P</td>
</tr>
<tr>
<td>n</td>
<td>20</td>
<td>27</td>
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</tr>
<tr>
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<td>25</td>
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</tr>
<tr>
<td>animal</td>
<td>15</td>
<td>7</td>
<td>20</td>
</tr>
<tr>
<td>silk</td>
<td>17</td>
<td>6</td>
<td>10</td>
</tr>
<tr>
<td>anthropogenic</td>
<td>1</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>other materials</td>
<td>8</td>
<td>4</td>
<td>1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>material</th>
<th>low altitude</th>
<th>high altitude</th>
<th>mean</th>
<th>standard deviation</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>n</td>
<td>67</td>
<td>67</td>
<td>50.0</td>
<td>0.71</td>
<td>1.00</td>
</tr>
<tr>
<td>plant</td>
<td>50</td>
<td>50</td>
<td>32.3</td>
<td>2.79</td>
<td>0.47</td>
</tr>
<tr>
<td>animal</td>
<td>33</td>
<td>25</td>
<td>23.4</td>
<td>2.80</td>
<td>1.00</td>
</tr>
<tr>
<td>silk</td>
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<td>21</td>
<td>8.5</td>
<td>2.19</td>
<td>0.43</td>
</tr>
<tr>
<td>anthropogenic</td>
<td>9</td>
<td>3</td>
<td>10.7</td>
<td>2.25</td>
<td>1.00</td>
</tr>
<tr>
<td>other materials</td>
<td>9</td>
<td>7</td>
<td>10.7</td>
<td>2.25</td>
<td>1.00</td>
</tr>
</tbody>
</table>

The indicator species analysis output includes the indicator values and Monte Carlo test of significance of observed maximum indicator values for materials found in nests from the climate categories: Low temperature / Low precipitation, Low temperature / High precipitation, High temperature / Low precipitation and High temperature / High precipitation; as well as two altitude categories: Low altitude and High altitude. Temperature is abbreviated to T and precipitation is abbreviated to P.

* Indicates that there is a significant correlation between the material type used in the nest and the climate or altitude category with the greater observed indicator value (α = 0.05). Significance can be assessed with a Bonferroni correction (i.e. α = 0.05), however this is considered unnecessary in this case (Perneger 1998).

^ The temperature, precipitation and altitude groups are determined from the residuals in the lower third and upper third percentile. Note that the total replicates does not equal the total number of nests in the study as nests from the 2/3 percentile were excluded from the indicator species analysis.

Statistics include the observed indicator values (percent of perfect indication, based on combining relative abundance values and relative frequency) for nests in each climate and altitude category, mean and standard deviation for the indicator value from randomised groups, as well as the P-value. The P-value is the proportion of randomized trials with an indicator value equal to or exceeding the observed indicator value.

Plant materials include sticks, twigs, rootlets, tendrils, bark, grass, runners, sedges, leaves, flowers, seed pods, plant-down, cotton, moss and lichen. Animal derived materials include fur, hair, wool and feathers. Silk products include spider silk, egg sacks and cocoons. Anthropogenic materials include processed cottons, cloth, paper, plastic and nylon. Other materials include faeces, mud and organic material.
(a) Climate

While many studies have found that nest size is related to the local climate conditions, such as temperature and rainfall (Briskie 1995; Collias and Collias 1971; Crossman et al. 2011; Kern 1984; Rohwer and Law 2010; Schaefer 1976), we found no evidence for such a trend. Rowher (2010) raised the possibility that increased nest size is a mal-adaptation to cool climates, as the fitness benefit is modest, and hence may be a product of random forces such as drift. On the other hand, large nests in cold environments have evolved multiple times in phylogenetically independent lineages and therefore it seems likely that climate is the driving factor (Briskie 1995; Kern 1984; Rohwer and Law 2010; Schaefer 1976). While our previous study found that there is variation in nest surface area and thickness within a species when accounting for parent mass (Chapter 2), this variation is not attributable to the mean climate conditions of the nest site according to the present study. However there is variation in nest conductance within a species once accounting for interspecific allometric relationships (Chapter 2) and we show here that this is largely due to climate effects.

While conductance increases with temperature and precipitation, the two factors do not act alone and therefore must be addressed simultaneously. This interaction between temperature and precipitation arises from the more pronounced increase in conductance at higher temperatures for nests built in areas with high rainfall, compared to areas with low rainfall (Figure 4.3). Nest dimensions do not vary with climate; therefore the material conductivity is the only significant factor driving the conductance relationship (Table 4.3). The interaction between temperature and precipitation extends to the conductivity of the nest materials (Figure 4.3), where conductivity has a positive relationship with ambient temperature for nests built in areas with high precipitation, but not in areas with low precipitation. This indicates that not only the ambient temperature, but also the precipitation of the breeding site, influences material selection during the nest construction phase. This is in line with several other studies that have found that nest material composition differs with respect to the prevailing weather at the nest site (Britt and Deeming 2011; Mainwaring and Hartley 2008; Rohwer and Law 2010).

In sites with low ambient temperatures, nest insulation may be important to maintain an appropriate microclimate for offspring and the incubating parent and therefore birds select materials during construction that have a low thermal conductivity, irrespective of the rainfall at the site. Birds breeding in cool climates use well-insulating materials to help prevent heat loss from the nest and this would in turn reduce the amount of energy expended by the incubating parents while on the nest, as well as the energy required to rewarm clutches following incubation recesses.

The significance of the interaction between the two climate variables becomes clear when interpreting the relationship in terms of nests constructed in warm climates but at the two extremes of precipitation. In warmer climates, the material choice differs for birds nesting in areas with high precipitation compared with those in areas of low precipitation. In warm and dry climates, birds use materials with a thermal conductivity that is
The structural and thermal properties of avian cup-shaped nests comparable to those used in cooler climates. This indicates that despite the birds being exposed to warmer temperatures, nest insulation is still important in preventing heat loss from clutches. However, birds breeding in warm and wet climates construct their nests with materials that have a higher thermal conductivity than those in dry climates, as indicated by the thermal conductivity for the nest as a whole, however the thermal conductivity of individual nest materials could not be assessed as desctructive sampling was not permitted on the nest specimens. The warmer temperatures may cause a relaxation in the need for insulation, thereby increasing the slope of the line. Wet materials have a higher thermal conductivity than dry materials and therefore clutches will cool more rapidly in a wet nest (Hilton et al. 2004). Consequently, there is likely to be strong selective pressure to minimise the degree and duration of water penetration into nesting materials and to accelerate the drying out process.

Materials with a high conductivity (such as sticks and grasses, rather than fur and wool) are possibly less absorptive and able to dry out faster following a rain event, to restore the insulating function of the nest. From the analysis of material usage, we can see that birds breeding in warm and wet climates use anthropogenic material (such as cloth and nylon) more frequently than those in all other climate groups, though not necessarily in greater proportions. However, this is only the case if a Bonferroni correction is not applied to the significance threshold (0.05), which would be reduced to 0.01 under a Bonferonni correction, rendering the P-value insignificant. A Bonferroni correction reduces the likelihood of Type I errors but simultaneously increases the rate of Type II errors (Perneger 1998). In addition, Bonferroni corrections are used when all null hypotheses (i.e. no significant effect of climate on material use by birds) are considered to be true simultaneously (for all material categories at once) (Perneger 1998). This is not necessarily the case for this analysis as the use of one category of nesting material does not influence the use of another; hence, the Bonferroni correction was not applied and the material usage differences accepted to be significant. By using anthropogenic materials, the birds may be able to build a structurally sound nest, with a low water-holding capacity. The thermal conductivity of the combination of materials used in the nest is likely to be of greater significance to a nest in wet environments. As birds breeding in warm and wet climates construct nests with highly conductive materials, any water absorbed will also be evaporated rapidly. The significance of these findings is that birds subjected to high levels of rainfall are able to construct a nest that will absorb less water and also dry out faster following a rain event. Birds that build nests in areas with high precipitation may also facilitate the drying out process by using a water-repellent outer layer or constructing the nest layers to maximise drainage (Hilton et al. 2004).

While some species travel great distances for anthropogenic nest materials (Surgey et al. 2012), the use and function of man-made materials in avian nests has rarely been addressed in previous studies. The use of anthropogenic materials (such as plastics, paper, cloth, nylon and threads) by Chinese bulbuls (Pycnonotus sinensis) is directly related to the availability of such materials, which is in turn correlated with urbanisation (Wang et al. 2009). Anthropogenic materials may also be selected by nest builders to supplement non-preferred materials in urban environments; for instance, the brown cacholote (Pseudoseisura lophotes) uses
wire, paper, plastic and scraps of nylon when thorny twigs are scarce (Nores and Nores 1994). Cigarette butts incorporated into nests of house sparrows (Passer domesticus) and house finches (Carpodacus mexicanus) reduces infestation by ectoparasites due to the presence of nicotine (Suárez-Rodríguez et al. 2013), while a signalling function has been dismissed for the use of cigarette butts in song thrush (Turdus philomelos) nest lining (Igic et al. 2009). This material may be used for its insulative properties or simply as convenient construction material (Igic et al. 2009; Suárez-Rodríguez et al. 2013). In Australia, the use of anthropogenic materials for avian nest construction is likely to be a relatively recent change with respect to the long time period over which avian nest construction behaviours would have evolved. In the present study, the earliest record of an anthropogenic material being incorporated in a nest is that of a varied sittella (Daphoenositta chrysoptera), where a small amount of light-weight paper (perhaps tissue) was used in a nest collected near Mount Compass, South Australia, in 1890, only a few years after settlement of the area. This suggests that birds have the potential to adapt nest construction behaviour relatively quickly in line with changes in material availability and warrants further study.

The PC eigenvalues allow us to determine the bioclimatic factors beyond ambient temperature and precipitation that are important in determining the thermal properties of nests. While annual mean temperature and annual precipitation explain the greatest proportion of the variation in the data; the mean monthly temperature range, isothermality (mean monthly temperature range divided by the temperature annual range, multiplied by 100), temperature seasonality and precipitation of the wettest month also contribute to a significant proportion of the variation (Table 4.1). Therefore it is these variables that have the greatest impact on nest design. For example, precipitation of the wettest month explains more of the variation in nest conductance than precipitation of the wettest quarter or the driest month/quarter. This indicates two things: firstly, that the upper extreme is important for nest construction (high precipitation matters more than low precipitation); and secondly, large quantities of rain over short periods are more important than similar quantities spread over a period of several months. It is important to note that 49 of the 201 nests included in the study were collected in regions where precipitation of the wettest month does not coincide with the breeding season of the species. For these birds, the precipitation of the wettest month during the breeding season differs from the precipitation of the wettest month at the annual scale by \(11 \pm 2\) mm, however the breeding season begins the month immediately following the wettest month in almost all cases. When precipitation of the wettest month is narrowed from the annual scale to include only the breeding season for each species and the PC analysis is repeated, the results are indistinguishable from those reported for annual bioclimatic variables.

(b) Altitude

The trend of increasing conductance with higher altitudes is contrary to what one would expect, as previous studies have found that nests constructed at high elevations have more insulation than those at low elevations (Kern and Van Riper 1984). However Kern and Van Riper’s (1984) study was unable to separate the effects
of altitude and temperature, which are intrinsically linked. The methods employed in the present study to determine the effect of altitude on nest structural and thermal properties account for the effect of ambient temperature, which would decrease by 4.3 °C over the altitudinal range of sites in this study (Campbell 1977). Thus, the relationship between altitude and conductance is detached from temperature and must be the result of an independent factor. However the mechanism responsible for the effect of altitude on conductance is unclear. Nest conductance is influenced by the thermal conductivity of the materials used in nest construction, the surface area of the nest, as well as the thickness of the nest. While each of these variables was analysed, none showed a significant relationship with altitude (Table 4.3). The thermal conductivity of the nest materials approached significance in the breeding season model and may be contributing to the significance in nest conductance. With altitude, the resistance of air to convective and evaporative heat transfer increases, but insignificantly in the altitude range of this study (Kandjov 1997). Furthermore, material conductivity will not be affected by altitude. Whether the non-significant association in this study is due to differences in material availability or intentional selection of materials is unclear, as we failed to detect a difference in the types of materials used by birds at different altitudes.

The nest collection sites in the present study spanned an altitudinal gradient up to only 667 m. This may be too small a difference to affect nest conductance, and the altitude range is a small proportion of that used by breeding birds. For example Tibetan ground tits (Pseudopodoces humilis) breed in burrows up to 5,500 m elevation and the Ecuadorian hillstar (Oreotrochilus chimboruzo jamesoni) breeds in cup-shaped nests up to 4,572 m (Corley Smith 1969; Ke and Lu 2009), where ambient temperature may be 30 °C lower than at sea level (Campbell 1977). Consequently, the ambiguous results may be a result of the small range over which nests were collected.

(c) Summary

It is clear that there is a strong relationship between parent mass and nest conductance that drives interspecific variation (Chapter 2), but within a species there is variation that is attributable to site-specific variables (such as climate and altitude) to which the birds are exposed. While this has generally only been qualitatively addressed, the methods employed here provide quantitative evidence that site selection and the local climate influences the construction of nests, through modification of the materials used, and therefore the rate of heat loss from the nest as a whole. This has important implications on the reproductive success of individuals breeding in different climates and may represent an adjustment to breeding in harsh conditions (Huey 1991).

The mean rainfall the nest localities receive ranges from 13 mm to 117 mm over the period of a month and from 154 mm to 1402 mm over the period of a year. Therefore, birds subjected to even greater rainfall extremes (such as those in monsoon areas) are likely to construct nests with a greater thermal conductivity and this warrants investigation. Furthermore, the nests included in the present study are from regions with mean breeding season temperatures ranging from 12 to 24 °C, a moderate range considering the often severe...
conditions in which birds are known to breed (Carey 2002). Studies that can take greater temperature extremes into account would be informative. In light of the ambiguous findings regarding the effect of altitude on nest thermal properties, further studies should also investigate nest conductance and material use across a considerable altitudinal gradient.

Breeding season climate averages over the period from 1950 to 2000 were used in this study – a period that includes considerable variation in the climate and should be reflected in the data. The climate over a single year or breeding season may exhibit less variation and prove more useful than long-term averages in detecting relationships with nest size and thickness. Further research could consider variation in nest morphology with climate at time-scales relative to the specific nests, by measuring a host of microclimate variables through the nest construction phase, to assess direct links between the nesting climate or site selection and the thermal properties of nests. For example, a study on great tits (Parus major) and blue tits (Cyanistes caeruleus) was conducted at the breeding season level directly to assess importance of local climate on nest material use, while first egg date was used for the same species in studies by Mainwaring et al. (2012) and Deeming et al. (2012). The finding that the local climate influences the choice of materials used by birds is significant; however, whether such modifications in nest material use and hence the total nest conductance adequately matches the needs of the parent and offspring is unknown. Therefore, further work could be extrapolated towards the functional significance of such relationships (e.g. if reproductive success is improved through superior nest construction).

Furthermore, since nest construction is influenced by the local climate conditions, rapid changes in the climate could have detrimental effects on the reproductive biology of the avian species studied here, as well as others that construct nests. It is likely to be the most heat-tolerant species that are in danger of further increases in environmental temperature (Somero 2011). There have been observed changes in the initiation date of nesting attempts associated with climate change, though it is unclear how reproductive performance will be affected by the constraints imposed on individuals by availability of nest materials due to climate change effects (Dunn 2006). Species that are flexible in their choice of materials may not be affected to the same degree as other species. In addition, there appear to be ecological and life history differences that affect individual species’ responses to warming temperatures. The interaction between the local climate and avian reproductive performance necessitates further study.
ACKNOWLEDGEMENTS

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CHAPTER 5

THE EFFECT OF WATER SATURATION ON THE RATE OF HEAT LOSS FROM NESTS OF THE TAWNY-CROWNED HONEYEATER (MELIPHAGIDAE: GLICIPHILLA MELANOPS)

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THE EFFECT OF WATER SATURATION ON THE RATE OF HEAT LOSS FROM NESTS OF THE TAWNY-CROWNED HONEYEATER (MELIPHAGIDAE: GLICIPHILLA MELANOPS)

Text in manuscript

HEENAN, C. B. (Candidate)

Lead study design, constructed equipment, collected all data and performed statistical analyses, interpreted data, wrote manuscript and acted as corresponding author

I hereby certify that the statement of contribution is accurate.

Signed Date 27/02/2013

PATON, D. C.

Assisted with collection of nest samples, contributed to planning of article and provided critical evaluation

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis.

Signed Date 27/02/2013
SEYMOUR, R. S.

Provided feedback on study design, supervised development of work, helped in data interpretation and manuscript evaluation

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis.

Signed ______________________ Date 27/02/2013
The structural and thermal properties of avian cup-shaped nests
ABSTRACT

Nests can become wet during a rainfall event and this can influence nest humidity and egg temperature, in turn affecting hatching success. The water content in nests is therefore important; however, the way in which saturation by rain influences the heat loss from the nest and consequently the energetics of the incubating bird is unclear. The dimensions and thermal properties of nests of *G. melanops* were measured in relation to varying levels of water content, and the energetics of the incubating female was assessed through temperature and attendance modelling. The data show that heat loss from a saturated nest is two and a half times greater than for a dry nest. This results in an increase in the energy required by the incubating female to maintain the nest cup at a temperature appropriate for egg development. The energy required for nest-warming on a cold and rainy day may exceed the capability of the female and hence a reproductive event could be compromised.

*Keywords:* bird nest; insulation; conductance; reproductive energetics; precipitation; rain
1. **INTRODUCTION**

The nest microclimate directly affects the thermoregulatory demands of reproducing birds, which will in turn influence the outcome of the breeding attempt and therefore lifetime reproductive success of an individual (Møller 1984; Reid et al. 2000b). The nest microclimate is therefore important but the effect of water in the nest (from rain, dew or absorption from the nest substrate) on the energetics of incubating birds has not been assessed.

Water itself may be used by birds to help maintain nest temperature and humidity. A well-known example is the black-necked stilt (*Himantopus mexicanus*), a bird that regularly dips its ventral feathers in water before returning to the nest to wet the eggs when ambient temperatures are high (Grant 1982). Little grebes (*Tachybaptus ruficollis*) cover their eggs with wet nest material when leaving the nest to forage and it is understood that this behaviour maintains the nest at the optimum temperature and humidity but may pose the problem of limiting water loss from eggs (Ar and Rahn 1980; Carey 2002; Prokop and Trnka 2011). However, birds nesting near water bodies (e.g. saltmarsh sharp-tailed sparrow (*Ammodramus caudacutus*)) can be at risk of clutch fatality when nests are flooded at high tide, though inundation is not always a death sentence provided chicks are able to retreat to higher ground (Gjerdrum et al. 2008).

Of interest is how rain can influence birds, their nests and reproduction. Rain has both positive and negative influences on avian reproduction. It can be beneficial for reproduction in some species, as it is often associated with increased food availability, and hence the onset of peak breeding conditions, as well as increased clutch sizes and more breeding attempts (Aslan and Yavuz 2010; Boulton et al. 2011; Zann et al. 1995). Conversely, rain can be detrimental because it can increase the rate of heat loss from the nest (Hilton et al. 2004), influence egg temperature and subject the clutch to conditions below optimum. Incubating goldcrests (*Regulus regulus*) have difficulty maintaining egg temperature at a suitable level when the nest has been exposed to rain and hence breeding success may be diminished (Haftorn 1978a; b). Rain also increases the humidity of nests, in turn reducing water loss from the eggs and lowering hatching success (Lundy 1969). Rainfall events may increase the number of predators during a breeding attempt and reduce nest survival, as is the case for the Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*) (Boulton et al. 2011). Some birds must abandon the nest in inclement weather to forage and meet their own energy demands and hence put the clutch at risk (Gates and Gysel 1978; Haftorn 1988; Morton et al. 1993); others increase nest attendance to protect the clutch at their own cost (Johnson and Best 1982).

Some species select sheltered roost sites (e.g. bananquits (*Coereba flaveola*)) or nest sites (such as the rocky-overhangs used by the Ecuadorian hillstar (*Oreotrochilus chimboruzo jamesoni*)) that provide protection from inclement weather and the associated high energy costs of incubating in wet nests (Corley Smith 1969; Merola-Zwartjes 1998). Birds such as woodpeckers (Family: Picidae) and Bachman's sparrows (*Aimophila aestivalis*) are able to prevent rain penetrating the nest by orientating cavity entrances downwards or directed away from prevailing storms (Conner 1975; Haggerty 1995).
Variations in nest construction and morphology are consistent with precipitation differences between sites (Collias and Collias 1984; Crossman et al. 2011; Rohwer and Law 2010) (see also Chapter 4). The structure of a nest influences its ability to protect the clutch from rain. The layers of a typical nest consist of the nest lining layer, the structural nest layer and the outer nest layer, as defined by Hansell and Deeming (2002). All nest layers moderate heat loss and at the same time function in contrasting ways to repel / retain water. The size of a nest and the amount of material used in construction influence the quantity of water it will absorb (Rohwer and Law 2010; Slagsvold 1989a). In addition, nest size is related to adult body size (Chapter 2), where small birds build nests with smaller openings that may provide more protection from rain than larger nests (Slagsvold 1989b).

The types and density of materials used in construction may influence the extent of water penetration, capacity for water absorption and the rate of evaporation (Hansell and Deeming 2002; Slagsvold 1989a). As a result, the materials used in nest construction can have a significant effect on the ability of the nest to protect the clutch from heat loss during a rainfall event (Chapter 4). For example, lichen is often cited as a material that is able to prevent water from penetrating into the nest layers (Hansell 1996; Hilton et al. 2004), while moss absorbs more water than other materials (Slagsvold 1989a). For the green-backed firecrown (Sephanoides sephanoides) and the white-sided hillstar (Oreotrochilus leucopleurus) the diversity of mosses and liverworts used in nest construction decreases along a precipitation gradient, though it is unclear whether this is due to concurrent changes in the availability of these materials or if birds are actively selecting fewer materials (Calvelo et al. 2006). While the thermoregulatory stresses during reproduction can be reduced by selecting sites that provide shelter from the elements (including rain and wind, Chapter 6), such savings may be surpassed by the protection afforded by a well-insulated nest (Reid et al. 2000b; Walsberg 1985).

Our earlier study on the thermal properties of dry nests involved conductive heat loss through whole nests across 36 passerine species (Chapter 2). Insulation was evaluated by measuring its inverse, the dry thermal conductance, which is the rate of heat flux (watts) moving across the nest wall per degree of temperature difference between the inside and outside of the nest, based on Newton’s Law of Cooling (Calder III and King 1974; Tracy 1972). Well-insulated nests have a low conductance and vice versa. However the effect of water content on nest insulation remains largely unquantified. Thermal conductivity of the nesting material of mound-building Australian brush turkeys (Alectura lathami) is known to vary by 8-fold, depending on water content, because the latent heat of vaporization causes enhanced heat flux by evaporation and condensation across a thermal gradient (Seymour and Bradford 1992). Thus the thermal consequences of moisture in nests could be substantial. Here we assess the thermal properties of cup-shaped nests under varying water content levels by measuring the “wet thermal conductance” (henceforth referred to as conductance), which includes heat moving by both conduction (flux due to direct contact) and evaporation-condensation. In addition, we determine the energy required by an incubating female to maintain nest temperature to understand the implications of a wet nest on reproductive success.
2. METHODS

(a) Nest collection

Seven tawny-crowned honeyeater (Meliphagidae: Gliciphila melanops Latham, 1802; (Christidis and Boles 2008)) nests were included in the study (nest images in Appendix 13). This species was selected for the study as individuals breed between July and December, when inclement weather in the breeding habitat is inevitable and honeyeater nests are known to become wet (Marchant and Higgins 2001; Pedler 2005).

Gliciphila melanops nest in open heath within canopy low to the ground (Figure A13.3 in Appendix 13) and nests can be easily located when incubating parents are flushed from the nest (Marchant and Higgins 2001). Nests were collected from Ngarkat Conservation Park, South Australia, between September 2009 and December 2010, with specific dates outlined in Table 5.1. All nests were collected under the National Parks and Wildlife Service research permit number K23393. Six of the nests were used to incubate two eggs, while ‘TCH 5’ was constructed but never laid in. Of the nests containing eggs, four nests were successful and fledged chicks, while the outcome of the breeding attempts for the remaining two nests is unknown.

Table 5.1. Collection dates and locations for nests of Gliciphila melanops used to determine the effect of water content on nest thermal properties

<table>
<thead>
<tr>
<th>nest ID</th>
<th>date collected</th>
<th>latitude</th>
<th>longitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>TCH 3</td>
<td>22/09/2009</td>
<td>35° 43' 0.000&quot;</td>
<td>140° 21' *</td>
</tr>
<tr>
<td>TCH 4</td>
<td>22/09/2009</td>
<td>35° 42' 0.000&quot;</td>
<td>140° 21' *</td>
</tr>
<tr>
<td>TCH 5</td>
<td>22/09/2009</td>
<td>35° 43' 15.782&quot;</td>
<td>140° 24' 03.411&quot;</td>
</tr>
<tr>
<td>TCH 12</td>
<td>1/10/2010</td>
<td>35° 52' 22.332&quot;</td>
<td>140° 29' 47.965&quot;</td>
</tr>
<tr>
<td>TCH 16</td>
<td>1/12/2010</td>
<td>35° 37' 57.276&quot;</td>
<td>140° 28' 59.809&quot;</td>
</tr>
<tr>
<td>TCH 17</td>
<td>1/12/2010</td>
<td>35° 38' 07.068&quot;</td>
<td>140° 28' 57.241&quot;</td>
</tr>
<tr>
<td>TCH 18</td>
<td>1/12/2010</td>
<td>35° 38' 00.683&quot;</td>
<td>140° 29' 07.222&quot;</td>
</tr>
</tbody>
</table>

* Latitude and longitude points could not be accurately obtained for TCH 3 and TCH 4 due to equipment malfunction.

Climate information was obtained courtesy of the Australian Government Bureau of Meteorology to understand the typical nesting conditions of the study species, as well as for use in energetic expenditure modelling (§4 Error! Reference source not found.). Climate data were recorded at Keith in South Australia (36.10° S, 143.6° E), approximately 54 km from the nest collection sites and the closest site where meteorology data were available. The rain and temperature conditions that the birds were exposed to in the duration of this study are shown in Figure 5.1. Note that the nests collected in 2009 and 2010 were constructed and collected before the end of the breeding season (Table 5.1). From Figure 5.1, it can be seen that nests constructed early in the 2009 breeding season, prior to collection, were exposed to higher than average July rainfall and slightly warmer temperatures throughout the breeding season. In the 2010 breeding...
season the nests were exposed to high August rains but more moderate temperatures. Note that all 2010 nests were collected prior to the large rainfall events in December.

![Figure 5.1](image.png)

**Figure 5.1.** Climate recorded at Keith, South Australia (36.10 °S, 143.6 °E; approximately 54 km from the nest collection sites) for a – total precipitation per month (mm); b – days of precipitation and c – mean maximum and minimum temperatures (°C) each month through the average *Gliciphila melanops* breeding season. Light grey columns represent the climate for 2009 and dark grey columns 2010. Dashed black lines represent the long-term average precipitation (years 1906 to 2011) and mean temperature (years 1947 to 2011). Data courtesy of the Australian Government, Bureau of Meteorology.

Nests were located by searching road-side patches of contiguous heath vegetation. On discovery, nests were identified with flagging tape (tied to an adjacent bush) and their position recorded with a GPS. Notes on the nesting location and plant host were also recorded. Nests were collected after several weeks, following chick-fledging. Nests were selected for measurement if they were in good condition. Any branches obscuring the opening of the nest were carefully removed with shears. Nest dimensions and thermal properties in relation to water content were measured between December 2010 and May 2011.
(b) **Descriptive properties and dimensions of nests**

Notes on the construction of each nest were made; including condition, attachment, material composition, nest shape and weave density. The physical dimensions of the nests were measured, including the nest thickness (X) and internal / external diameter (d₁ and dₑ) and height (hᵢ and hₑ), to enable calculations of the geometric mean surface area of the nest (Ā), according to Chapter 2.

Nests were weighed on a Scout portable precision balance (model SC6010, Ohaus Corp., Florham Park, New Jersey) when fresh, following initial desiccation, during measurements on wet nests and following final desiccation.

The volume of material in the nest wall (Vₙ) was calculated as half of the volume for a prolate spheroid based on external nest dimensions, minus half of the volume of a prolate spheroid based on internal nest dimensions (Equation 5.1).

\[
Vₙ = \frac{2}{3} \pi \left( hₑ \frac{dₑ²}{4} - hᵢ \frac{dᵢ²}{4} \right)
\]

for an even-walled deep cup nest \((\frac{dᵢ}{2} < hᵢ \text{ and } \frac{dₑ}{2} < hₑ)\)

\[
Vₙ = \frac{2}{3} \pi \left( dₑ \frac{hₑ²}{2} - dᵢ \frac{hᵢ²}{2} \right)
\]

for an even-walled open bowl nest \((\frac{dᵢ}{2} > hᵢ \text{ and } \frac{dₑ}{2} > hₑ)\)

\[
Vₙ = \frac{2}{3} \pi \left( hₑ \frac{dₑ²}{4} - hᵢ \frac{dᵢ²}{4} \right)
\]

for an uneven-walled nest where \(\frac{dimuth}{2} < hₑ \text{ but } \frac{dₑ}{2} > hᵢ\)

\[
Vₙ = \frac{2}{3} \pi \left( dₑ \frac{hₑ²}{2} - hᵢ \frac{dᵢ²}{4} \right)
\]

for an uneven-walled nest where \(\frac{dₑ}{2} > hₑ \text{ but } \frac{dᵢ}{2} < hᵢ\)

where the symbols are:

\[
\begin{align*}
Vₙ &= \text{Nest wall volume (cm}³) \\
hₑ &= \text{External nest height (cm)} \\
dₑ &= \text{External nest diameter (cm)} \\
hᵢ &= \text{Internal nest height (cm)} \\
dᵢ &= \text{Internal nest diameter (cm)}
\end{align*}
\]

The density of the nest was calculated to determine how the nest weave differs for each nest. Nest density \((ρ, \text{g cm}⁻³)\) was calculated as the nest mass \((Mₙ)\) divided by the nest wall volume \((Vₙ, \text{Equation 5.1})\).

Nest dimensions were measured prior to wetting experiments and again following desiccation to determine if nest-wetting affected overall nest shape.
(c) **The effect of water on nest thermal properties**

Nests were saturated in order to assess their thermal properties, which involved submerging each nest in water for 30 s. The nest was then transferred to a humidifier (glass desiccator with a pool of water in the base) for up to 60 min to allow the excess water to drip out and equilibrate the nest to 100 % water content (saturated).

Measurements of the thermal properties of wet *G. melanops* nests were carried out in a 10 °C constant temperature (CT) cabinet that was equipped with open trays of water and wet towels hanging from the rails. This was performed to increase the humidity of the cabinet and prevent drying of the nest during a 30 min cabinet re-cooling period. Air flow around the nest was minimised to eliminate the effect of forced convection on the measurements by placing a large cardboard box around the equipment within the cabinet. The nest was lined with aluminium foil to prevent forced convection through the nest.

As in our previous study (Chapter 2), the opening of the nest was insulated with Styrofoam and cotton padding (Figure 5.2). However, to inhibit the movement of the Styrofoam and padding during measurements, and prevent it from contributing to the measured mass, the nest was measured upside down. While this may affect the flow of heat through the nest, the Styrofoam padding ensures that the majority of the heat flows through the nest wall. Equipment cables were supported horizontally such that they would not influence the mass recorded. The nest, heating equipment and padding was supported by a thin wire mesh stand to allow for free convection around the nest system.

**i. Water content and rate of evaporation**

Prior to the study, fresh nests were placed in a glass desiccator filled with silica gel for 110 h to remove moisture from the nesting material, so that water gain during saturation could be accurately measured (MH$_2$O$_{satd}$). Once the nest properties had been measured for wet nests (§ 2(c)), nests were placed in a desiccator to dry out completely again. After approximately 5 months of desiccation in the chamber, the nests were oven dried on a bed of silica gel at 65 °C for 50 h and then 100 °C for a further 24 h (Broggi and Senar 2009; Prokop and Trnka 2011). The oven-drying process was considered complete when the nests no longer decreased in mass. This was conducted to confirm the dry nest weight (M$_{dry}$).
The structural and thermal properties of avian cup-shaped nests


The nest and equipment rested on a Scout portable precision balance, so that the mass of the nest could be tracked throughout the experiments. The balance was zeroed following placement of the nest on the equipment, such that the mass of evaporated water ($M_{H_2O_{evap}}$) could be determined throughout the wetting treatments. The mass of the water absorbed by the nest when saturated ($M_{H_2O_{satd}}$) was calculated, according to Equation 5.2. The mass of the nest at any particular time during the treatment ($M_{Nt}$) was determined according to Equation 5.3, where the mass of the evaporated water ($M_{H_2O_{evap}}$) was determined directly from the electronic balance. Therefore, the mass of water in the nest at any particular time ($M_{H_2O_t}$) was calculated with Equation 5.4 and the water content ($\%H_2O_t$) as a percentage of the mass of water in a saturated nest ($M_{H_2O_{satd}}$) could thus be determined according to Equation 5.5.

$$M_{H_2O_{satd}} = M_{Nsatd} - M_{Ndry} \quad (5.2)$$

$$M_{Nt} = M_{Nsatd} - M_{H_2O_{evap}} \quad (5.3)$$

$$M_{H_2O_t} = M_{H_2O_{satd}} - M_{H_2O_{evap}} \quad (5.4)$$
\[
\%\text{H}_2\text{O}_t = \frac{\text{MH}_2\text{O}_t}{\text{MH}_2\text{O}_{\text{satd}}} \times 100
\]  
(5.5)

where the symbols are:
- \(\text{MH}_2\text{O}_{\text{satd}}\) = Mass of water in the nest when saturated (g)
- \(\text{MN}_{\text{satd}}\) = Mass of the nest when saturated (g)
- \(\text{MN}_{\text{dry}}\) = Mass of the nest when desiccated (g)
- \(\text{M}_{\text{n}}\) = Mass of the nest at time, \(t\) (g)
- \(\text{MH}_2\text{O}_{\text{evap}}\) = Mass of the evaporated water (g)
- \(\text{MH}_2\text{O}_t\) = Mass of water in the nest at time, \(t\) (g)
- \(\%\text{H}_2\text{O}_t\) = Water content in the nest at time, \(t\) (%)

The rate of evaporation (\(\text{MH}_2\text{O}\)) was calculated according to Equation 5.6. The heat production at 0 % (\(\text{HP}_{0\%}\)) was determined from the linear regression equation of heat production on water content for each nest, as the nest only dried out completely following the oven-drying process.

\[
\dot{\text{MH}}_2\text{O} = \frac{\text{HP}_{x\%} - \text{HP}_{0\%}}{\text{H}_v}
\]  
(5.6)

where the new symbols are:
- \(\dot{\text{MH}}_2\text{O}\) = Rate of evaporation (mg s\(^{-1}\))
- \(\text{HP}_{x\%}\) = Heat production at measured water content, \(x\) (W or J s\(^{-1}\))
- \(\text{HP}_{0\%}\) = Heat production at 0 % water content (W or J s\(^{-1}\))
- \(\text{H}_v\) = Latent heat of vaporization, 2.259 (J mg\(^{-1}\)) (O’Connor 1974)

**ii. Total nest conductance**

Once the nests had been placed in the temperature control cabinet and it had cooled to 10 °C, the total conductance (\(G\), mW °C\(^{-1}\)) of the nests was measured by placing an artificial heat source inside the nest and measuring the heat flow out through the wall (\(\Phi\)), in relation to the temperature difference across the wall (\(\Delta T\)), as described in Chapter 2. As before, the surface of the foil was heated to 40 °C and the heated air within the nest was circulated with a fan mounted below the heat source. Here, the fan was a 20 mm Sunon Maglev green motor fan (1.3 to 1.6 CFM, model GM0501PFV1-8, Kaohsiung, Taiwan).

The total power (\(\Phi\)) required to keep a stable nest temperature was calculated by multiplying the voltage and current from the globe and adding this to the product of voltage and current from the fan, according to Equation 2.2.2 (Chapter 2). Copper-constantan thermocouples were placed against the nest to measure the average temperature gradient across the nest wall, which were calibrated according to Chapter 6.
Using the temperature gradient across the nest wall and the power required to keep a stable nest temperature, the total conductance of the system ($G_{TOT}$, mW °C⁻¹) was calculated using Equation 2.3 (Chapter 2). The total conductance of the system ($G_{TOT}$) is equal to the sum of the nest conductance ($G$) and the Styrofoam lid conductance ($G_{LID}$). The conductance of the lid was measured according to Chapter 2. This was then subtracted from the total conductance of the nest system to obtain a value for nest conductance. Because of the difference in the linear regression elevations, the nest conductance values were standardised by dividing the conductance for each measurement by the conductance at 0 % water content, according to Equation 5.7. The conductance at 0 % water content was calculated from the untransformed linear regression for each nest.

$$G_{ST} = \frac{G_t}{G_{0\%}}$$  \hspace{1cm} (5.7)

where the new symbols are:

- $G_{ST}$ = Standardised nest conductance
- $G_t$ = Nest conductance at time, $t$ (mW °C⁻¹)
- $G_{0\%}$ = Nest conductance at 0 % water content (mW °C⁻¹)

**iii. Surface-specific nest conductance**

The surface-specific conductance ($G_A$, W °C⁻¹ m⁻²) was calculated by dividing the total conductance by the geometric mean surface area of the nest.

**iv. Nest material thermal conductivity**

The thermal conductivity (k, mW °C⁻¹ m⁻¹) of the materials used in each nest was calculated using the surface area and thickness of the nest, according to Equation 2.8 of Chapter 2.

**d) Measurement frequency**

Measurements of the nest mass ($M_N$), relative humidity of the cabinet ($RHE$), voltage (V), current (I) and internal/external temperatures ($T_I$ and $T_E$) were recorded at the following intervals: every 10 min until 1 h, every 15 min until 2 h, every 30 min until 10 h and every 60 min until 30 h. Measurements were then made sporadically thereafter, as long as each new measurement was followed by another two measurements, an hour apart, to confirm a stable trend. Measurements ceased when nest water content no longer decreased at a significant rate, which occurred between 44 and 82.5 h.

**e) Statistical analyses**

Statistical analyses were performed in JMP IN (SAS Institute (2001), version 4.0.4). Comparisons of mean values of nest wall and base thickness, as well as comparisons of nest dimensions before and after wetting were analysed with a Student’s t-test. Data that met the assumptions required for parametric tests,
including normality (Shapiro-Wilk W test) and equal variance were subjected to a multiple regression analysis. Nest identification was included as a random variable in all multiple regression models, as individual points from a single nest are not independent. Analysis of differences between slopes of individual nests was analysed with an Analysis of Covariance (ANCOVA) by including an interaction term for nest identification and the explanatory variable of interest. The slope of the relationship between water content and the thermal properties of the nests was assessed against nest mass, density and surface area and nest thickness. Surface area was not included in the slope analysis for surface-specific conductance, as surface-specific conductance is independent of nest surface area. The surface-specific conductance and thermal conductivity of the nests was assessed against the date they were collected with a linear regression analysis to test if storage time affects the nest thermal properties.

Data that did not meet the assumptions required for parametric tests were transformed, where appropriate. Conductance data were subjected to a square inverse transformation \((1/G^2)\), while the square-root of the conductivity data \((\sqrt{k})\) and rate of evaporation \((\sqrt{M_{H_2O}})\) were analysed. As nest water content remained stable at 100 % for the first 10 to 60 seconds, but thermal properties were yet to stabilise, these erratic values were excluded from linear regression analyses. Consequently, linear regression analyses for conductance, standardised conductance, surface-specific conductance and material conductivity included 411 data points from seven nests. An additional two values for the rate of evaporation from nest TCH 3 were excluded from the analysis as calculations suggested negative evaporation (i.e. an error) due to the erratic nature of the drying process. The relationship between nest water content and time elapsed did not have constant spread of residuals and data transformation failed to improve the fit; however, the residuals were normally distributed \((W = 0.98, P < W = 0.11)\). The relationship was assessed with a third-order polynomial and hence all 428 data points were included to obtain an accurate fit (initial values were not excluded, as for the linear regression). As the data for drying time did not meet all of the assumptions required for polynomial regression, reliance on the statistical outcome should be approached with caution.

The significance value was set at 0.05 for all analyses. Data are expressed as mean ± 95 % confidence interval.
3. RESULTS

(a) Descriptive properties and dimensions of nests

Of the seven nests measured in this study, one was constructed in *Babingtonia behrii*, one in *Banksia marginata*, two in *Banksia ornata* and three in *Allocasuarina pusilla*. All nests are cup-shaped (internal nest depth greater than internal radius) supported at the base, positioned within the vertical fork of the respective species. Six of the nests were classed as having a medium outer weave and a dense inner weave, with the remaining nest ('TCH 18') having a dense weave throughout. Nests were constructed 10 to 40 cm from the base of the plant, where plants were generally 40 to 150 cm tall.

Nests were constructed with bark, grass stems and blades, *Banksia* sp. leaves, grass seed heads, plant down, lichen or moss, spider silk and spider egg sacks. Nests were lined with *Banksia* sp. and other species of plant down, small down feathers, grass stems and blades, grass seed heads and in one nest some small leaves. All material appeared to be relatively dry upon collection. Nests contained between 3 and 8 types of nesting material (4.6 ± 1.1, mean ± 95 % C.I.).

The nest dimensions of *G. melanops* nests in this study are reported in Table 5.2. The nest floor is thicker than the wall of the nest (*t*12 = 3.01, *P* = 0.011, N = 7). Mean nest dimensions were not affected by the nest-wetting treatment (N = 7), including nest volume (*t*12 = 0.63, *P* = 0.54), density (*t*12 = -0.056, *P* = 0.96), mean nest thickness (*t*12 = 0.88, *P* = 0.40) and mean surface area (*t*12 = 0.72, *P* = 0.49). While the external dimensions of diameter (*t*12 = -0.60, *P* = 0.56) and height (*t*12 = 2.15, *P* = 0.053) did not significantly change as a result of the experiment, internal diameter increased (*t*12 = -2.87, *P* = 0.014) and internal height decreased (*t*12 = 3.13, *P* = 0.0088).

Table 5.2. Mean nest dimensions for *Gliciphila melanops*

<table>
<thead>
<tr>
<th>nest parameter</th>
<th>mean ± 95 % C.I.</th>
</tr>
</thead>
<tbody>
<tr>
<td>nest mass (M_n, g)</td>
<td>23.4 ± 7.3</td>
</tr>
<tr>
<td>nest volume (V_n, cm³)</td>
<td>218.7 ± 65.9</td>
</tr>
<tr>
<td>nest density (p, g cm⁻³)</td>
<td>0.11 ± 0.02</td>
</tr>
<tr>
<td>wall thickness (X_w, cm)</td>
<td>1.47 ± 0.39</td>
</tr>
<tr>
<td>floor thickness (X_f, cm)</td>
<td>3.22 ± 1.07</td>
</tr>
<tr>
<td>mean nest thickness (X, cm)</td>
<td>2.35 ± 0.57</td>
</tr>
<tr>
<td>internal surface area (A_i, cm²)</td>
<td>65.96 ± 6.24</td>
</tr>
<tr>
<td>external surface area (A_e, cm²)</td>
<td>174.30 ± 28.64</td>
</tr>
<tr>
<td>mean surface area (Ā, cm²)</td>
<td>106.64 ± 12.15</td>
</tr>
<tr>
<td>internal diameter (d_i, cm)</td>
<td>5.51 ± 0.21</td>
</tr>
<tr>
<td>external diameter (d_e, cm)</td>
<td>8.46 ± 0.86</td>
</tr>
<tr>
<td>internal height (h_i, cm)</td>
<td>4.26 ± 0.37</td>
</tr>
<tr>
<td>external height (h_e, cm)</td>
<td>7.78 ± 0.88</td>
</tr>
</tbody>
</table>

Statistics include the mean ± 95 % C.I. (N = 7).
(b) Water content and rate of evaporation

The nests of *G. melanops* weighed 23.4 ± 7.3 g when fresh and this reduced to 20.6 ± 6.4 g following the oven-drying process. Nests absorbed between 25.9 g and 76.3 g (47.4 ± 14.4 g, mean ± 95 % C.I.) of water prior to the experiment. The quantity of water absorbed by the nest was significantly influenced by the mass of the nest and therefore the quantity of material \( F_{1,5} = 19.88, P = 0.007 \). Nest drying time was not linear, but rather approximated a third-order polynomial (Figure 5.3, Time: \( F_{1,6} = 1164.2, P < 0.0001 \); Time\(^2\): \( F_{1,412} = 398.8, P < 0.0001 \); Time\(^3\): \( F_{1,412} = 164.7, P < 0.0001 \)). There were significant differences in the drying time between nests \( (F_{6,412} = 14.1, P < 0.0001) \), but the polynomial explained 97.1 % of the variation in the data once accounting for nest differences. The time taken for a nest to dry was significantly affected by the mean thickness of the nest \( (F_{1,5} = 7.66, P = 0.040) \).

![Figure 5.3. Relationship between the time elapsed since initial saturation (t, h) and water content (%H\(_2\)O) for cup-shaped nests of *Gliciphila melanops*. Each point represents the water content at a given time for the seven nests. The third-order polynomial fit for the data is also represented for the combined data (black line), based on predicted values but ID effects not included.](image)

Upon termination of the measurements the nests averaged 7.1 ± 1.9 % water content. Drying time was slow, as the relative humidity in the cabinet was maintained at a high level; averaging 90.3 ± 0.58 %.

There was an increase in the rate of evaporation with water content \( (F_{1,6} = 552.3, P < 0.0001) \); however, the rate of evaporation differed between nests \( (F_{6,395} = 11.5, P < 0.0001) \).

(c) Nest thermal properties

There is a significant effect of water content on effective nest conductance (Figure 5.4, \( F_{1,6} = 49.6, P = 0.0004 \)), as well as a significant difference between nests \( (F_{6,397} = 81.6, P < 0.0001) \). As each nest responded
to water content in a different way, it is impossible to form a general prediction equation for water content and conductance. However, all of the individual regressions were significant.

Because of the difference in the linear regression elevations the nest conductance values were standardised (Equation 5.7). With standardisation of conductance values (rendering the values unitless), water increases heat loss from the nest by $2.65 \pm 0.17$ ($F_{1,6} = 276.4, P < 0.0001$). While there is a significant difference in the slope of the relationships between standardised conductance and water content for individual nests ($F_{6,397} = 30.0, P < 0.0001$), the linear regression explained 95.9% of the variation in the data.

![Figure 5.4. Relationship between the water content (%H$_2$O) and conductance (G) for cup-shaped nests of Gliciphila melanops. Individual points represent the nest conductance at a given water content for the seven nests. The linear regression fit for the combined data is represented by a black line (± 95% C.I., grey lines), based on mean values for individual regressions but ID effects not included. The elevation of values has not been standardised.](image)

Surface-specific nest conductance increases with greater water content in the nest ($F_{1,6} = 47.1, P = 0.0005$). There is a significant difference in the slope of the relationships between surface-specific nest conductance and water content between nests ($F_{6,397} = 181.5, P < 0.0001$); however, the linear regression explained 97.6% of the variation in the data.

The thermal conductivity of the materials used in nest construction also increases with greater water content in the nest (Figure 5.5, $F_{1,6} = 100.4, P < 0.0001$) where the regression explained 98.3% of the variation in the data; and again there are differences between nests ($F_{6,397} = 88.7, P < 0.0001$). Nests ‘TCH 3’, ‘TCH 12’ and ‘TCH 17’ have a similar material conductivity, which is higher than that of ‘TCH 4’, ‘TCH 5’, ‘TCH 16’ and ‘TCH 18’.
Figure 5.5. Relationship between the water content (%H$_2$O) and material conductivity (k, mW °C$^{-1}$ m$^{-1}$) for cup-shaped nests of *Gliciphila melanops*. Individual points represent the material conductivity at a given water content for the seven nests. The linear regression fit for the combined data is represented by a black line (± 95% C.I., grey lines), based on mean values for individual regressions but ID effects not included. The elevation of values has not been standardised.

The slope of the relationship between water content and conductance for an individual nest is not related to the mass, density, nest thickness or mean surface area of the nests ($F_{4,2} = 2.45, P = 0.31$). Nor is the slope of the relationship between water content and surface-specific conductance related to mass, density or thickness ($F_{3,3} = 2.99, P = 0.20$). However, the slope of the relationship between water content and material conductivity for an individual nest is related to the mass, density, nest thickness and surface area of the nests ($F_{4,2} = 47.3, P = 0.021$). Nests with a high density, thick wall or large surface area have a greater slope than those with low values and nests with a low mass have a greater slope.

The surface-specific conductance and thermal conductivity of the nests was assessed against the date they were collected to test if storage time influenced the results, where nests TCH 3, 4 and 5 were collected on day 1, TCH 12 on day 369 and TCH 16, 17 and 18 on day 429. There was no significant difference in the surface-specific conductance ($F_{1,6} = 1.65, P = 0.26, N = 7$) or thermal conductivity ($F_{1,6} = 0.021, P = 0.89, N = 7$) across collection dates.
4. ENERGY EXPENDITURE MODEL

In order to understand the impact that nest water content has on the incubating bird, we used the conductance from dry and wet nests to model the energetics of the female. This included calculations of the rate of energy expenditure (EE, J s\(^{-1}\)), the daily energy expenditure (DEE, KJ d\(^{-1}\)) and nesting energy expenditure (NEE, KJ).

Nesting energy expenditure (NEE) was calculated as the total energy required for the incubation and brooding periods combined (a 27 d breeding attempt), taking place between July and December (Marchant and Higgins 2001). Values obtained represent the energy required by the incubating female to maintain the temperature of the nest during attendance, but does not include energy expended while off the nest (foraging and territorial displays) or for self-maintenance (basal metabolism). The heat lost from a nest depends on the thermal conductance as well as the temperature difference across the nest wall (Calder III and King 1974; Tracy 1972), thus these factors formed the basis of the model, as outlined below:

(a) Model components and assumptions

i. Nest temperature

*Gliciphila melanops* nest air temperature (\(T_N\)) is maintained between 15 and 30 °C in winter when the parent is in attendance (Pedler 2005), thus the median of these two values (22.5 °C) was used to represent nest temperature. Nest temperature rapidly equilibrates with ambient temperature (\(T_A\)) when the incubating parent takes leave to forage (Pedler 2005) and this was assumed to take approximately 30 s. Nest temperature increases rapidly on resumption of incubation and, likewise, this was assumed to take approximately 30 s. When ambient temperature exceeds 22.5 °C in summer, nest temperature is assumed to match ambient temperature, with no active cooling by the parent.

ii. Ambient temperature and precipitation

Diurnal variation in ambient temperature was calculated according to Ephrath *et al.* (1996), incorporating mean minimum and maximum temperature values (Figure 5.1.c) obtained from the Australian Government, Bureau of Meteorology (includes the years 1947 to 2011). Calculation of diurnal cycles of ambient temperature consisted of a sinusoidal expression during the daytime and an exponential expression during the night (Ephrath *et al.* 1996). In line with suggestions of Ephrath *et al.* (1996) the effect of buoyancy (\(T_B\)) was kept constant at 15 °C, the time coefficient (\(\tau\)) was set as 4 h and the delay in maximum temperature with respect to the time of maximum solar height (\(P\)) was set as 1 h. The time at which the maximum solar height occurs (LSH, h), as well as sunrise and sunset times for the months in question (July and December), were obtained from www.timeanddate.com (created by Steffen Thorsen) using values for the middle day of each month in 2010 with the location set to Adelaide (approximately 187 km from the nest collection sites). These times influenced the model through the values of day length (DL, h), sunset time (\(ts\), h) and night length (\(\eta\), h).
iii. **Recess length and frequency**

The difference between nest temperature and ambient temperature is dependent on the attendance of the incubating parent, and hence recess length and duration was accounted for in the model. Data on nest attendance by *G. melanops* was obtained from Pedler (2005). Incubation recesses take place between 0600 and 1700 h (Pedler 2005). Recess length during dry days varies from 3.5 min between 0600 and 0700 h to 6.1 min from 1300 to 1400 h. Recess length increases steadily between these two times in a linear fashion and declines steadily thereafter. Recesses during periods of rain were assumed to be only 62.8% of the duration of recesses on dry days (as is the case for *Phylidonyris albifrons*); hence recesses on days of rain vary from 2.2 to 3.8 min in duration. The modified recess length during rain was applied for a 24 h period, irrespective of the duration of a rain event. *Gliciphila melanops* make 3.9 trips off the nest between 0600 and 0700 h and up to 5.7 trips between 0700 and 0800 h. However, since the number of trips off the nest does not differ with time of day the mean of these two values was used (4.8 trips per h).

iv. **Nest conductance**

The conductance of a dry nest (G_{0%}) was used on dry days and the conductance from a saturated nest (G_{100%}) was used on days of rain. The G_{100%} rate of heat loss from a nest on rainy days was applied for a 24 h period only, despite reports that nests take several days to dry (Pedler 2005).

v. **Determination of heat loss and energy expenditure**

The rate of heat loss from the nest in a 10 s period (Φ, W) was calculated as the conductance from the nest (G_{x%}) multiplied by the temperature difference across the nest wall (ΔT = T_N – T_A). The rate of energy expenditure (EE, W) of the incubating female was assessed from attendance patterns. The rate of heat loss in each interval was multiplied by 10 s to obtain the Joules of energy expended to incubate (1 W = 1 J s⁻¹), the sum of which gave the daily energy expenditure (DEE). This was determined for a dry or wet day at the two temperature extremes of the breeding season: July and December. The nesting energy expenditure (NEE) was determined by combining the DEE under dry and wet conditions for a 27 d period with the ratio of dry: precipitation days expected in July and December. The mean number of days of precipitation was obtained from the Australian Government Bureau of Meteorology for the nearest weather station (Keith, South Australia), with mean data including the years 1800 to 2011 (Figure 5.1.b).
(b) Model outcomes

From the energy expenditure model we find that the rate of energy expenditure (EE, Figure 5.6) varies with time of day, according to incubation patterns and ambient temperature. The daily energy expended to maintain nest temperature (DEE, Figure 5.7) in the warm months of December ranges from 12 KJ d\(^{-1}\) on a dry day to 33 KJ d\(^{-1}\) when it rains. However the cool ambient temperature in July results in a DEE of 36 KJ d\(^{-1}\) on a dry day, up to 103 KJ d\(^{-1}\) when rain occurs. This equates to a NEE of between 447 to 1873 KJ, depending on when a reproductive event occurs within the breeding season.

(c) Model accuracy and improvements

The accuracy of the model could be improved and adjusted for various scenarios; however, it provides reasonable values of EE, DEE and NEE for the conditions outlined in the methodology. Firstly, NEE may be greater than that reported here as the increased rate of heat loss on a wet day was only applied for a 24 h period even though nests can take several days to dry (Pedler 2005); and the model did not account for changes in the rate of conductance during nest drying, rather calculations were based on G\(_{100\%}\) or G\(_{0\%}\) only. The model demonstrates the implications of a rain event resulting in a nest that is saturated. For the nests we studied, between 26 and 76 g of water was required to saturate a nest. Given the mean diameter of a *G. melanops* nest, these values would correspond to a rainfall event of between 4.6 to 13.5 mm. While rainfall between July and December at the nearest weather station is typically of the order of 3.6 to 4.3 mm d\(^{-1}\), large rainfall events of up to 56 mm d\(^{-1}\) have been recorded (Bureau of Meteorology). Therefore it is not unreasonable to suggest a nest could become saturated. However, nests are constructed in bushes, which may provide some protection and nest attendance by the parent may reduce nest-wetting further. Minor rain events could result in values for EE that are less than those reported here and females may have behavioural adaptations to reduce nest wetting (beyond increased nest attendance) that were not accounted for in the model. In addition, values for DEE may be intermediate to those of dry and wet days (*i.e.* the extremes) when a rain event occurs in conditions conducive to rapid evaporation of water from the nest. Nest egg temperature is maintained about the average nest air temperature, with a maximum of 42.2 °C (Pedler 2005); thus the nest air temperatures used in the model here may underestimate the full energetic cost of incubation but provide a fair approximation of mean temperatures that the incubating bird is exposed to. As nestlings grow and become homeothermic, their metabolic heat production may help to offset the energy required by the parent and this would also depend on the number of hatchlings (Cooper *et al.* 2005; Turner 2002). Furthermore, the energetic cost of incubation calculated in the present study does not include the energy expended on self-maintenance, foraging or territorial display; nor does it take the heat production of the hatchlings into account.
Figure 5.6. Daily fluctuation in energy expenditure (EE, J s$^{-1}$) on a day in July without rain (grey solid line) or with rain (grey dotted line) and in December without rain (black solid line) or with rain (black dotted line). Vertical lines indicate incubation recesses.

Figure 5.7. Modelled daily energy expenditure (DEE) in KJ d$^{-1}$ and Kcal d$^{-1}$ on a day without rain (open points) or with rain (black points) in July (circles) and December (squares). Values obtained from modelling assume that the nest is either dry or saturated, where nests require 26 to 76 g of water to become saturated.
5. DISCUSSION

The results of this study show that water penetration into the nesting material increases conductance of G. melanops nests by up to two and a half times the rate seen in a dry nest – a consequence of the increased material conductivity for a wet nest. As a result, additional energy is required by the incubating parent to keep clutches warm when nests become wet. These findings agree with previous studies where materials experimentally placed in nests and artificially-constructed nests were reported to have a higher thermal conductivity when wet (Hilton et al. 2004; Reid et al. 2002a). The higher nest conductance for wet nests implies that there should be strong selective pressure for birds to reduce the degree and duration of nest-wetting and to facilitate the nest drying process (Hilton et al. 2004). This can be achieved by selecting an appropriate nest site, using well-insulated materials or selecting materials for their water-repellent nature. If a nest becomes wet, the mean incubation time could be maintained if clutches are rewarmed promptly.

The conductance, thermal conductivity and the rate of evaporation from nests at different levels of water content all show significant variation between nests. As a result, general equations cannot be produced and used for predictive purposes with any accuracy. In addition, there appears to be no consistency in the cause of the differences – variation in the rate of conductance and evaporation is not related to nest properties; though conductivity is related to nest size. Previous findings on a range of passerine species show that smaller nests dry out faster than larger nests, as they absorb less water and they have a higher surface:volume ratio (Slagsvold 1989a; b). This suggests that birds breeding in wet environments may benefit from constructing smaller nests than dry-habitat-dwelling counterparts. In fact, nests of yellow warblers (Dendroica petechia) breeding in regions with high rainfall are smaller, absorb less water and are less insulated than those of drier habitats (Rohwer and Law 2010). Contrary to logic, a well-ventilated nest might provide better insulation than a less ventilated one, as water will be evaporated more effectively (Hansell and Deeming 2002; Chapter 4 and 6). In addition, nest material choice may reflect the breeding climate (Chapter 4) or a particular nest site (Slagsvold 1989a; b), as less absorptive materials are suited to habitats with high rainfall or exposed nest sites. As G. melanops nests are regularly exposed to rainfall, the use of poorly absorptive materials on the outer layer (such as lichen and grass stems) may help to prevent water penetration, while the soft and absorptive materials were largely used for nest lining only.

There are a number of factors that need to be considered when interpreting the consequence of a wet nest for the energetic costs to birds. Is the energy required for incubation within the metabolic range expected for the species? If not, additional energy will need to be obtained, but how much is required and is the additional energy available in terms of food resources? If so, is an individual capable of obtaining the required quantity of food and processing the energy? Here, we address these matters in turn.

First, the energy required to maintain the temperature of a dry nest for a day (§ 4) is within the calculated daily cost of living for an 18 g bird, between 65 to 83 KJ d⁻¹ (MacMillen and Carpenter 1977; Nagy 2005; Nagy et al. 1999; Tatner and Bryant 1993; Weathers et al. 1996). The DEE for a wet nest in the warm month of
December is also within the calculated range, but the DEE of a wet nest in July far exceeds the metabolic cost of living for a bird this size (§ 4). This would result in an energy deficit that would force the incubating female to take extended incubation recesses to forage and replenish her own energy reserves or sacrifice body fat reserves with the risk of reduced reproductive success (Erikstad and Tveraa 1995; Hilton et al. 2004).

Based on a metabolisable energy factor of 16 KJ g\(^{-1}\) dry matter (Nagy et al. 1999) a female G. melanops incubating on a rainy day in July would need to consume 6.4 g of dry matter per day, just to meet the demands of maintaining nest temperature. This is notably higher than the 0.8 g required on a dry December day and the 4.7 g required in total (for all activities) per day in non-incubating individuals (Nagy et al. 1999). However, floral nectar is often abundant within Ngarkat Conservation Park in winter, with inflorescences producing nectar crops with 1 g (dry mass) of sugar (reviewed by Paton 1996). With large numbers of flowering inflorescences (approximately 1,000 per hectare), G. melanops should have little difficulty accessing the necessary resources to meet increased costs in winter at this site.

The question of foraging ability, however, is not clear-cut. The DEE for a dry day would mean that the incubating female would need to acquire between 0.05 and 0.14 KJ min\(^{-1}\) while off the nest, which increases to 0.64 KJ min\(^{-1}\) on a cold and rainy day. Similar sized honeyeaters can harvest up to 0.5 g min\(^{-1}\) of sucrose from floral resources, equating to 9 KJ min\(^{-1}\); well above that required in inclement weather (Mitchell and Paton 1990). However, digestive physiology is apparently the major limiting factor in the energy uptake of nectarivorous birds, resulting in long periods between feeding events (Diamond et al. 1986). This may limit the foraging bout frequency of G. melanops such that the DEE may not be compensated by the appropriate intake of energy (Diamond et al. 1986). In addition, the calculated foraging ability of a bird this size is only 0.23 KJ min\(^{-1}\), based on allometric equations of Bryant and Westerterp (1980; cited by Tatner and Bryant 1993), which is only 36% of the foraging rate required on a cold and rainy day.

For G. melanops it is possible that a female would be capable of increasing her energy intake to cope with the increased cost of nest-warming on cold and rainy days. However, if floral resources in other locations are poor and a bird is unable to meet such energy demands, it may abandon the nest altogether (Gates and Gysel 1978; Haftorn 1988; Hilton et al. 2004; Morton et al. 1993). While this study is concerned with G. melanops, white-fronted honeyeaters (Phylidonyris albifrons) have been observed abandoning nests in the same habitat during inclement weather (Pedler 2005). It is possible, therefore, that P. albifrons are subjected to pressures of increased heat loss from wet nests.

In summary, the present study hypothesises the importance of nest design and construction for the thermal properties of nests – small variations in nest design can have significant impacts on the insulative value of a nest. Furthermore, the effect of water content on nest conductance, and the consequence of this for the energetics of the incubating parent, reinforces the view that nest site selection is crucial for birds.
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CHAPTER 6

THE EFFECT OF WIND ON THE RATE OF HEAT LOSS
FROM AVIAN CUP-SHAPED NESTS

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THE EFFECT OF WIND ON THE RATE OF HEAT LOSS FROM AVIAN CUP-SHAPED NESTS

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HEenan, C. B. (Candidate)

Lead study design, constructed equipment, collected all data and performed statistical analyses, interpreted data, wrote manuscript and acted as corresponding author

I hereby certify that the statement of contribution is accurate.

Signed Date 27/02/2013

SEYMOUR, R. S.

Provided feedback on study design, supervised development of work, helped in data interpretation and manuscript evaluation

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis.

Signed Date 27/02/2013
ABSTRACT

Forced convection can significantly influence the heat loss from birds and their offspring but effects may be reduced by using sheltered micro-sites such as cavities or constructing nests. The structural and thermal properties of the nests of two species, the spiny-cheeked honeyeater (Acanthagenys rufogularis) and yellow-throated miner (Manorina flavigula), were measured in relation to three wind speeds. Nest dimensions differ between the two species, despite the similar body mass of the incubating adults; however, nest conductance is comparable. As wind speed increases, so does the rate of heat loss from the nests of both species, and further still during incubation recesses. The significance of forced convection through the nest is a near-doubling in heat production required by the parent, even when incubating at relatively low wind speeds. This provides confirmation that selecting a sheltered nest site is important for avian reproductive success.

Keywords: bird nest; insulation; thermal conductance; reproductive energetics; wind; convection; Acanthagenys rufogularis; Manorina flavigula
1. INTRODUCTION

The microclimate properties that are critical to adult birds include wind, radiation, air temperature and humidity, and these directly affect the thermoregulatory demands with which a bird must cope (Walsberg 1985; 1986; Webb and King 1983a). Wind, which is forced convection (henceforth referred to as convection), is often considered to be more important for heat loss than conduction and evaporation (Southwick and Gates 1975; Webb and King 1983a; b). The energetics of a variety of avian species exposed to wind has been explored using doubly-labelled water, time energy budgets and respirometry techniques in wind tunnels (Bakken 1990; Buttemer et al. 1986; Goldstein 1983; Wolf and Walsberg 1996). Webster and Weathers (1988) found that heat production in verdins (Auriparus flaviceps) can rise by nearly 30 % when wind speed increases from 1.8 to 10.8 km h⁻¹, whereas Tracy (1972) argued that heat loss may vary by up to 100 % for some individuals under different wind speed conditions.

Energy demands of thermostasis may be greatest when roosting or during reproduction (Hilton et al. 2004; Reid et al. 2000b; Walsberg 1985). Therefore, it is expected that there would be strong selective pressure for birds to minimise thermoregulatory stresses to the individual and offspring. Reducing air movement over birds moderates their convective heat loss and this can be achieved by using sheltered microsites such as cavities and domed nests (Hilton et al. 2004; With and Webb 1993). Of primary interest here is how convection can influence heat loss from the nest of reproducing individuals, as the rate of heat loss can influence the outcome of a breeding attempt and consequently lifetime reproductive success (D’Alba et al. 2009; Reid et al. 2000b). Reproduction in birds via oviparity necessitates developmental conditions to be modulated externally, provided by the reproducing birds through modification of their own metabolism (Reid et al. 2002a; Webb 1993). While the energetics of birds under different wind regimes has only been investigated in non-incubating individuals, it is expected that wind would also increase the rate of heat loss for reproducing birds. Appropriate nest site selection can reduce heat loss through convection, however, such savings may be small compared to those produced by the addition of an insulating nest (Kim and Monaghan 2005; Walsberg 1985). Consequently, nests might be expected to be shaped by selection over evolutionary time to approach functional optima and reflect the microclimate conditions to which birds are exposed, including convection (Reid et al. 2002a).

Nest structure and placement has been reported widely in the literature in recent years, as the importance of such structures has become more apparent (reviewed by Hansell 2000). Methods for determining the effect of wind on heat loss from the nest largely consist of either heat loss modelling (Webb and King 1983b) or nest orientation correlations (Austin 1974; Facemire et al. 1990; Ricklefs and Hainsworth 1969). Nest orientation is expected to change the nest microenvironment due to the effects of wind and thus sparrow (Ammodramus savannarum and Aimophila aestivalis) and meadowlark (Stunella magna) nests are primarily oriented away from prevailing winds (Haggerty 1995; Long et al. 2009). Appropriate nest site selection by orange-tufted sunbirds (Nectarinia osea) reduces the exposure of nestlings to wind by up to five-fold compared to other
available nest sites (Sidis et al. 1994). Woodpecker (Picidae) nest orientations provide shelter from the wind and rain (Conner 1975), while nest orientation for a variety of avian species is correlated with modified nest temperatures (Austin 1976; Hadley 1969; Inouye et al. 1981; Orr 1970; Reller 1972; Tieleman et al. 2008).

There may be differences in nest structure that contribute to reductions in convective heat loss (Calder III 1973; Kern 1984). Palmgren and Palmgren (1939) were the first to assess the influence of convection on nests thermal properties and found that heat loss increases in turbulent conditions by 44 % in the common rosefinch (Carpodactus erythrinus) to 91 % in the chaffinch (Fringilla coelebs). Kern (1984) found that elevated nests of the white-crowned sparrow (Zonotrichia leucophrys) were better insulated than ground nests and proposed that the increased insulation may offset the increased convective cooling to which they are exposed. Pectoral sandpiper (Calidris melanotos) nest structure is an example of how a compromise can be found between multiple unfavourable variables (Reid et al. 2002a). While deep nest scrapes would reduce convective heat loss from eggs, the eggs would in turn experience cooler ground temperatures. Scrapes are therefore constructed such that the eggs are positioned at an optimal depth for minimising forced convection as well as the rate of heat loss to the substrate. The choice of materials used for nest construction may also be partly driven by the need to reduce convective heat loss. For example, mosses are woven into the outer layer of giant conebill (Oreomanes fraseri) nests and this fills air spaces to improve the nest structure and reduce penetration by wind currents (Cahill et al. 2008).

There is a paucity in the knowledge regarding the effect of wind on the insulative properties of exposed nests and how wind may influence the heat loss from the clutch, and in turn, the energetics of the incubating parent. Our earlier study on the thermal properties of nests involved conductive heat loss through whole nests in essentially still air (Chapter 2). The results from 36 species of birds with body masses ranging from 8 to 360 g demonstrated that cup-shaped nests were constructed primarily for support rather than insulation. Insulation was evaluated by measuring its inverse, thermal conductance. This is the rate of heat flux (watts) moving across the nest wall, per degree of temperature difference between the inside and outside of the nest, based on Newton’s Law of Cooling (Calder III and King 1974; Tracy 1972). Well-insulated nests have a low conductance and vice versa. The present study is designed to investigate the role of convective heat transfer through cup-shaped nests of two species with similar body masses, but of different nest construction, thin versus thick walls. Here, the thermal conductance is again measured, but within a wind-tunnel. In the present study, the ‘effective’ thermal conductance and ‘effective’ material conductivity is measured (henceforth referred to as conductance and conductivity, respectively), as both thermal properties in this context include the effects of conductive and convective heat flow. If nest wall structure is important in preventing heat loss via convection, then we expect that there would be differences in nest conductance that are related to the thickness of the nest wall or the conductivity of the nest material in windy conditions. Furthermore, we compare the heat loss from nests where the opening is sealed with a Styrofoam lid to those without a lid. This was conducted to reflect differences in heat loss from attended and unattended nests.
2. METHODS

Nests were borrowed from the South Australian Museum ornithology collection and were selected for measurement if they were in a good condition and had no branches obscuring the opening of the nest. Nests that were damaged were excluded from analyses. Nests were collected between 1976 and 1992, with collection information missing for five out of the 15 nests. For those where collection date was known, there was no significant difference in the year the nest was collected when comparing the two species ($X^2 = 1.86, \text{DF} = 1, P = 0.17$). All nests were from museum collections, stored in a similar way, which should have reduced any bias resulting from degradation and storage. Notes on the construction of each nest were made; including condition, attachment, materials, nest shape and weave density.

(a) Study species

A total of eight spiny-cheeked honeyeater (Acanthagenys rufogularis Gould, 1838) and seven yellow-throated miner (Manorina flavigula Gould, 1840) nests were measured. The two species were selected as they both have similar parent masses (50 g and 55 g, respectively) but different nest structure (Figure 6.1). While M. flavigula nests have larger dimensions, A. rufogularis constructs a nest with a denser wall compared to M. flavigula. In addition, the nest dimensions for A. rufogularis are lower than what would be predicted for an incubating parent of this size, while nests of M. flavigula are larger than predicted (Chapter 2).

The two species have largely overlapping geographical distributions throughout Australia and breed in similar habitats, usually open woodland or shrubland in arid and semi-arid zones (Marchant and Higgins 2001). Both species are capable of breeding year-round but most of the breeding occurs between June/July through to March. While A. rufogularis tends to construct their nests suspended in the top or outer edge of plant canopies (1 to 3 m above ground), M. flavigula nests are regularly found in dense canopy close to the trunk of the plant (4 to 5 m above ground).

(b) Nest dimensions

The physical dimensions of the nests were measured with callipers and a micrometer to the nearest millimetre, including the nest thickness ($X$, Figure 2.1, Chapter 2), internal and external diameter ($d$) and height ($h$). Those nests without supporting structures attached were weighed on a Mettler digital analytical balance (model AE163, Zürich, Switzerland). The internal and external nest surface area ($A$) was approximated using the equation for half of a prolate spheroid (Equation 2.1, Chapter 2), using values for internal and external diameters and heights. The average surface area ($\bar{A}$) was calculated as the geometric mean of the internal and external surface area. Nest volume was calculated as half of the volume for a prolate spheroid based on external dimensions, minus half of the volume of a prolate spheroid based on internal dimensions (Equation 5.1, Chapter 5). The density of the nest was calculated for each species. Nest density ($\rho$, g cm$^{-3}$) was calculated as the nest mass ($M_N$) divided by the nest volume ($V_N$).
Figure 6.1. A nest of *Acanthagenys rufogularis* and *Manorina flavigula*. The nest of *A. rufogularis* (left) is smaller and has thinner nest walls than *M. flavigula* (right) but a greater nest wall density.

(c) **Wind tunnel**

A wind tunnel was constructed to enable wind speed surrounding the nest to be controlled and measured (Figure 6.2). The wind tunnel consisted of a long cardboard box (35.5 cm width; 36.5 height; 139 cm length), divided into three main chambers: the settling chamber, the test section and the diffuser. The settling chamber consisted of a filter made from a double-layer fly-wire mesh screen. This was used to prevent large airborne particles from entering the chamber and causing undesirable turbulence in the flow (Mehta and Bradshaw 1979; Pennycuick *et al.* 1997). A 4 cm wide honeycomb screen made from plastic straws (1 cm in diameter), glued together in alternating layers, was placed towards the end of the settling chamber. The honeycomb screen acts to straighten the flow, reducing turbulence, as well as eliminating the cross-flow component (Bradshaw and Pankhurst 1964; Mehta and Bradshaw 1979). A second honeycomb screen was placed at the beginning of the diffuser.
The structural and thermal properties of avian cup-shaped nests

Figure 6.2. The wind tunnel used to alter experimental wind conditions. Sections include the settling chamber, test section and diffuser. Wind flows in direction of arrows. 1. Wind tunnel air inlet; 2. Wind filter; 3. Inlet honeycomb screen; 4. Outlet honeycomb screen; 5. Axial fan; 6. Test section access door; 7. Mesh base; 8. Nest. Not drawn to scale.

The test section was situated between the two honeycomb screens, with access provided by an outward-opening door. The door was sealed closed during the experiments with metal corner brackets clipped in place with Velcro.

A duct mounted axial fan (ø150 mm, model MT132, Fantech, Dandenong, Australia) was placed at the outlet end to suck wind through the tunnel. The speed of the fan was manipulated with a variable voltage transformer (model Voltac SB-5 IKVA, Yokoyama Electric Co. Ltd., Japan) by varying the voltage from 0 to 240 V. The maximum wind speed achievable was 3.4 km h⁻¹.

Wind speed was measured with a hot-wire anemometer (model AM-4204HA, Lutron Electronic, Coopersburg, USA) at radial interval positions through the centre of the test section when the fan was at its maximal speed. This was to ensure that wind speed was relatively consistent at all points in the chamber and that differences in measurements would not result from slight changes in nest placement. Wind speed varied slightly throughout the chamber test section, ranging from 2.7 to 3.1 km h⁻¹ (± 7 %) during the test runs. The anemometer was also turned sideways and moved throughout the chamber to confirm that movement of air through the tunnel was laminar and did not consist of turbulent flow or produce a cross-flow component.

The nest was placed in the centre of the test-section on a 4 cm high wire-mesh strip to allow for free airflow around it. The cross-sectional area of the wind tunnel blocked by the nest ranged from to 2 to 9 % (mean 5 ± 1 %). The anemometer was suspended above the lid of the nest to measure the wind-speed, which was recorded for each nest and treatment. Nest measurements were repeated at three wind speeds: 0, 0.8 and 3.1 km h⁻¹. These speeds are described in this paper as 'still', 'calm' and 'light air', respectively, according to Beaufort scale definitions in Allaby (2002).

We tried to maintain a consistent wind speed by setting the variable voltage regulator to the same output each time, the average speed detected (Table 6.1) surrounding the open nests differed for each species for the light air treatment ($X^2 = 5.53$, DF = 1, $P = 0.019$) but not within the calm ($X^2 = 0.13$, DF = 1, $P = 0.72$) treatment. There was no significant difference in the wind speed detected around sealed nests for each
species within both the calm ($X^2 = 1.64$, DF = 1, $P = 0.20$) and the light air treatment ($X^2 = 3.16$, DF = 1, $P = 0.075$). Wind speed in the still air treatments was consistently 0 km h$^{-1}$.

**Table 6.1. Comparison of wind speeds between open and sealed treatments for nests of *Acanthagenys rufogularis* and *Manorina flavigula***

<table>
<thead>
<tr>
<th>species</th>
<th>treatment</th>
<th>wind speed (km h$^{-1}$)</th>
<th>calm</th>
<th>light air</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acanthagenys rufogularis</em></td>
<td>open</td>
<td>0.76 ± 0.04</td>
<td>3.03 ± 0.10</td>
<td></td>
</tr>
<tr>
<td></td>
<td>sealed</td>
<td>0.71 ± 0.02</td>
<td>3.06 ± 0.04</td>
<td></td>
</tr>
<tr>
<td><em>Manorina flavigula</em></td>
<td>open</td>
<td>0.77 ± 0.04</td>
<td>3.19 ± 0.08</td>
<td></td>
</tr>
<tr>
<td></td>
<td>sealed</td>
<td>0.74 ± 0.04</td>
<td>3.14 ± 0.07</td>
<td></td>
</tr>
</tbody>
</table>

Statistics include the mean ± 95 % C.I.

The anemometer was inserted into the nest space through a hole in the nest lid to determine the proportion of wind passing through the nest wall under light air conditions. The wind detected in the nest cavity of *A. rufogularis* was 0.6 ± 0.1 km h$^{-1}$ and for *M. flavigula* the nest cavity wind speed was 0.8 ± 0.1 km h$^{-1}$. The ratio of the internal nest wind speed to tunnel wind speed was then compared for the two species. The ratio for nest:tunnel wind speed was 0.2 ± 0.1 for *A. rufogularis* and 0.3 ± 0.1 for *M. flavigula*, with no significant difference between the two species ($F_{1,13} = 0.65$, $P = 0.44$). This was repeated for four nest orientations (nest ID tag facing the front, left, back and right side) along the horizontal axis of rotation. There was no significant difference in the ratio of wind entering the nest cavity to that in the tunnel, irrespective of nest orientation ($F_{1,13} = 2.00$, $P = 0.18$).

**(d) Total nest conductance**

The total thermal conductance (G, mW °C$^{-1}$) of the nests was measured by placing an artificial heat source inside the nest and measuring the heat flow out through the wall (Φ), in relation to the temperature difference across the wall (ΔT). The methods of Chapter 2 were used where applicable, with exceptions outlined below. All measurements were carried out in a 10 °C constant temperature room.

An artificial egg heater consisted of a 3.35 mm thick aluminium sphere with a diameter of 3.8 cm (3003 alloy, Sharpe Products Inc., New Berlin, USA), within which the heating equipment was placed (Figure 6.3). The egg was heated internally to 40 °C with a 20 W (12 V, 1.67 A) globe (Mirabella International, Tullamarine, Australia). The heated air within the sphere was circulated with a 1.6 cm (3.3 V) fan (Copal Electronics, Tokyo, Japan), mounted above the heat source. The temperature inside the sphere was measured with a LM35DZ temperature sensor and the power supplied to the globe was varied to achieve constant temperature (Chapter 2). The opening of the nest was insulated with a 23 mm thick layer of Styrofoam and cotton padding sealed the lip against air leaks.

The voltage supplied to the globe was recorded in a chart application using AD Instruments Powerlab (model ML750, Castle Hill, Australia) and the current sent through the globe was measured with a multimeter (model QM1538, Digitech). The power used to operate the egg fan (\( \Phi_{FAN} \)) is released as heat and this is added to the power requirement of the globe (\( \Phi_{GLOBE} \)). The total power (\( \Phi \)) required to keep a stable nest temperature was calculated by multiplying the voltage and current from the globe and adding this to the product of voltage and current from the fan, according to Equation 2.2 (Chapter 2).

Two copper-constantan thermocouples ensheathed in polyethylene tubing were placed on the surface of the egg heater, one at the top and one at the bottom, between the egg heater and nest interface. A third thermocouple was placed outside the nest to measure the wind tunnel temperature. The temperature of the wind tunnel fluctuated slightly, within and between treatments, ranging from 10.8 to 12.3 °C (11.4 ± 0.1) for the closed treatments and 10.5 to 15.2 °C (11.6 ± 0.2) for the open treatments. Temperatures were logged on a portable data logger (model OM-SQ2020-IF8, Omega, Stamford, USA). Thermocouples were calibrated prior to the study by placing them into water of four different temperatures and plotting the thermocouple temperature reading against the temperature reading from a precision calibrated mercury-in-glass thermometer. The resulting calibration regression was used to correct the thermocouple readings.

The equipment was set up to heat the nest for each treatment, followed by an equilibration period of between 30 and 45 min. Measurements were obtained once the heat production rate had stabilised.

The temperature gradient used for calculations was that between the average of the egg heater surface temperatures (\( T_{Egg} \)) and the wind tunnel air temperature (\( T_A \)). Using the temperature gradient and the power
required to keep a stable nest temperature, the total thermal conductance of the system \( (G_{\text{TOT}}, \text{mW } ^\circ\text{C}^{-1}) \) was calculated using Equation 6.1.

\[
G_{\text{TOT}} = \frac{\Phi}{T_{\text{EGG}} - T_A}
\]  

(6.1)

where the new symbols are:

- \( G_{\text{TOT}} \) = System thermal conductance (mW \(^\circ\text{C}^{-1}\))
- \( \Phi \) = Heat production rate (mW)
- \( T_{\text{EGG}} \) = Egg heater surface temperature (°C)
- \( T_A \) = Ambient temperature (°C)

The total conductance of the system includes the conductance of the nest, air within the nest and the Styrofoam lid conductance. The surface area \( (A_{\text{LID}}) \) and surface-specific conductance of the lid \( (G_{A,\text{LID}}) \) was calculated according to Chapter 2. For each nest, the surface-specific lid conductance was multiplied by the surface area of the nest opening to obtain the total lid conductance \( (G_{\text{LID}}) \) for each nest. This was subtracted from the total conductance of the nest system to obtain a value representing the conductance from the egg heater surface to the outside of the nest, from here on referred to as total conductance.

This method was repeated for \( A. \text{rufogularis} \) and \( M. \text{flavigula} \) nests without a lid for the calm and light air wind treatments to determine the effect of wind on heat loss from eggs during incubation recesses. To determine the influence of the nest in general, the egg heater was measured in the chamber without the protection of a nest.

(e) Surface-specific nest conductance

The surface-specific conductance \( (G_A, \text{W } ^\circ\text{C}^{-1} \text{ m}^{-2}) \) was calculated by dividing the total conductance by the geometric mean surface area of the nest.

(f) Thermal conductivity

The thermal conductivity \( (k, \text{mW } ^\circ\text{C}^{-1} \text{ m}^{-1}) \) of the nest material was calculated using the surface area and thickness of the nest, according to Equation 6.2.

\[
k = \frac{G_X}{A}
\]  

(6.2)
where the new symbols are:

- \( k \) = Material thermal conductivity (mW °C\(^{-1}\) m\(^{-1}\))
- \( G \) = Nest thermal conductance (mW °C\(^{-1}\))
- \( X \) = Mean nest thickness (m)
- \( \bar{A} \) = Geometric mean of the internal and external surface area (m)

Thermal conductivity relates to the nest (nest material and air spaces between materials) and air within the nest cavity in the present study, as thermocouples were placed against the artificial heat source and external surfaces of the nest wall. While there are likely to be boundary layer effects that influence the thermal properties of nests, these were not accounted for due to the indefinite limits of boundary layers and increasing boundary layer thickness with nest size.

**Statistical analyses**

Statistical analyses were performed in JMP IN (SAS Institute (2001), version 4.0.4). Data that met the assumptions required for parametric tests, including normality (Shapiro-Wilk W test) and equal variance (O’Biens test), were subjected to an analysis of variance (ANOVA). Data that did not meet the assumptions required for parametric tests were analysed using the Wilcoxon / Kruskal-Wallis Chi-squared test. Comparisons of species mean values within treatments were made using post-hoc Tukey-Kramer HSD.

An indicator species analysis was performed in PC-Ord (McCune and Mefford (1999), version 5.0) to test whether the materials used in nest construction differed between the two species. An indicator species is the characteristic species of a group; thus a species with a high indicator value occurs frequently in one group and not in other groups (Dufrêne and Legendre 1997). In this test, the materials used in construction are the indicator species and the nest species are groups. The analysis was based on indicator values (percent of perfect indication, based on combining relative abundance values and relative frequency) calculated with the methods of Dufrêne and Legendre (1997) and a Monte Carlo one-sided test of significance of the observed maximum indicator value for materials found in *A. rufogularis* and *M. flavigula* nests. The Monte Carlo test yields a \( P \)-value, which is the proportion of randomised trials with an indicator value equal to or exceeding the observed indicator value, based on 1000 permutations.

An alpha value of 0.05 was used for all analyses. Data are expressed as mean ± 95% confidence interval.
3. RESULTS

Nest dimensions differed between *A. rufogularis* and *M. flavigula*, despite the similar body mass of the incubating adults (Table 6.2). *Manorina flavigula* had a greater nest mass, greater nest volume, thicker nest wall, greater surface area, as well as greater diameter and height (both internal and external). However, *A. rufogularis* constructed a nest with a denser nest wall compared to *M. flavigula*.

Table 6.2. Nest dimensions for cup-shaped nests of *Acanthagenys rufogularis* and *Manorina flavigula*

<table>
<thead>
<tr>
<th>nest variable</th>
<th>Acanthagenys rufogularis</th>
<th>Manorina flavigula</th>
<th>test statistic</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>nest mass (M₅₀, g)</td>
<td>10.30 ± 1.48</td>
<td>41.46 ± 7.53</td>
<td>25.93 ^</td>
<td>0.0009 *</td>
</tr>
<tr>
<td>nest volume (V₅₀, cm³)</td>
<td>105.09 ± 27.24</td>
<td>745.61 ± 125.83</td>
<td>10.50 ^</td>
<td>0.0012 *</td>
</tr>
<tr>
<td>nest density (ρ, g cm⁻³)</td>
<td>0.12 ± 0.07</td>
<td>0.06 ± 0.01</td>
<td>9.67 ^</td>
<td>0.014 *</td>
</tr>
<tr>
<td>nest thickness (X, cm)</td>
<td>0.93 ± 0.19</td>
<td>2.96 ± 0.38</td>
<td>96.39 ^</td>
<td>&lt; 0.0001 *</td>
</tr>
<tr>
<td>surface area (Ā, cm²)</td>
<td>122.46 ± 12.08</td>
<td>233.01 ± 16.82</td>
<td>113.64 ^</td>
<td>&lt; 0.0001 *</td>
</tr>
<tr>
<td>internal diameter (dᵢ, cm)</td>
<td>7.48 ± 0.34</td>
<td>9.10 ± 0.46</td>
<td>32.18 ^</td>
<td>&lt; 0.0001 *</td>
</tr>
<tr>
<td>external diameter (dₑ, cm)</td>
<td>9.09 ± 0.59</td>
<td>15.37 ± 1.04</td>
<td>10.50 ^</td>
<td>0.0012 *</td>
</tr>
<tr>
<td>internal height (hᵢ, cm)</td>
<td>4.58 ± 0.56</td>
<td>5.29 ± 0.33</td>
<td>4.84 *</td>
<td>0.028 *</td>
</tr>
<tr>
<td>external height (hₑ, cm)</td>
<td>5.64 ± 0.66</td>
<td>8.07 ± 0.51</td>
<td>31.35 ^</td>
<td>&lt; 0.0001 *</td>
</tr>
</tbody>
</table>

Statistics include the mean ± 95 % C.I., the F-ratio (^) for parametric tests or Chi-square statistic/ X² (*) for non-parametric tests, as well as the P-value.

* Indicates that there is a significant difference between the dimensions for each species (α = 0.05).

N = 8 for *Acanthagenys rufogularis* and N = 7 for *Manorina flavigula* except nest mass and density which has N = 3 and 7 (respectively). DF = 1,13 for all parametric comparisons except nest mass and density which has DF = 1,8. Non-parametric comparisons have a DF = 1. The replicate for the nest mass and density measurements is lower as some nests were excluded from analysis due to the attachment of supporting branches.

Surface area (Ā) is the geometric mean of the internal (Aᵢ) and external (Aₑ) surface areas.

Of the eight *A. rufogularis* nests measured: four contained solid plant material such as stems, vines, rootlets and bark; five contained flat plant material such as leaves; all contained materials from graminoids such as grasses, sedges and rushes; all contained soft plant material (commonly known as plant down); five contained animal products such as wool, fur, hair and feathers; and all contained silk products from arachnids such as silk thread and egg sacs. Of the seven *M. flavigula* nests measured: all contained solid plant material; two contained flat plant material; six contained materials from graminoids; two contained soft plant material; all contained animal products and all contained silk products from arachnids. In addition, one nest contained man-made material (nylon). An indicator species analysis showed that the materials present in the nests did not differ between each species, with the exception of soft plant material (Table 6.3). Soft plant material occurred more often in *A. rufogularis* nests than in *M. flavigula* nests. Solid plant material was also found marginally more often in *M. flavigula* nests than in *A. rufogularis* nests, though the difference was not significant.
Table 6.3. Indicator species analysis output for materials found in *Acanthagenys rufogularis* and *Manorina flavigula* nests

<table>
<thead>
<tr>
<th>material</th>
<th>observed indicator value</th>
<th>indicator value from randomised groups</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>Acanthagenys rufogularis</em></td>
<td><em>Manorina flavigula</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td>mean</td>
<td>standard deviation</td>
<td></td>
</tr>
<tr>
<td>graminoids</td>
<td>54</td>
<td>40</td>
<td>53.6</td>
</tr>
<tr>
<td>soft plant material</td>
<td>78</td>
<td>6</td>
<td>49.9</td>
</tr>
<tr>
<td>solid plant material</td>
<td>17</td>
<td>67</td>
<td>46.9</td>
</tr>
<tr>
<td>flat plant material</td>
<td>43</td>
<td>9</td>
<td>36.1</td>
</tr>
<tr>
<td>animal products</td>
<td>24</td>
<td>62</td>
<td>49.9</td>
</tr>
<tr>
<td>arachnid silk</td>
<td>50</td>
<td>50</td>
<td>50.0</td>
</tr>
</tbody>
</table>

The indicator species analysis output includes the indicator values and Monte Carlo test of significance of observed maximum indicator values for materials found in *Acanthagenys rufogularis* and *Manorina flavigula* nests. Statistics include the observed indicator values (percent of perfect indication, based on combining relative abundance values and relative frequency) for nests of each species, mean and standard deviation for the indicator value from randomised groups, as well as the $P$-value. The $P$-value is the proportion of randomized trials with an indicator value equal to or exceeding the observed indicator value. * Indicates that there is a significant correlation between the material type used in the nest and the species with the greater observed indicator value ($\alpha = 0.05$).

N = 8 for *Acanthagenys rufogularis* and N = 7 for *Manorina flavigula*.

There was a significant effect of wind speed on nest conductance for both species (Figure 6.4.a, $X^2 = 30.30$, DF = 5, $P < 0.0001$). There was no significant difference in the mean nest conductance for *A. rufogularis* and *M. flavigula*, within each wind speed treatment (Tukey-Kramer HSD). The control (heat source with no protection from a nest) had a conductance that was 250% greater than the nests of both species in still conditions and the difference increased to 290% in light air (Figure 6.4.a); however the increase could not be analysed statistically as the control was not replicated. The conductance of the nest under the light air condition was greater than the still and calm conditions for both species; however the conductance was no greater in calm conditions than it was in still conditions for either *A. rufogularis* or *M. flavigula*.

There was a significant effect of wind speed on surface-specific nest conductance for *A. rufogularis* and *M. flavigula* (Figure 6.4.b, $X^2 = 37.19$, DF = 5, $P < 0.0001$). There was a significant difference in the mean surface-specific conductance for *A. rufogularis* and *M. flavigula*, within each wind speed treatment (Tukey-Kramer HSD). The surface-specific conductance of *A. rufogularis* nests was greater than *M. flavigula* for all three wind conditions. The surface-specific nest conductance in both species was significantly greater in light air than in calm or still conditions, which were not significantly different.
Figure 6.4. The effect of wind speed on nest conductance. Relationship between wind speed (km h$^{-1}$) and a – total conductance (G, mW °C$^{-1}$) and b – surface specific conductance (G$_A$, W °C$^{-1}$ m$^{-2}$) for cup-shaped nests of Acanthagenys rufogularis (black line) and Manorina flavigula (grey line). The total conductance of the control (uncovered heat source) is also shown (dashed line). Each point represents the mean ± 95 % C.I. for each treatment mean. Points that share common symbols (a,b,c) are those that are not significantly different according to a Tukey-Kramer HSD. Wind speed treatments consist of still, calm and light air.
There was a significant effect of wind speed on thermal conductivity of the nest material for *A. rufogularis* and *M. flavigula* (Table 6.4, $F_{5,39} = 27.90, P < 0.0001$). *Manorina flavigula* had a significantly greater mean thermal conductivity compared with *A. rufogularis*, within each wind speed treatment, as confirmed with the Tukey-Kramer HSD. The thermal conductivity under the light air condition was greater than the still and calm conditions for both species; however, it was no greater in calm conditions than it was in still conditions for either *A. rufogularis* or *M. flavigula*.

**Table 6.4. Comparison of the structural and thermal properties of nests of *Acanthagenys rufogularis* and *Manorina flavigula* under each wind speed treatment**

<table>
<thead>
<tr>
<th>species</th>
<th>nest thickness (X)</th>
<th>surface area (Å)</th>
<th>wind speed</th>
<th>total conductance (G)</th>
<th>surface-specific conductance (G_A)</th>
<th>thermal conductivity (k)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acanthagenys rufogularis</em></td>
<td>0.93 ± 0.19</td>
<td>122.46 ± 12.08</td>
<td>still</td>
<td>48.4 ± 2.7</td>
<td>4.0 ± 0.4</td>
<td>36.7 ± 6.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>calm</td>
<td>51.3 ± 5.3</td>
<td>4.2 ± 0.5</td>
<td>38.7 ± 6.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>light air</td>
<td>82.7 ± 6.8</td>
<td>6.8 ± 0.8</td>
<td>63.0 ± 11.8</td>
</tr>
<tr>
<td><em>Manorina flavigula</em></td>
<td>2.96 ± 0.38</td>
<td>233.01 ± 16.82</td>
<td>still</td>
<td>45.1 ± 5.4</td>
<td>2.0 ± 0.3</td>
<td>56.8 ± 7.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>calm</td>
<td>47.1 ± 5.1</td>
<td>2.1 ± 0.3</td>
<td>59.7 ± 8.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>light air</td>
<td>83.9 ± 10.3</td>
<td>3.6 ± 0.6</td>
<td>105.5 ± 12.3</td>
</tr>
</tbody>
</table>

Statistics include the mean ± 95 % C.I.
Surface area (Å) is the geometric mean of the internal (A_I) and external (A_E) surface areas.

There was a significant effect of wind speed on heat loss from the nests of *A. rufogularis* and *M. flavigula* when sealed and open (Figure 6.5, $X^2 = 76.89, DF = 11, P < 0.0001$). There was a significant increase in the mean heat loss from *A. rufogularis* and *M. flavigula* as wind speed increased (Tukey-Kramer HSD). This was the case for both sealed and open nests. Heat loss from sealed *A. rufogularis* nests increased by 34 % between the two wind speed treatments (calm and light air only), and by 24 % from open nests. Heat loss from sealed *M. flavigula* nests increased by 39 % between the two wind speed treatments and by 20 % from open nests.

Within the calm treatment, there was no significant difference between the heat loss from *A. rufogularis* nests when open, compared with open *M. flavigula* nests. Nor was there a significant difference in the heat loss from sealed nests for either species. However, heat loss from the open nests was significantly higher than sealed nests for both species in calm conditions (22 % higher for *A. rufogularis* and 19 % for *M. flavigula*). Within the light air treatment, there was no significant difference in the heat loss from nests of *M. flavigula*, when sealed or open. However, open nests of *A. rufogularis* had a 12 % greater rate of heat loss than sealed nests.
Figure 6.5. The effect of wind speed on heat loss from nests. Relationship between wind speed (km h\(^{-1}\)) and heat loss (W) from cup-shaped nests of *Acanthagenys rufogularis* (black) and *Manorina flavigula* (grey) while nests are sealed (circles with solid lines) and open (square points with dashed lines). Each point represents the mean ± 95% C.I. for each treatment mean. Points that share common symbols (a,b,c,d) are those that are not significantly different according to a Tukey-Kramer HSD. Wind speed treatments consist of calm and light air.
4. DISCUSSION

(a) Still conditions

Nest conductance in still conditions is influenced by the thermal conductivity, the surface area and the thickness of the nest (Equation 6.2). The similarity in nest conductance between the two species results from a smaller surface area and lower thermal conductivity in A. rufogularis being compensated by a thinner nest (Table 6.4). *Manorina flavigula*, on the other hand, has a greater surface area and higher conductivity, but a much thicker nest. Given that the species have similar body masses and therefore comparable metabolic rates in accordance with allometric relationships (Bennett and Harvey 1987), the rate of heat loss from the nest appears independent of nest structure. The materials present in the nests do not differ between each species, with the exception of plant down, which is found more frequently in nests of *A. rufogularis* (Table 6.3). Plant down is made up of many plant fibres such that it resembles fur and appears to be good insulation. The prevalence of plant down in *A. rufogularis* nests is likely the reason that their thermal conductivity is lower (Table 6.4).

Despite differences in density (g cm$^{-3}$) between nests of the two species, density does not reflect the ability of the nest to prevent convective heat loss, but rather the fineness of weave is the important factor. The inner lining of the *M. flavigula* nest is densely woven but the main structure of the nest (the majority of the material) is quite loosely woven. On the other hand, the nest of *A. rufogularis* has a medium weave throughout, resulting in a greater overall nest density. This heterogeneous layered structure (Figure 6.1) means that is not possible in this study to compare heat loss from the nests in terms of the fineness of weave. Future work on convective heat loss from nests could assess nests that have a consistent structure throughout to determine if nest weave influences heat loss.

Nest conductance for *M. flavigula* and *A. rufogularis* is much lower than that predicted for their parent mass; predicted values being between 117 and 120 mW °C$^{-1}$ for the two species (Chapter 2). The former study measured conductance of the nest wall only, as the inner surface of the nest was covered with aluminium foil that prevented air flow through the wall. The present study was designed to permit flow through the nest, so the surface temperature of the artificial egg heater was measured, not nest wall temperature. Thus there was additional resistance to heat flow from the egg heater to the nest wall due to the air within the nest, decreasing the effective conductance. However comparisons using this method are just as valid as when looking at the nest wall alone.

(b) The effect of wind

i. Sealed nests

Light air flowing around the nest, compared to calm conditions, results in significant increases of between 71 to 86 % in total conductance and surface-specific conductance in both species. The increase in conductance
with wind speed is caused by disruption of the boundary layer around the nest and passage of air through it. The boundary layer is the still layer of air at the nest-environment interface (Calder III and King 1974).

Heat is transported through the boundary layer by conduction and is then transferred from the boundary layer largely by radiation and convection. The thickness of the boundary layer is a function of the wind velocity and the structure of the nest surface. For example, nests with a loose weave and plenty of sticks penetrating from the surface would have a thicker boundary layer than nests with a smooth weave. By increasing the wind speed around the nest, heat loss from the boundary layer is facilitated (Mitchell 1985).

In addition, wind enters the nest material and convects heat away, as shown by the increase in the thermal conductivity with greater wind speeds (Table 6.4). While conductance is influenced by the nest dimensions and thermal conductivity, the dimensions of the nest do not change with increasing wind speed; hence the increase in conductance must be a result of the increase in convection through the nest. While the nest wall reduces the wind speed within the nest cup compared to the tunnel, wind speeds of 0.6 km h\(^{-1}\) and 0.8 km h\(^{-1}\) were detected in the nest in the light air condition for *A. rufogularis* and *M. flavigula*, respectively. The lower wind speed within *A. rufogularis* nests indicates that the nest wall provides more protection from the wind and may also contribute to the lower thermal conductivity of the nest in comparison to *M. flavigula*. It is also reasonable to assume that the wind speed within the nest increases with the wind speed in the tunnel, increasing the thermal conductivity at higher wind speeds.

The consequence of increased wind currents around and through the nests in these experiments would be a near-doubling in heat production required by the parent when incubating at the experimental wind speeds. There are clear energetic costs to some birds when wind speeds increase (D’Alba et al. 2009; Pinowski et al. 2006) however convection is known to influence the choice of roosting site for non-breeding birds as well. Goldfinches (*Carduelis tristis*) save 12 % of their energy by roosting in sheltered sites, whereas heat loss from the Carolina and mountain chickadees (*Parus carolinensis* and *Poecile gambeli*) is reduced by 38 to 100 % when using sheltered sites, primarily a result of reduced exposure to wind (Buttemer 1985; Cooper 1999; Mayer et al. 1982). Keep in mind, also, that birds nesting in the wild would be subjected to wind speeds greater than those measured here and therefore the effect of wind on conductance may be more pronounced in natural systems. In addition, wind has unpredictable fluctuations in speed and direction (turbulence) in natural systems, which was not replicated here (Mitchell 1976). It is likely that there is an ever-increasing effect of wind on convective heat loss from nests, which could considerably influence the incubation cost for the parent (Mitchell 1985). Further work on convective heat loss from birds’ nests under stronger wind conditions should investigate this idea.

### ii. Open nests

As the rate of heat loss from open nests is greater than for sealed nests in calm air, when an incubating bird takes leave to forage in calm conditions, the clutch will be subjected to rates of heat loss between 19 to 22 % higher. This can increase developmental time and decrease hatching success (Deeming and Ferguson 1991;
When wind speed increases to light air, unsealed *A. rufogularis* nests lose 11% more heat than sealed nests under comparable wind conditions. However, the difference between sealed and open nests does not hold true for *M. flavigula* – the sealed nest loses heat at the same rate as the open nest. The disparity between the responses of the nests of these species may be related to the nest structure. The majority of *M. flavigula* nests have an uneven nest rim and when viewing them from the side, many small twigs can be seen extending above the nest lip horizon at an angle. This is rarely seen in the case of *A. rufogularis* nests. It may be that there is a greater opportunity for air leaks to occur in the sealed treatments for *M. flavigula*, compared to nests of *A. rufogularis*. The consequence of this may be that the rate of heat loss under light air conditions for *M. flavigula* nests appears more pronounced than it would be if an incubating parent was sitting on the nest, moulding their underbelly to the nest edges. Alternatively, the rate of heat loss from *M. flavigula* nests in light air may not increase when the lid is removed, as the coarse outer structure may help to break up the flow of air around the nest to deflect some of it away from the nest opening.

If the rates of heat loss between treatments accurately represent those of attended versus unattended nests, then it means that unattended *M. flavigula* clutches may not cool as fast as *A. rufogularis* clutches at increased wind speeds. This would have some bearing on the rates of nest attendance between the two species where *M. flavigula* could take longer recesses and forage for greater periods, in turn reducing the cost of reproduction for this species, as occurs in other species (Carey 2002; Eikenaar *et al.* 2003; Kristjansson and Jonsson 2011; Møller 1991).

### iii. No nest

The control treatment enables the nest data to be put into perspective. The conductance from the heat source with no protection from a nest (control) nearly tripled in light air conditions compared to when surrounded by a nest. This demonstrates that the nest does in fact help to ameliorate heat loss from the clutch by 58 to 65%, potentially reducing the energetic cost of incubation to the parent. Ar and Sidis (2002) found that the nest of the blackbird (*Turdus merula*) helped reduce heat loss from eggs in still air by 25 to 30% however cooling times were halved when wind speed increased to 2.7 km h\(^{-1}\). In the present study, the difference in conductance from the uncovered heat source and the heat source protected by a nest increased with wind speed, suggesting that the presence of a nest becomes even more important as wind speed increases. Our findings provide further support for the benefit of selecting sheltered nest sites (D’Alba *et al.* 2009). In addition to the nest itself, the surrounding vegetation can be important. This is the case for the song sparrow (*Melospiza melodia*), where nests are constructed on the lee side of the plant, such that surrounding shrubs reduce wind speed around the nest by 73% (Kern *et al.* 1993).

### (c) Summary

Here we have shown that in still air, the two species have a similar nest conductance, a result of differences in nest dimensions. The thickness of a nest is largely driven by the need to support the clutch and incubating parent when comparing over a broad range of bird sizes (Chapter 2). In addition, the size of the inner nest cup...
is somewhat determined by the size of incubating parent and clutch. Therefore, it could be argued that the overall construction of a nest is fixed to some extent. However, in habitats where there are extreme temperature changes, the nature of the nest may be essential to the development of the clutch and the efficiency of temperature regulation of the young (Ricklefs and Hainsworth 1968; 1969). Therefore, the highly contrasting nest dimensions yet comparable conductance values may be indicative of the plasticity in nest design within a species, with the ultimate objective of achieving an appropriate nest microclimate. However, small birds (such as those studied here) may have more flexibility regarding structural design of nests than larger birds that may be more restricted (Chapter 2). Furthermore, as nest thickness increases with parent mass (Chapter 2), the clutches of large birds may be protected from convection to a greater extent than those of small birds.

Exposing the sealed nests to greater wind speeds, raises nest conductance via a concurrent increase in the thermal conductivity. Contrary to predictions based on convective heat loss, conductance is similar in the two species, although they construct their nests in different parts of the canopy. Acanthagenys rufogularis does not increase the insulative value of the nest to account for the poorer protection from wind afforded by its location near the ends of branches. Manorina flavigula nests would potentially have greater protection from the elements due to the dense canopy near the trunk, but the nest has a thick nest wall, further adding to the protection of the offspring.

The significance of convection through the nest is a near-doubling in heat production required by the parent when incubating in light air conditions. However, this may be more or less extreme for other species, depending on the ability of the nest to impede wind currents (Webb 1993). Heat is lost from nests more rapidly during parental recesses for both species at low wind speeds, with a minimal increase in heat loss for A. rufogularis in light air. This would result in an immediate increase in heat loss from the clutch, thereby lengthening development time and reducing hatching success or chick survival (Lundy 1969; Olson et al. 2006; Wachob 1996). The incubating or brooding parent will also be affected following a recess as extra energy will be expended to rewarm the clutch (Biebach 1986; Vleck 1981). In conclusion, building a thermally favourable nest helps to save parental energy (Hilton et al. 2004), however, convection increases conductance of heat from the nest and therefore selecting an appropriate nest site that provides additional shelter is important for avian reproductive success.
ACKNOWLEDGEMENTS

We thank the South Australian Museum (in particular, Dr Philippa Horton) for use of their nest collection and invaluable nest knowledge. We appreciate the assistance of Richard Norrish (the University of Adelaide) for designing and constructing the controlled temperature power monitor circuit, as well as Georgina Allan for constructing the wind tunnel honeycomb. We also thank the reviewers for their useful comments and improving the clarity of the text.
The Effect of Wind on the Rate of Heat Loss from Avian Cup-Shaped Nests

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Abstract

Forced convection can significantly influence the heat loss from birds and their offspring but effects may be reduced by using sheltered micro-sites such as cavities or constructing nests. The structural and thermal properties of the nests of two species, the spiny-cheeked honeyeater (Acanthagenys nufugularis) and yellow-throated miner (Manorina flavigula), were measured in relation to three wind speeds. Nest dimensions differ between the two species, despite the similar body mass of the incubating adults, however nest conductance is comparable. As wind speed increases, so does the rate of heat loss from the nests of both species, and further still during incubation recesses. The significance of forced convection through the nest is a near-doubling in heat production required by the parent, even when incubating at relatively low wind speeds. This provides confirmation that selecting a sheltered nest site is important for avian reproductive success.

Introduction

The microclimate properties that are critical to adult birds include wind, radiation, air temperature and humidity, and these directly affect the thermoregulatory demands with which a bird must cope [1-3]. Wind, which is forced convection (henceforth referred to as convection), is often considered to be more important for heat loss than conduction and evaporation [3-5]. The energetics of a variety of avian species exposed to wind has been explored using doubly-labelled water, time energy budgets and respirometry techniques in wind tunnels [6-9]. Webster and Weathers [10] found that heat production in verdins (Acanthis flavirostris) can rise by nearly 30% when wind speed increases from 1.8 to 10.8 km h⁻¹, whereas Tracy [11] argued that heat loss may vary by up to 100% for some individuals under different wind speed conditions.

Energy demands of thermoregulation may be greatest when roosting or during reproduction [1,12,13]. Therefore, it is expected that there would be strong selective pressure for birds to minimise thermoregulatory stresses to the individual and offspring. Reducing air movement over birds moderates their convective heat loss and this can be achieved by using sheltered micro-sites such as cavities and domed nests [13,14]. Of primary interest here is how convection can influence heat loss from the nest of reproducing individuals, as the rate of heat loss can influence the outcome of a breeding attempt and consequently lifetime reproductive success [12,15]. Reproduction in birds via oviparity necessitates developmental conditions to be modulated externally, provided by the reproducing birds through modification of their own metabolism [16,17]. While the energetics of birds under different wind regimes has only been investigated in non-incubating individuals, it is expected that wind would also increase the rate of heat loss for reproducing birds. Appropriate nest site selection can reduce heat loss through convection, however such savings may be small compared to those produced by the addition of an insulating nest [1,18]. Consequently, nests might be expected to be shaped by selection over evolutionary time to approach functional optima and reflect the microclimate conditions to which birds are exposed, including convection [16].

Next structure and placement has been reported widely in the literature in recent years, as the importance of such structures has become more apparent [reviewed by 19]. Methods for determining the effect of wind on heat loss from the nest largely consist of either heat loss modelling [4] or nest orientation correlations [20,21]. Nest orientation is expected to change the nest microenvironment due to the effects of wind and thus sparrow (Passer domesticus) and meadowlark (Sturnella magna) nests are primarily oriented away from prevailing winds [22,23]. Woodpecker (Picidae) nest orientations provide shelter from the wind and rain [24], while nest orientation for a variety of avian species is correlated with modified nest temperatures [25-30].

There may be differences in nest structure that contribute to reductions in convective heat loss [31,32]. Palmegren and Palmegren [33] were the first to assess the influence of convection on nest insulation and found that heat loss increases in turbulent conditions by 44% in the common rooschel (Caprimulgus europaeus) to 91% in the chaffinch (Fringilla coelebs). Kern [31] found that elevated nests of the white-crowned sparrow (Zonotrichia leucophrys) were better insulated than ground nests and proposed that the increased insulation may offset the increased convective cooling to which they are exposed. Pectoral sandpiper (Calidris melanotos) nest structure is an example of how a compromise can be found between multiple unfavourable variables [16]. While deep nest
scrapes would reduce convective heat loss from eggs, the eggs would in turn experience cooler ground temperatures. Scrapes are therefore constructed such that the eggs are positioned at an optimal depth for minimising forced convection as well as the rate of heat loss to the substrate. The choice of materials used for nest construction may also be partly driven by the need to reduce convective heat loss [34].

There is a paucity in the knowledge regarding the effect of wind on the insulative properties of exposed nests and how wind may influence the heat loss from the clutch, and in turn, the energetics of the incubating parent. Our earlier study on the thermal properties of nests involved conductive heat loss through whole nests in essentially still air [35]. The results from 36 species of birds with body masses ranging from 8 to 301 g demonstrated that cup-shaped nests were constructed primarily for support rather than insulation. Insulation was evaluated by measuring its inverse, thermal conductance. This is the rate of heat flux (watts) moving across the nest wall, per degree of temperature difference between the inside and outside of the nest, based on Newton's Law of Cooling [11,36]. Well-insulated nests have a low conductance and vice versa. The present study is designed to investigate the role of convective heat transfer through cup-shaped nests of two species with similar body masses, but of different nest construction, thin versus thick walls. Here, the thermal conductance is again measured, but within a wind-tunnel. In the present study, the ‘effective’ thermal conductance and ‘effective’ material conductivity is measured (henceforth referred to as conductance and conductivity, respectively, as both thermal properties in this context include the effects of convective and conductive heat flow.

If nest wall structure is important in preventing heat loss via convection we expect that there would be differences in nest conductance that are related to the thickness of the nest wall or the conductivity of the nest material in windy conditions. Furthermore, we compare the heat loss from nests where the opening is sealed with a Styrofoam lid to those without a lid. This was conducted to reflect differences in heat loss from attended and unattended nests.

**Methods**

Nests were borrowed from the South Australian Museum ornithology collection and were selected for measurement if they were in a good condition and had no branches obstructing the opening of the nest. Nests that were damaged were excluded from analyses. Nests were collected between 1976 and 1992, with collection information missing for five out of the 15 nests. For those where collection date was known, there was no significant difference in the year the nest was collected when comparing the two species ($\chi^2=1.86$, $\text{DF}=1$, $P=0.17$). All nests were from museum collections, stored in a similar way, which should have reduced any bias resulting from degradation and storage. Notes on the construction of each nest were made; including condition, attachments, materials, nest shape and weave density.

(a) Study species

A total of eight spiny-cheeked honeyeater (*Acanthagenys rufigularis* Gould, 1840) nests were measured. The two species were selected as they both have similar parent masses (50 g and 55 g, respectively), however different nest structure (Figure 1). While *M. flavigula* nests have larger dimensions, *A. rufigularis* constructs a nest with a denser wall compared to *M. flavigula*. In addition, the nest dimensions for *A. rufigularis* are lower than what would be predicted for a bird of this size, while nests of *M. flavigula* are larger than predicted [35].

The two species have largely overlapping geographical distributions throughout Australia and breed in similar habitats, usually open woodland or shrubland in arid and semi-arid zones [37]. Both species are capable of breeding year-round but most of the breeding occurs between June/July through to March. While *A. rufigularis* tends to construct their nests suspended in the top or outer edge of plant canopies (1 to 3 m above ground), *M. flavigula* nests are regularly found in dense canopy close to the trunk of the plant (4 to 3 m above ground).

(b) Nest dimensions

The physical dimensions of the nests were measured with callipers and a micrometer to the nearest millimetre, including the nest thickness ($X$, Figure 2), internal and external diameter ($d$) and height ($h$). Those nests without supporting structures attached were weighed on a Mettler digital analytical balance (model AE165, Zürich, Switzerland).

The internal and external nest surface area ($A_t$) was approximated using the equation for half of a prolate spheroid (Equation 1 of Heenan & Seymour [35]), using values for internal and external diameters and heights. The average surface area ($A_t$) was calculated as the geometric mean of the internal and external surface area. Nest volume was calculated as half of the volume for a prolate spheroid based on external dimensions, minus half of the volume of a prolate spheroid based on internal dimensions (Equation 1 of Heenan, Paton & Seymour [38], in Preparation). The density of the nest was calculated for each species. Nest density $(\rho, \text{g cm}^{-3})$ was calculated as the nest mass ($MN$) divided by the nest volume ($VN$).

(c) Wind tunnel

A wind tunnel was constructed to enable wind speed surrounding the nest to be controlled and measured (Figure 3). The wind tunnel consisted of a long cardboard box (35.5 cm width; 36.5 height; 139 cm length), divided into three main chambers: the settling chamber, the test section and the diffuser. The settling chamber consisted of a filter made from a double-layer wire-mesh screen. This was used to prevent large airborne
particles from entering the chamber and causing undesirable turbulence in the flow [39,40]. A 4 cm wide honeycomb screen made from plastic straws (1 cm in diameter), glued together in alternating layers, was placed towards the end of the settling chamber. The honeycomb screen acts to straighten the flow, reducing turbulence, as well as eliminating the cross-flow component [39,41]. A second honeycomb screen was placed at the beginning of the diffuser.

The test section was situated between the two honeycomb screens, with air access provided by an outward-opening door. The door was sealed closed during the experiments with metal corner brackets clipped in place with Velcro.

A desk mounted axial fan (Ø10 mm, model MT132, Fantech, Dandenong, Australia) was placed at the outlet end to suck wind through the tunnel. The speed of the fan was manipulated with a variable voltage regulator (model Voltaux SB-3 IRUKA, Yokokama Electric Co., Ltd., Japan) by varying the voltage from 0 to 240 V. The maximum wind speed achievable was 3.4 km h⁻¹.

Wind speed was measured with a hot-wire anemometer (model AM-420WHA, Lafron Electronic, Cooperburg, USA) at radial interval positions through the centre of the test section when the fan was at its maximal speed. This was to ensure that wind speed was relatively consistent at all points in the chamber and that differences in measurements would not result from slight changes in nest placement. Wind speed varied slightly throughout the chamber test section, ranging from 2.7 to 3.1 km h⁻¹ (2.7%) during the test runs. The anemometer was also turned sideways and moved throughout the chamber to confirm that movement of air through the tunnel was laminar and did not consist of turbulent flow or produce a cross-flow component.

The nest was placed in the centre of the test section on a 4 cm high wire-mesh strip to allow for free air-flow around it. The cross-sectional area of the wind tunnel blocked by the nest ranged from 2.9% (mean 3.1%). The anemometer was suspended above the lid of the nest to measure wind speed, which was recorded for each nest and treatment. Nest measurements were repeated at three wind speeds: 0.0, 0.6 and 3.1 km h⁻¹. These speeds are described in this paper as 'still', 'calm' and 'light air', respectively, according to Beaufort scale definitions in Allaby [42].

We tried to maintain a consistent wind speed by setting the variable voltage regulator to the same output each time, the average speed detected (Table 1) surrounding the open areas differed for each species for the light air treatment (X² = 5.55, DF = 1, P = 0.019) but not within the calm (X² = 0.15, DF = 1, P = 0.72) treatment. There were no significant differences in the wind speed detected around sealed nests for each species within both the calm (X² = 1.64, DF = 1, P = 0.20) and the light air treatment (X² = 3.16, DF = 1, P = 0.075). Wind speed in the still air treatments was consistently 0 km h⁻¹.

The anemometer was inserted into the nest space through a hole in the nest lid to determine the proportion of wind passing through the nest wall under light air conditions. The wind detected in the nest cavity of A. nigergalis was 0.6±0.1 km h⁻¹ and for M. flavigula the nest cavity wind speed was 0.8±0.1 km h⁻¹. The ratio of the internal nest wind speed to tunnel wind speed was then compared for the two species. The ratio for nest tunnel wind speed was 0.2±0.1 for A. nigergalis and 0.3±0.1 for M. flavigula, with no significant difference between the two species (t = 0.65, P = 0.44). This was repeated for four nest orientations (nest ID tagging the front, left, back and right side) along the horizontal axis of rotation. There was no significant difference in the ratio of wind entering the nest cavity to that in the tunnel, irrespective of nest orientation (t = 2.00, P = 0.18).

(d) Total nest conductance

The total thermal conductance (G, mW °C⁻¹) of the nests was measured by placing an artificial heat source inside the nest and...
measuring the heat flow out through the wall (Φe) in relation to the temperature difference across the wall (ΔT). The methods of Heenan & Seymour [35] were used where applicable, with exceptions outlined below. All measurements were carried out in a 10°C constant temperature room.

An artificial egg heater consisted of a 3.3 mm thick aluminium sphere with a diameter of 3.8 cm (3005 alloy, Sharpe Products Inc., New Berlin, USA), within which the heating equipment was placed (Figure 4). The egg was heated internally to 40°C with a 20 W (12 V, 1.67 Ω) globe (Mirabella International, Tullamarine, Australia). The heated air within the sphere was circulated with a 1.6 cm (3.3 V) fan (Copal Electronics, Tokyo, Japan), mounted above the heat source. The temperature inside the sphere was measured with a LM35DZ temperature sensor and the power supplied to the globe was varied to achieve constant temperature [35]. The opening of the nest was insulated with a 23 mm thick layer of Styrofoam and cotton padding sealed the lip against air leaks.

The voltage supplied to the globe was recorded in a chart application using AD Instruments Powerlab (model ML750, Castle Hill, Australia) and the current sent through the globe was measured with a multimeter (model QM153B, Digitron). The power used to operate the egg fan (Φf,fan) is released as heat and this is added to the power requirement of the globe (Φe,LMN). The total power (Φw) required to keep a stable nest temperature was calculated by multiplying the voltage and current from the globe and adding this to the product of voltage and current from the fan, according to Equation 2 of Heenan & Seymour [35].

Two copper-constantan thermocouples embedded in polyethylene tubing were placed on the surface of the egg heater, one at the top and one at the bottom, between the egg heater and nest interface. A third thermocouple was placed outside the nest to measure the wind tunnel temperature. The temperature of the wind tunnel fluctuated slightly, within and between treatments, ranging from 10.8 to 12.3°C (11.4±0.6°C) for the closed treatments and 10.5 to 13.3°C (11.6±1.3°C) for the open treatments. Temperatures were logged on a portable data logger (model OM-SQ2020-IFh, Omev, Stamford, USA). Thermocouples were calibrated prior to the study by placing them into water of four different temperatures and plotting the thermocouple temperature reading against the temperature reading from a precision calibrated mercury-in-glass thermometer. The resulting calibration regression was used to correct the thermocouple readings.

The equipment was set up to heat the nest for each treatment, followed by an equilibration period of between 30 and 45 min. Measurements were obtained once the heat production rate had stabilised.

The temperature gradient used for calculations was that between the average of the egg heater surface temperatures (Teg) and the wind tunnel air temperature (T0). Using the temperature gradient and the power required to keep a stable nest temperature, the total thermal conductance of the system (GNET, mW °C⁻¹) was calculated using Equation 1.

\[
G_{\text{NET}} = \frac{\Phi}{T_{\text{eg}} - T_0}
\]

Where the symbols are:

- \(G_{\text{NET}}\): System thermal conductance (mW °C⁻¹)
- \(\Phi\): Heat production rate (mW)
- \(T_{\text{eg}}\): Egg heater surface temperature (°C)
- \(T_0\): Ambient temperature (°C)

The total conductance of the system includes the conductance of the nest, air within the nest and the Styrofoam lid conductance. The surface area (A_LMN), surface-specific conductance of the lid (G_LMN) was calculated according to Heenan and Seymour [35]. For each nest, the surface-specific lid conductance was multiplied by the surface area of the nest opening to obtain the total lid conductance (G_LMN) for each nest. This was subtracted from the total conductance of the nest system to obtain a value representing the conductance from the egg heater surface to the outside of the nest, from here on referred to as total conductance.

This method was repeated for A. rufifacies and M. flavigula nests without a lid for the calm and light air wind treatments to determine the effect of wind on heat loss from eggs during incubation recesses. To determine the influence of the nest in general, the egg heater was measured in the chamber without the protection of a nest.
(e) Surface-specific nest conductance

The surface-specific conductance \( (G_s, \text{W} \cdot \text{C}^{-1} \cdot \text{m}^{-2}) \) was calculated by dividing the total conductance by the geometric mean surface area of the nest.

(f) Thermal conductivity

The thermal conductivity \( (k, \text{mW} \cdot \text{C}^{-1} \cdot \text{m}^{-1}) \) of the nest material was calculated using the surface area and thickness of the nest, according to Equation 2.

\[
k = \frac{G}{X} \quad \text{(2)}
\]

Where the symbols are:

- \( k \) = Material thermal conductivity (\( \text{mW} \cdot \text{C}^{-1} \cdot \text{m}^{-1} \))
- \( G \) = Nest thermal conductance (\( \text{mW} \cdot \text{C}^{-1} \))
- \( X \) = Nest wall thickness (m)
- \( A \) = Geometric mean of the internal and external surface area (m)

(g) Statistical analyses

Statistical analyses were performed in JMP IN (SAS Institute Inc., version 4.0.6). Data that met the assumptions required for parametric tests, including normality (Shapiro-Wilks W test) and equal variance (O’Brien test), were subjected to an analysis of variance (ANOVA). Data that did not meet the assumptions required for parametric tests were analysed using the Wilcoxon/Kruskal-Wallis Chi-squared test. Comparisons of species mean values within treatments were made using post-hoc Tukey-Kramer HSD.

An indicator species analysis was performed in PC-Ord (MjM Software, version 5.6) to test whether the materials used in nest construction differed between the two species. The analysis was based on indicator values (percent of perfect indication, based on combining relative abundance values and relative frequency) and a Monte Carlo test of significance of the observed maximum indicator value for materials found in A. rufogularis and M. flavigula nests.

An alpha value of 0.05 was used for all analyses. Data are expressed as mean ± 95% confidence interval.

Results

Nest dimensions differed between A. rufogularis and M. flavigula, despite the similar body mass of the incubating adults (Table 2). M. flavigula had a greater nest mass, greater nest volume, thicker nest wall, greater surface area, as well as greater diameter and height (both internal and external). However, A. rufogularis constructed a nest with a denser nest wall compared to M. flavigula.

Of the eight A. rufogularis nests measured, four contained solid plant material such as stems, vines, roots, and twigs; two contained flat plant material such as leaves; all contained materials from graminoids such as grasses, sedges and rushes; and all contained soft plant material (commonly known as plant down); five contained animal products such as wool, fur, hair and feathers; and all contained silk products from arachnids such as silk thread and egg sacs. Of the seven M. flavigula nests measured; all contained solid plant material; two contained flat plant material; six contained materials from graminoids; two contained soft plant material; all contained animal products and all contained silk products from arachnids. In addition, one nest contained man-made material (nylon). An indicator species analysis showed that the materials present in the nests did not differ between each species, with the exception of soft plant material (Table 3). Soft plant material occurred more often in A. rufogularis nests than in M. flavigula nests. Solid plant material was also found marginally more often in M. flavigula nests than in A. rufogularis nests, though the difference was not significant.

There was a significant effect of wind speed on nest conductance for both species (Figure 5A; \( X^2 = 30.30, \text{DF} = 5, P<0.0001 \)). There was no significant difference in the mean nest conductance for A. rufogularis and M. flavigula within each wind speed treatment (Tukey-Kramer HSD). The control (unprotected heat source) had a conductance that was 250% greater than the nests of both species in still conditions and the difference increased to 250% in light air (Figure 5A); however, the increase could not be analysed statistically as the control was not replicated. The conductance of the nest under the light air condition was greater than the still and calm conditions for both species; however the conductance was no greater in calm conditions than it was in still conditions for either A. rufogularis or M. flavigula.

| Table 2. Nest dimensions for cup-shaped nests of Acanthagenys rufogularis and Manornia flavigula. |
|-------------------------------------------------|-------------------------------------------------|-------------------------------------------------|-------------------------------------------------|
| Dimension | Acanthagenys rufogularis | Manornia flavigula | Test statistic | \( P \)-value |
|-------------------------------------------------|-------------------------------------------------|-------------------------------------------------|-------------------------------------------------|
| Nest mass (\( M_{\text{nest}} \), g) | 10.36±1.48 | 41.48±7.53 | 25.93* | 0.0000* |
| Nest volume (\( V_{\text{nest}} \), cm\(^3\)) | 105.59±27.24 | 745.61±125.83 | 10.50* | 0.0012* |
| Nest density (\( \rho \), g cm\(^{-3}\)) | 0.12±0.07 | 0.06±0.01 | 9.67* | 0.014* |
| Nest thickness (\( X \), cm) | 0.93±0.19 | 2.96±0.38 | 90.39* | <0.0001* |
| Surface area (\( A \), cm\(^2\)) | 122.46±12.08 | 233.01±168.2 | 113.04* | <0.0001* |
| Internal diameter (\( d_{\text{in}} \), cm) | 7.48±0.34 | 9.10±0.46 | 32.18* | <0.0001* |
| External diameter (\( d_{\text{out}} \), cm) | 9.09±0.59 | 13.87±1.04 | 105.38* | 0.0012* |
| Internal height (\( h_{\text{in}} \), cm) | 4.58±0.56 | 5.29±0.53 | 4.64* | 0.008* |
| External height (\( h_{\text{out}} \), cm) | 5.64±0.66 | 6.07±0.53 | 31.35* | <0.0001* |

Statistics include the mean ± 95% confidence interval; the F-test (*) for parametric tests or Chi-square test(\( X^2 \)) for non-parametric tests, as well as the \( P \)-value. \( * \) indicates that there is a significant difference between the dimensions for each species (\( \alpha = 0.05 \)).

\( N = 8 \) for Acanthagenys rufogularis and \( N = 7 \) for Manornia flavigula except nest mass and density which has \( N = 3 \) and \( 7 \) (respectively). \( \text{DF} = 1,13 \) for all parametric comparisons except nest mass and density which has \( \text{DF} = 1,18 \). Non-parametric comparisons have a \( \text{DF} = 1 \). The replicate for the nest mass and density measurements is lower as some nests were excluded from analysis due to the attachment of supporting branches.

Surface area \( (A) \) is the geometric mean of the internal \( (A_{\text{in}}) \) and external \( (A_{\text{out}}) \) surface areas.

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Table 3. Indicator species analysis output for materials found in Acathagnes rufugalis and Manorina flavigula nests.

<table>
<thead>
<tr>
<th>Material</th>
<th>Observed indicator value</th>
<th>Indicator value from randomised groups</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Acanthagnes rufugalis</td>
<td>Manorina flavigula</td>
</tr>
<tr>
<td>Graminoids</td>
<td>54</td>
<td>40</td>
</tr>
<tr>
<td>Soft plant material</td>
<td>78</td>
<td>6</td>
</tr>
<tr>
<td>Solid plant material</td>
<td>17</td>
<td>6</td>
</tr>
<tr>
<td>Flat plant material</td>
<td>43</td>
<td>9</td>
</tr>
<tr>
<td>Animal products</td>
<td>24</td>
<td>62</td>
</tr>
<tr>
<td>Arachnid silk</td>
<td>50</td>
<td>50</td>
</tr>
</tbody>
</table>

The indicator species analysis output includes the indicator values and Monte Carlo test of significance of observed maximum indicator values for materials found in Acanthagnes rufugalis and Manorina flavigula nests. Statistics include the observed indicator values (percent of perfect indication, based on combining relative abundance and relative frequency) for nests of each species, mean and standard deviation for the indicator value from randomised groups, as well as the P-value. The P-value is the proportion of randomised trials with an indicator value equal to or exceeding the observed indicator value.

There was a significant effect of wind speed on surface-specific nest conductance for *A. rufugalis* and *M. flavigula* (Figure 3B, $F_1, 39 = 37.19, DF = 5, P < 0.001$). There was a significant difference in the mean surface-specific conductance for *A. rufugalis* and *M. flavigula*, within each wind speed treatment (Tukey-Kramer HSD). The surface-specific conductance of *A. rufugalis* nests was greater than *M. flavigula* for all three wind conditions. The surface-specific nest conductance in both species was significantly greater in light air than in calm or still conditions, which were not significantly different.

There was a significant effect of wind speed on thermal conductivity of the nest material for *A. rufugalis* and *M. flavigula* (Table 4, $F_1, 27 = 57.30, P < 0.0001$). *M. flavigula* had a significantly greater mean thermal conductivity compared with *A. rufugalis*, within each wind speed treatment, as confirmed with the Tukey-Kramer HSD. The thermal conductivity under the light air condition was greater than the still and calm conditions for both species; however it was no greater in calm conditions than it was in still conditions for either *A. rufugalis* or *M. flavigula*.

There was a significant effect of wind speed on heat loss from the nests of *A. rufugalis* and *M. flavigula* when sealed and open (Figure 6, $F_1, 37 = 76.89, DF = 1, P < 0.0001$). There was a significant increase in the mean heat loss from *A. rufugalis* and *M. flavigula* as wind speed increased (Tukey-Kramer HSD). This was the case for both sealed and open nests. Heat loss from sealed *A. rufugalis* nests increased by 34% between the two wind speed treatments (calm and light air only), and by 24% from open nests. Heat loss from sealed *M. flavigula* nests increased by 59% between the two wind speed treatments and by 20% from open nests.

Within the calm treatment, there was no significant difference between the heat loss from *A. rufugalis* nests when open, compared with open *M. flavigula* nests. Nor was there a significant difference in the heat loss from sealed nests for either species. However, heat loss from the open nests was significantly higher than sealed nests for both species in calm conditions (22% higher for *A. rufugalis* and 19% for *M. flavigula*). Within the light air treatment, there was no significant difference in the heat loss from nests of *M. flavigula*, when sealed or open. However, open nests of *A. rufugalis* had a 12% greater rate of heat loss than sealed nests.

**Discussion**

(a) Still conditions

Nest conductance in still conditions is influenced by the thermal conductivity, the surface area and the thickness of the nest (Equation 2). The similarity in nest conductance between the two species results from a smaller surface area and lower thermal conductivity in *A. rufugalis* being compensated by a thinner nest (Table 4). *M. flavigula*, on the other hand, has a greater surface area and higher conductivity, but a much thicker nest. Given that the species have similar body masses and therefore comparable metabolic rates [35], the rate of heat loss from the nest appears independent of nest structure. The materials present in the nests do not differ between each species, with the exception of plant down, which is found more frequently in nests of *A. rufugalis* (Table 3) and consequently their thermal conductivity is lower (Table 4). Plant down is made up of many plant fibres such that it resembles fur and appears to be good insulation.

Despite differences in density (g cm$^{-3}$) between nests of the two species, density does not reflect the ability of the nest to prevent convective heat loss, but rather the fineness of weave is the important factor. The inner lining of the *M. flavigula* nest is densely woven but the main structure of the nest (the majority of the material) is quite loosely woven. On the other hand, the nest of *A. rufugalis* has a medium weave throughout, resulting in a greater overall nest density. This heterogeneous layered structure (Figure 1) means that it is not possible in this study to compare heat loss from the nests in terms of the fineness of weave. Future work on convective heat loss from nests could assess nests that have a consistent structure throughout to determine if nest weave influences heat loss.

(b) The effect of wind

i) Sealed nests. Light air flowing around the nest results in significant increases of between 71 to 86% in total conductance and surface-specific conductance in both species. The increase in conductance with wind speed is caused by disruption of the boundary layer around the nest and passage of air through it. The boundary layer is the still layer of air at the nest-environment interface [36].

Heat is transported through the boundary layer by conduction and is then transferred from the boundary layer largely by radiation and convection. The thickness of the boundary layer is a function of the wind velocity and the structure of the nest surface. For example, nests with a loose weave and plenty of sticks penetrating from the surface would have a thicker boundary layer than nests with a smooth weave. By increasing the wind speed around the nest, heat loss from the boundary layer is facilitated [44].
Figure 5. The effect of wind speed on nest conductance. Relationship between wind speed (km h⁻¹) and (A) total conductance (G, mW°C⁻¹) and (B) surface specific conductance (Gₛ, W°C⁻¹ m⁻²) for cup-shaped nests of Acrocephalus rufivirgatus (black line) and Manoella flavigula (grey line). The total conductance of the control (uncovered heat source) is also shown (dashed line). Each point represents the mean ± 95% CI for each treatment mean. Points that share common symbols (a,b,c) are those that are not significantly different according to a Tukey-Kramer HSD. Wind speed treatments consist of still, calm and light air.
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In addition, wind enters the nest material and convects heat away, as shown by the increase in the thermal conductivity with greater wind speeds (Table 4). While conductance is influenced by the nest dimensions and thermal conductivity, the dimensions of the nest do not change with increasing wind speed; hence the increase in conductance must be a result of the increase in convection through the nest. While the nest wall reduces the wind speed within the nest cup compared to the tunnel, wind speeds of 0.6 km h⁻¹ and 0.8 km h⁻¹ were detected in the nest in the light air condition for A. rufivirgatus and M. flavigula, respectively. The lower wind speed within A. rufivirgatus nests indicates that the nest wall provides more protection from the wind and may also contribute to the lower thermal conductivity of the nest in comparison to M. flavigula. It is also reasonable to assume that the wind speed within the nest increases with the wind speed in the tunnel, increasing the thermal conductivity at higher wind speeds.

The consequence of increased wind currents around and through the nests in these experiments would be a near-doubling in heat production required by the parent when incubating. There are clear energetic costs to some birds when wind speeds increase [15,45] however convection is known to influence the choice of roosting site for non-breeding birds as well. Goldfinches (Carduelis tristis) save 12% of their energy by roosting in sheltered sites, whereas heat loss from the Carolina and mountain chickadees (Parus carolinensis and Poecile gambeli) is reduced by 38 to 100% when using sheltered sites, primarily a result of reduced exposure to wind [46–48]. Keep in mind, also, that birds nesting in the wild would be subjected to wind speeds greater than those measured here and therefore the effect of wind on conductance may be more pronounced in natural systems. In addition, wind has unpredictable fluctuations in speed and direction (turbulence) in natural systems, which was not replicated here [49]. It is likely that there is
Table 4. Comparison of the thermal and structural properties of nests of Acanthagenys rufogularis and Manorina flavigula under each wind speed treatment.

<table>
<thead>
<tr>
<th>Species</th>
<th>Nest thickness (K)</th>
<th>Surface area (A)</th>
<th>Wind speed</th>
<th>Total conductance (G)</th>
<th>Surface-specific conductance (Qa)</th>
<th>Thermal conductivity (h)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>cm</td>
<td>cm²</td>
<td>mW °C⁻¹ m⁻²</td>
<td>W °C⁻¹ m⁻²</td>
<td>mW °C⁻¹ m⁻¹</td>
<td></td>
</tr>
<tr>
<td>Acanthagenys</td>
<td>0.93 ± 0.19</td>
<td>122.46 ± 12.08</td>
<td>still</td>
<td>48.4 ± 2.7</td>
<td>4.0 ± 0.4</td>
<td>36.7 ± 5.0</td>
</tr>
<tr>
<td>rufogularis</td>
<td></td>
<td></td>
<td>calm</td>
<td>51.3 ± 5.3</td>
<td>4.2 ± 0.5</td>
<td>38.7 ± 6.8</td>
</tr>
<tr>
<td>light air</td>
<td>82.7 ± 6.8</td>
<td>6.8 ± 0.8</td>
<td>63.0 ± 11.8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Manorina flavigula</td>
<td>2.96 ± 0.38</td>
<td>233.01 ± 16.82</td>
<td>still</td>
<td>46.1 ± 3.4</td>
<td>2.9 ± 0.3</td>
<td>56.8 ± 7.1</td>
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<td>light air</td>
<td>47.1 ± 5.4</td>
<td>3.1 ± 0.3</td>
<td>59.7 ± 8.9</td>
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<td></td>
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<tr>
<td>light air</td>
<td>83.9 ± 10.3</td>
<td>3.6 ± 0.6</td>
<td>105.5 ± 12.3</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Statistics include the mean ± 95% confidence interval. Surface area (A) is the geometric mean of the internal (A₁) and external (A₂) surface areas.

an ever-increasing effect of wind on convective heat loss from nests, which could considerably influence the incubation cost for the parent [44]. Further work on convective heat loss from birds’ nests under stronger wind conditions should investigate this idea.

ii) Open nests. As the rate of heat loss from open nests is greater than for sealed nests in calm air, when an incubating bird takes leave to forage in calm conditions, the clutch will be subjected to rates of heat loss between 10 to 22% higher. This can increase developmental time and decrease hatching success [30–52]. When wind speed increases to light air, unsealed A. rufogularis nests lose 11% more heat than sealed nests under comparable wind conditions. However, the difference between sealed and open nests does not hold true for M. flavigula – the sealed nest loses heat at the same rate as the open nest. The disparity between the responses of the nests of these species may be related to the nest structure. The majority of M. flavigula nests have an uneven nest rim and when viewing them from the side, many small twigs can be seen extending above the nest lip horizon at an angle. This is
rarely seen in the case of A. nygadensis nests. It may be that there is a greater opportunity for air leaks to occur in the sealed treatments for M. fasciata, compared to nests of A. nygadensis. The consequence of this may be that the rate of heat loss under light air conditions for M. fasciata nests appears more pronounced than it would be if an incubating parent was sitting on the nest, moulding their underbody to the nest edges. Alternatively, the rate of heat loss from M. fasciata nests in light air may not increase when the lid is removed, as the coarse outer structure may help to break up the flow of air around the nest to deflect some of it away from the nest opening.

If the rates of heat loss between treatments accurately represent those of attended versus unattended nests, then it means that unattended M. fasciata clutches may not cool as fast as A. nygadensis clutches at increased wind speeds. This would have some bearing on the rates of nest attendance between the two species where M. fasciata could take longer recesses and forage for greater periods, in turn reducing the cost of reproduction for this species, as occurs in other species [53–56].

10. No nest. The control treatment enables the nest data to be put into perspective. The conductance from the heat source with no protection from a nest (control) nearly tripled in light air conditions compared to when surrounded by a nest. This demonstrates that the nest does in fact help to ameliorate heat loss from the clutch by 50 to 65%, potentially reducing the energetic cost of incubation to the parent. Aar and Sids [57] found that the nest of the blackbird (Turdus merula) helped reduce heat loss from eggs in still air by 25 to 30% however cooling times were halved when wind speed increased to 2.7 km h⁻¹. In the present study, the difference in conductance from the uncovered heat source and the heat source protected by a nest increased with wind speed, suggesting that the presence of a nest becomes even more important as wind speed increases. Our findings provide further support for the benefit of selecting sheltered nest sites [13]. In addition to the nest itself, the surrounding vegetation can be important. This is the case for the song sparrow (Melospiza melodia), where nests are constructed on the lee side of the plant, such that surrounding shrubs reduce wind speed around the nest by 73% [58].

(c) Summary

Here we have shown that in still air, the two species have a similar nest conductance, a result of differences in nest dimensions. The thickness of a nest is largely driven by the need to support the clutch and incubating parent when comparing over a broad range of bird sizes [35]. In addition, the size of the inner nest cup is somewhat determined by the size of incubating parent and clutch. Therefore, it could be argued that the overall construction of a nest is fixed to some extent. However, in habitats where there are extreme temperature changes, the nature of the nest may be essential to the development of the clutch and the efficiency of temperature regulation of the young [20,29]. Therefore, the highly contrasting nest dimensions yet comparable conductance values may be indicative of the plasticity in nest design within a species, with the ultimate objective of achieving an appropriate nest microclimate. However, small birds (such as those studied here) may have more flexibility regarding structural design of nests than larger birds that may be more restricted [33]. Furthermore, as nest thickness increases with parent mass [35], the clutches of large birds may be protected from convection to a greater extent than those of small birds.

Exposing the sealed nests to greater wind speeds, raises nest conductance via a concurrent increase in the thermal conductivity. Contrary to predictions based on convective heat loss, conductance is similar in the two species, although they construct their nests in different parts of the canopy. A. nygadensis does not increase the insulative assistance of the nest to achieve the poorer protection from wind afforded by its location near the ends of branches. M. fasciata nests would potentially have greater protection from the elements due to the dense canopy near the trunk, but the nest has a thick nest wall, further adding to the protection of the offspring. The significance of convection through the nest is a near-doubling in heat production required by the parent when incubating in light air conditions. However, this may be more or less extreme for other species (University of Adelaide) to impede wind currents [17]. Heat lost from nests more rapidly during parental recesses for both species at low wind speeds, with a minimal increase in heat loss for A. nygadensis in light air. This would result in an immediate increase in heat loss from the clutch, thereby lengthening development time and reducing hatching success or chick survival [52,60,61]. The incubating or brooding parent will also be affected following a recess as extra energy will be expended to rewarm the clutch [62,63]. In conclusion, building a thermally favourable nest helps to save parental energy [13], however convection increases conductance of heat from the nest and therefore selecting an appropriate nest site that provides additional shelter is important for avian reproductive success.

Acknowledgments

We thank the South Australian Museum (in particular, Dr Philippa Horton) for use of their nest collection and invaluable nest knowledge. We appreciate the assistance of Richard Nunn (the University of Adelaide) for designing and constructing the controlled temperature power monitor circuit, as well as Georgina Alais for constructing the wind tunnel hexacomb. We also thank the reviewers for their useful comments and improving the clarity of the text.

Author Contributions

Conceived and designed the experiments: CBH RSS. Performed the experiments: CBH. Analyzed the data: CBH. Wrote the paper: CBH RSS. Designed and constructed the wind tunnel: CBH RSS.

References

The structural and thermal properties of avian cup-shaped nests


CHAPTER 7

CONCLUSION

The energy invested to maintain egg temperature and re-warm clutches that have cooled during incubation recesses can influence the outcome of current or subsequent breeding attempts and is therefore of importance to the lifetime reproductive success of birds (Reid et al. 2000b; Tinbergen and Williams 2002). The energetic demand of incubation varies within and between species, where differences arise from the body mass of the incubating parent (Williams 1996), the microclimate within and around the nest (Walsberg 1985), patterns of nest attendance (de Heij et al. 2008), egg morphology (Turner 2002) and the thermal properties of the nest (Walsberg 1978). Ultimately, the energetic cost of incubation is determined by the rate at which heat energy is lost from the clutch and incubating parent (Hilton et al. 2004). Therefore the thermal properties of nests are important to birds, though few researchers have attempted to quantify the heat loss from nests.

The present study details our investigations of the thermal properties of avian nests, quantified in terms of the nest conductance (the inverse of insulation). Nest conductance is influenced by the materials used in nest construction, the surface area of the nest cavity and the thickness of the nest wall. Therefore, we address each of these factors and consider how and why materials and dimensions vary in nests. The analyses look inter- and intra-specifically, while accounting for phylogenetic relatedness, to give a well-rounded view of nest design.

By measuring nest structural and thermal properties for 36 species of Australian passerines and assessing the data allometrically (i.e. relative to the body mass of the incubating parent), we show that nest design is influenced by the size of the parent and clutch. The surface area and volume of the nest cup is influenced by the clutch surface area and volume, respectively, as well as the size of the incubating parent. Larger birds lay larger eggs and construct larger nests which, in turn, have a higher thermal conductance. However, egg size becomes a smaller proportion of the female mass for larger birds than we would expect, suggesting that large females allocate a relatively smaller proportion of their energetic reserves to a reproductive attempt compared to small birds. Egg size and clutch size are not only influenced by the absolute mass of the female, but also by the ratio of male body mass to female body mass, or sexual size dimorphism. There appears to be a trade-off between egg size and clutch size that is driven by the relative size of the sexes within a species, such that the overall volume of a clutch is defined only by the absolute size of the bird. In addition to the eggs, sexual size dimorphism influences the mass and density of the nest.

However, structural support for the parent and clutch is the primary factor driving nest thickness. A change in nest thickness with the combined mass of the parent and clutch has a direct influence on the conductance of nests, such that structurally adequate nests achieve a lower thermal conductance (higher insulation) than expected, as they increase in size. This suggests that the nest does provide sufficient insulation to ameliorate
heat loss from the parent, at least in large birds. However, this assumes that the parent, nest and the clutch within are in a steady-state condition (continuous incubation in a dry nest with no wind).

When exposed to windy conditions, the rate of heat loss from the nest increases, which is likely to have direct consequences on the energetics of the incubating parent. When the nest becomes wet the thermal conductivity of the materials increases, which also increases the total nest conductance. Again, the energetics of the incubating bird will be affected. The increase in nest conductance with convection and precipitation may not be an issue if the parent can modify incubation attendance patterns, in order to forage and obtain sufficient food resources, to counter the high energetic demand of incubation. In addition, the choice of materials used in nest construction can reduce the energetic cost of maintaining the nest temperature in wet conditions. By constructing a nest with anthropogenic materials, or natural materials with a high thermal conductivity, birds breeding in warm and wet climates can accelerate the nest drying process to reduce the overall cost of incubation.

There are a number of factors that influence nest construction that were not considered in the present study. As well as providing a thermal barrier and structural support, birds’ nests provide environments in which the parent can moderate the humidity and gas composition around the eggs (Ar and Sidis 2002; Hansell and Deeming 2002; Seymour and Ackerman 1980), provide camouflage and concealment from predators (Crossman et al. 2011; Hansell 1996; Orr 1970; Prokop and Trnka 2011), control ectoparasites (Clark and Mason 1985; 1988; Wimberger 1984), as well as display for mate attraction (Broggi and Senar 2009; Brouwer and Komdeur 2004; Palomino et al. 1998). In addition, nest size or design may be constrained due to the energetic cost of construction (Wiebe and Swift 2001; Withers 1977), the time required to construct a nest (Mainwaring and Hartley 2008), predation during material collection and the conspicuousness of a nest once construction is complete (Franklin 1995; Mayer et al. 2009; Møller 1990). Therefore it is possible that some of the interspecific variation in nest dimensions or materials within our data may be accounted for by other factors and requires further study. It would be of interest to assess nest construction and thermal properties as well as egg morphology of non-passerines, as the two avian groups are known to differ allometrically for some variables (Peters 1983; Schmidt-Nielsen 1984). For example, egg mass for passerines scales with adult mass with an exponent of 0.73 (Ricklefs 1974), while for non-passerines the exponent is 0.68 (Cabana et al. 1982). In addition, metabolic rates of the two avian groups is known to differ (Lasiewski and Dawson 1967; McKechnie et al. 2006) and therefore the energetic cost of incubation may also be influenced by avian phylogenetic grouping.

At the beginning of this dissertation we asked if the nest provides sufficient insulation to ameliorate heat loss from the parent and which factors influence conductance. In summary, the parent, clutch and local climate conditions influence nest conductance, via the thermal properties of the materials used in nest construction and variation in the nest dimensions. While low temperatures, wind and rain can increase heat loss from the nest, nests are effectively over-insulated for the sake of structural support and so incubation may only be energetically demanding for small birds or in extreme weather conditions. Furthermore, birds are
known to select nest sites that offer appropriate shelter from the elements to further reduce heat loss, or exposure to solar radiation to increase heat gain (D’Alba et al. 2009; Horvath 1964; Kim and Monaghan 2005; Tieleman et al. 2008).
The structural and thermal properties of avian cup-shaped nests
APPENDICES

APPENDIX 1: IMAGES OF CUP-SHAPED NESTS OF AUSTRALIAN PASSERINES
APPENDIX 2: THE THERMAL PROPERTIES OF AVIAN CUP-SHAPED NESTS
APPENDIX 3: THE PHYSICAL DIMENSIONS AND MASS OF AVIAN CUP-SHAPED NESTS
APPENDIX 4: THE VOLUME, DENSITY AND SURFACE AREAS OF AVIAN CUP-SHAPED NESTS
APPENDIX 5: IMAGES OF EGGS OF AUSTRALIAN PASSERINES
APPENDIX 6: OOMORPHOLOGY MACRO
APPENDIX 7: ELECTRONIC SUPPLEMENTARY MATERIAL
APPENDIX 8: SHAPE PARAMETERS OF AVIAN EGGS
APPENDIX 9: AVIAN EGG SIZE
APPENDIX 10: MATERIAL USE IN AVIAN CUP-SHAPED NESTS
APPENDIX 11: METHODS OF ATTACHMENT BETWEEN CUP-SHAPED NESTS AND HOST BRANCH
APPENDIX 12: COLLECTION LOCATION, ATTACHMENT METHOD, WEAVE AND NEST MATERIAL USE FOR CUP-SHAPED NESTS OF AUSTRALIAN PASSERINES
APPENDIX 13: NESTS OF GLICIPHILA MELANOPS
Figure A1.1.a. Nest of *Acanthorhynchus tenuirostris* (1/3).
Figure A1.1.b. Nest of *Acanthorhynchus tenuirostris* (2/3).
The structural and thermal properties of avian cup-shaped nests

Figure A1.1.c. Nest of *Acanthorhynchus tenuirostris* (3/3).
Figure A1.2. Nest of *Anthochaera carunculata*. 
Figure A1.3. Nest of Anthochaera chrysoptera.
Figure A1.4. Nest of *Colluricincla harmonica*. 
Figure A1.5. Nest of Corcorax melanorhamphos.
Figure A1.6. Nest of *Cracticus torquatus*.
Figure A1.7. Nest of *Daphoenositta chrysoptera*. 
Figure A1.8. Nest of *Eopsaltria australis*. 
The structural and thermal properties of avian cup-shaped nests

Figure A1.9. Nest of *Grallina cyanoleuca*. 
Figure A1.10.a. Nest of *Lichenostomus chrysops* (1/2).
Figure A1.10.b. Nest of *Lichenostomus chrysops* (2/2).
Figure A1.11. Nest of *Lichenostomus cratitius*. 
The structural and thermal properties of avian cup-shaped nests

Figure A1.12. Nest of Lichenostomus leucotis.
Figure A1.13. Nest of *Lichenostomus ornatus*.
The structural and thermal properties of avian cup-shaped nests

Figure A1.14. Nest of *Lichenostomus penicillatus*. 
Figure A1.15. Nest of *Lichenostomus plumulus*.
The structural and thermal properties of avian cup-shaped nests

Figure A1.16. Nest of *Lichenostomus virescens*. 
Figure A1.17. Nest of *Lichmera indistincta*.
The structural and thermal properties of avian cup-shaped nests

Figure A1.18. Nest of *Manorina flavigula*. 
Figure A1.19. Nest of *Melanodryas cucullata*.
The structural and thermal properties of avian cup-shaped nests

Figure A1.20. Nest of *Melanodryas vittata*.
Figure A1.21. Nest of *Microeca fascinans*. 
Figure A1.22. Nest of *Oriolus sagittatus*. 
Figure A1.23. Nest of *Pachycephala inornata*.
The structural and thermal properties of avian cup-shaped nests

Figure A1.24. Nest of *Pachycephala olivacea*. 
Figure A1.25. Nest of *Pachycephala pectoralis*. 
Figure A1.26. Nest of *Pachycephala rufiventris*. 
Figure A1.27. Nest of *Pachycepha  rufogularis*. 
The structural and thermal properties of avian cup-shaped nests

Figure A1.28. Nest of *Petroica goodenovii*. 
Figure A1.29. Nest of *Petroica multicolour*. 
Figure A1.30. Nest of Psophodes nigrogularis.
Figure A1.31. Nest of *Rhipidura albiscapa*.
The structural and thermal properties of avian cup-shaped nests

Figure A1.32. Nest of *Rhipidura leucophrys*. 
Figure A1.33. Nest of Strepera versicolor.
The structural and thermal properties of avian cup-shaped nests

Figure A1.34. Nest of *Struthidea cinerea*.
Figure A1.35. Nest of *Turdus merula*.
Figure A1.36. Nest of *Zosterops lateralis*. 
## APPENDIX 2: THE THERMAL PROPERTIES OF AVIAN CUP-SHAPED NESTS

<table>
<thead>
<tr>
<th>bird species</th>
<th>N</th>
<th>parent mass (g)</th>
<th>total nest conductance (G, mW °C⁻¹)</th>
<th>surface-specific nest conductance (Gₐ, W °C⁻¹ m⁻²)</th>
<th>thermal conductivity (k, mW °C⁻¹ m⁻¹)</th>
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<tr>
<td>Acanthorhynchus tenuirostris</td>
<td>6</td>
<td>11</td>
<td>77.40 ± 5.61</td>
<td>10.46 ± 2.08</td>
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<td>107.37 ± 19.84</td>
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<td>Microeca fascinans</td>
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<td>173.42 ± 47.00</td>
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<tr>
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<td>8.03 ± 2.78</td>
<td>132.83 ± 22.57</td>
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<tr>
<td>Pachycephala inornata</td>
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<td>98.98 ± 14.16</td>
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<td>210.30</td>
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<td>40</td>
<td>77.51</td>
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<td>127.24 ± 55.64</td>
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<tr>
<td>Pachycephala pectoralis</td>
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<td>25</td>
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<td>9.15 ± 0.96</td>
<td>136.00 ± 14.45</td>
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<td>Pachycephala rufigularis</td>
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<td>6.35 ± 1.27</td>
<td>141.49 ± 30.74</td>
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<tr>
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<td>26.15 ± 12.84</td>
<td>278.19 ± 59.38</td>
</tr>
<tr>
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<td>13</td>
<td>96.99 ± 46.98</td>
<td>15.96 ± 10.90</td>
<td>127.24 ± 55.64</td>
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<tr>
<td>Psophodes nigrogularis</td>
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<td>98.43 ± 4.45</td>
<td>5.90 ± 2.05</td>
<td>167.79 ± 47.44</td>
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<tr>
<td>Rhipidura albiscapa</td>
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<td>8</td>
<td>75.32 ± 7.92</td>
<td>14.21 ± 1.85</td>
<td>219.97 ± 43.17</td>
</tr>
<tr>
<td>Rhipidura leucophrys</td>
<td>9</td>
<td>18</td>
<td>91.14 ± 14.02</td>
<td>12.88 ± 1.71</td>
<td>128.06 ± 21.88</td>
</tr>
<tr>
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<td>232.69</td>
<td>3.27</td>
<td>274.65</td>
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<tr>
<td>Struthidea cinerea</td>
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<td>122.83 ± 53.91</td>
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<tr>
<td>Turdus merula</td>
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<td>89.10 ± 6.82</td>
<td>3.50 ± 0.31</td>
<td>116.43 ± 10.51</td>
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<tr>
<td>Zosterops lateralis</td>
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<td>11</td>
<td>114.91 ± 19.20</td>
<td>19.91 ± 4.43</td>
<td>145.35 ± 28.51</td>
</tr>
</tbody>
</table>

Values represent the mean ± 95 % C.I. for a species of bird.

* Values that do not have a listed confidence interval were not measured with significant replication to enable calculation of a confidence interval.
APPENDIX 3: THE PHYSICAL DIMENSIONS AND MASS OF AVIAN CUP-SHAPED NESTS

<table>
<thead>
<tr>
<th>bird species</th>
<th>N</th>
<th>nest surface area (Å, cm$^2$)</th>
<th>nest thickness (X, cm)</th>
<th>internal diameter (d$_I$, cm)</th>
<th>external diameter (d$_E$, cm)</th>
<th>internal height (h$_I$, cm)</th>
<th>external height (h$_E$, cm)</th>
<th>nest mass (M$_N$, g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthorhynchus tenuirostris</td>
<td>6.5</td>
<td>77.79 ± 15.45</td>
<td>1.17 ± 0.36</td>
<td>5.20 ± 0.44</td>
<td>7.68 ± 0.40</td>
<td>3.82 ± 1.08</td>
<td>4.92 ± 1.38</td>
<td>5.06 ± 1.82</td>
</tr>
<tr>
<td>Anthochaera carunculata</td>
<td>9.7</td>
<td>236.89 ± 45.40</td>
<td>2.99 ± 0.66</td>
<td>9.27 ± 0.52</td>
<td>16.54 ± 1.49</td>
<td>5.36 ± 0.86</td>
<td>7.71 ± 1.34</td>
<td>46.72 ± 16.13</td>
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<tr>
<td>Anthochaera chrysoptera</td>
<td>8.8</td>
<td>132.17 ± 19.03</td>
<td>1.64 ± 0.37</td>
<td>8.33 ± 0.16</td>
<td>12.07 ± 0.88</td>
<td>3.75 ± 0.42</td>
<td>5.15 ± 0.57</td>
<td>15.04 ± 2.85</td>
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<td>Colluricincia harmonica</td>
<td>4.4</td>
<td>223.02 ± 49.30</td>
<td>3.30 ± 1.26</td>
<td>8.25 ± 0.47</td>
<td>14.04 ± 2.65</td>
<td>5.66 ± 1.22</td>
<td>9.35 ± 3.09</td>
<td>111.58 ± 98.16</td>
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<tr>
<td>Corcorax melanorhamphos</td>
<td>4.0</td>
<td>647.82 ± 222.38</td>
<td>4.57 ± 1.37</td>
<td>17.78 ± 1.09</td>
<td>22.71 ± 2.01</td>
<td>8.28 ± 3.34</td>
<td>14.95 ± 3.64</td>
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<td>Cracticus torquatus</td>
<td>2.2</td>
<td>266.22 ± 34.83</td>
<td>3.19 ± 0.97</td>
<td>10.20 ± 0.59</td>
<td>18.14 ± 2.12</td>
<td>5.35 ± 0.29</td>
<td>6.67 ± 1.50</td>
<td>14.84 ± 3.14</td>
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<tr>
<td>Daphoenositta chrysoperta</td>
<td>3.2</td>
<td>84.25 ± 10.64</td>
<td>1.97 ± 0.23</td>
<td>5.40 ± 0.34</td>
<td>6.36 ± 0.45</td>
<td>3.77 ± 0.51</td>
<td>7.23 ± 0.35</td>
<td>17.45 ± 3.12</td>
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<td>Eopsaltria australis</td>
<td>9.7</td>
<td>93.45 ± 9.95</td>
<td>2.09 ± 0.69</td>
<td>5.95 ± 0.27</td>
<td>7.86 ± 0.40</td>
<td>3.45 ± 0.22</td>
<td>6.67 ± 1.50</td>
<td>14.84 ± 3.14</td>
</tr>
<tr>
<td>Grallina cyanoleuca</td>
<td>8.0</td>
<td>294.02 ± 28.44</td>
<td>3.19 ± 0.97</td>
<td>10.20 ± 0.59</td>
<td>13.65 ± 0.64</td>
<td>6.82 ± 0.27</td>
<td>10.40 ± 1.32</td>
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</tr>
<tr>
<td>Lichenostomus chrysops</td>
<td>7.2</td>
<td>75.47 ± 6.85</td>
<td>0.84 ± 0.27</td>
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<td>7.25 ± 0.69</td>
<td>3.80 ± 0.51</td>
<td>4.67 ± 0.67</td>
<td>5.30 ± 2.30</td>
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<td>Lichenostomus cratitius</td>
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<td>94.33 ± 6.21</td>
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<td>7.91 ± 0.56</td>
<td>4.38 ± 0.39</td>
<td>5.78 ± 0.92</td>
<td>10.27 ± 1.65</td>
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<tr>
<td>Lichenostomus leucotis</td>
<td>4.1*</td>
<td>107.68 ± 16.11</td>
<td>1.29 ± 0.78</td>
<td>5.48 ± 0.20</td>
<td>7.32 ± 0.43</td>
<td>5.58 ± 0.88</td>
<td>7.23 ± 1.44</td>
<td>8.00</td>
</tr>
<tr>
<td>Lichenostomus omnatus</td>
<td>1*,1*</td>
<td>63.86</td>
<td>0.47</td>
<td>4.90</td>
<td>6.06</td>
<td>4.00</td>
<td>4.35</td>
<td>2.70</td>
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<tr>
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<td>82.36 ± 12.70</td>
<td>1.09 ± 0.47</td>
<td>5.33 ± 0.21</td>
<td>7.31 ± 0.58</td>
<td>4.10 ± 0.54</td>
<td>5.28 ± 0.97</td>
<td>4.40</td>
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<td>92.21</td>
<td>1.62</td>
<td>5.40</td>
<td>8.88</td>
<td>3.90</td>
<td>5.40</td>
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<td>Lichenostomus virescens</td>
<td>7.6</td>
<td>98.30 ± 15.60</td>
<td>1.17 ± 0.21</td>
<td>6.10 ± 0.58</td>
<td>8.53 ± 0.54</td>
<td>4.10 ± 0.49</td>
<td>5.23 ± 0.54</td>
<td>6.95 ± 2.13</td>
</tr>
<tr>
<td>Lichmera indistincta</td>
<td>5.1*</td>
<td>58.37 ± 3.14</td>
<td>0.88 ± 0.14</td>
<td>4.75 ± 0.30</td>
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<td>3.18 ± 0.43</td>
<td>4.01 ± 0.24</td>
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<td>2.89 ± 0.46</td>
<td>9.24 ± 0.49</td>
<td>15.47 ± 1.10</td>
<td>5.80 ± 0.33</td>
<td>8.47 ± 0.67</td>
<td>40.77 ± 7.93</td>
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<td>Melanodryas cucullata</td>
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<td>95.50 ± 5.97</td>
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<td>6.00 ± 0.15</td>
<td>8.46 ± 0.50</td>
<td>3.82 ± 0.23</td>
<td>5.51 ± 0.53</td>
<td>21.65 ± 2.54</td>
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<td>6.90</td>
<td>9.30</td>
<td>3.60</td>
<td>4.60</td>
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<td>2.05 ± 0.29</td>
<td>3.15 ± 1.27</td>
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<td>233.51 ± 26.05</td>
<td>1.66 ± 1.01</td>
<td>10.35 ± 1.27</td>
<td>13.87 ± 0.57</td>
<td>5.65 ± 0.88</td>
<td>7.20 ± 0.78</td>
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<td>4.33 ± 0.77</td>
<td>5.64 ± 1.22</td>
<td>26.69 ± 7.38</td>
</tr>
<tr>
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<td>1*,1*</td>
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<td>5.27</td>
<td>7.20</td>
<td>11.28</td>
<td>4.60</td>
<td>13.10</td>
<td>71.20</td>
</tr>
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<td>bird species</td>
<td>N^</td>
<td>nest surface area (A, cm²)</td>
<td>nest thickness (X, cm)</td>
<td>internal diameter (d₁, cm)</td>
<td>external diameter (dₑ, cm)</td>
<td>internal height (h₁, cm)</td>
<td>external height (hₑ, cm)</td>
<td>nest mass (Mₙ, g)</td>
</tr>
<tr>
<td>------------------------------</td>
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<td>------------------------</td>
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<td>---------------------------</td>
<td>--------------------------</td>
<td>--------------------------</td>
<td>---------------------</td>
</tr>
<tr>
<td>Pachycephala pectoralis</td>
<td>19</td>
<td>97.69 ± 7.51</td>
<td>1.50 ± 0.10</td>
<td>6.42 ± 0.13</td>
<td>9.10 ± 0.35</td>
<td>3.56 ± 0.30</td>
<td>5.22 ± 0.35</td>
<td>9.74 ± 1.40</td>
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<tr>
<td>Pachycephala rufiventris</td>
<td>7</td>
<td>86.49 ± 14.04</td>
<td>1.14 ± 0.21</td>
<td>6.58 ± 0.41</td>
<td>8.88 ± 0.65</td>
<td>3.25 ± 0.55</td>
<td>4.39 ± 0.58</td>
<td>8.12 ± 1.67</td>
</tr>
<tr>
<td>Pachycephala rufogularis</td>
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<td>163.21 ± 22.00</td>
<td>2.30 ± 0.54</td>
<td>7.03 ± 0.52</td>
<td>11.87 ± 1.33</td>
<td>5.17 ± 0.55</td>
<td>7.35 ± 0.76</td>
<td>50.83 ± 13.31</td>
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<tr>
<td>Petroica goodenovii</td>
<td>3</td>
<td>54.60 ± 12.08</td>
<td>1.19 ± 0.56</td>
<td>4.47 ± 0.13</td>
<td>5.88 ± 0.45</td>
<td>3.00 ± 0.41</td>
<td>4.67 ± 1.31</td>
<td>-</td>
</tr>
<tr>
<td>Petroica multicolor</td>
<td>3</td>
<td>67.77 ± 20.74</td>
<td>0.90 ± 0.29</td>
<td>4.87 ± 0.40</td>
<td>6.80 ± 0.49</td>
<td>3.70 ± 0.99</td>
<td>4.53 ± 1.54</td>
<td>11.70 ± 4.48</td>
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<tr>
<td>Psophodes nigrogularis</td>
<td>5</td>
<td>183.98 ± 49.16</td>
<td>3.17 ± 1.44</td>
<td>7.98 ± 0.40</td>
<td>12.76 ± 0.82</td>
<td>4.80 ± 1.08</td>
<td>8.74 ± 3.59</td>
<td>48.52 ± 21.46</td>
</tr>
<tr>
<td>Rhipidura albiscapa</td>
<td>14</td>
<td>53.94 ± 4.04</td>
<td>1.53 ± 0.20</td>
<td>4.35 ± 0.17</td>
<td>5.55 ± 0.15</td>
<td>2.90 ± 0.33</td>
<td>5.35 ± 0.39</td>
<td>-</td>
</tr>
<tr>
<td>Rhipidura leucophrys</td>
<td>9</td>
<td>70.88 ± 5.07</td>
<td>1.02 ± 0.17</td>
<td>5.75 ± 0.27</td>
<td>7.38 ± 0.34</td>
<td>3.02 ± 0.13</td>
<td>4.24 ± 0.25</td>
<td>13.43 ± 5.94</td>
</tr>
<tr>
<td>Strepera versicolor</td>
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<td>710.82</td>
<td>8.39</td>
<td>16.60</td>
<td>35.56</td>
<td>6.90</td>
<td>14.20</td>
<td>-</td>
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<tr>
<td>Struthidea cinerea</td>
<td>2</td>
<td>364.50 ± 45.59</td>
<td>2.47 ± 0.74</td>
<td>12.16 ± 0.12</td>
<td>15.26 ± 0.39</td>
<td>7.74 ± 0.67</td>
<td>11.13 ± 2.02</td>
<td>218.81 ± 54.06</td>
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<tr>
<td>Turdus merula</td>
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<td>256.44 ± 19.20</td>
<td>3.34 ± 0.23</td>
<td>9.41 ± 0.58</td>
<td>14.77 ± 0.87</td>
<td>5.68 ± 0.49</td>
<td>9.68 ± 0.51</td>
<td>-</td>
</tr>
<tr>
<td>Zosterops lateralis</td>
<td>21</td>
<td>61.56 ± 6.04</td>
<td>0.78 ± 0.10</td>
<td>5.42 ± 0.37</td>
<td>7.26 ± 0.43</td>
<td>3.05 ± 0.27</td>
<td>3.69 ± 0.26</td>
<td>3.66 ± 0.64</td>
</tr>
</tbody>
</table>

Values represent the mean ± 95% C.I. for a species of bird.
* Values that do not have a listed confidence interval were not measured with significant replication to enable calculation of a confidence interval.
^ Replicate values (N) separated by commas indicate the replicate for the nest dimensions, followed by the replicate for the nest mass measurements. Multiple nests and species could not be included in nest mass analysis due to the attachment of supporting branches.
### APPENDIX 4: THE VOLUME, DENSITY AND SURFACE AREAS OF AVIAN CUP-SHAPED NESTS

<table>
<thead>
<tr>
<th>bird species</th>
<th>N^</th>
<th>nest cup volume (V&lt;sub&gt;CUP&lt;/sub&gt;, cm³)</th>
<th>nest wall volume (V&lt;sub&gt;N&lt;/sub&gt;, cm³)</th>
<th>nest wall density (ρ, g cm&lt;sup&gt;-3&lt;/sup&gt;)</th>
<th>nest opening surface area (A&lt;sub&gt;LID&lt;/sub&gt;, cm²)</th>
<th>internal nest surface area (A&lt;sub&gt;I&lt;/sub&gt;, cm²)</th>
<th>external nest surface area (A&lt;sub&gt;E&lt;/sub&gt;, cm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthorhynchus tenuirostris</td>
<td>6.5</td>
<td>52.54 ± 11.06</td>
<td>97.43 ± 43.49</td>
<td>0.06 ± 0.02</td>
<td>21.44 ± 3.79</td>
<td>55.80 ± 10.10</td>
<td>109.56 ± 26.51</td>
</tr>
<tr>
<td>Anthochaera carunculata</td>
<td>9.8</td>
<td>244.48 ± 61.78</td>
<td>785.74 ± 301.44</td>
<td>0.07 ± 0.02</td>
<td>67.88 ± 7.76</td>
<td>148.37 ± 28.53</td>
<td>384.63 ± 86.02</td>
</tr>
<tr>
<td>Anthochaera chrysoptera</td>
<td>8.7</td>
<td>120.17 ± 22.66</td>
<td>229.58 ± 85.49</td>
<td>0.07 ± 0.02</td>
<td>54.47 ± 2.05</td>
<td>93.35 ± 11.33</td>
<td>188.64 ± 35.10</td>
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<tr>
<td>Colluricincla harmonica</td>
<td>4.4</td>
<td>200.36 ± 43.31</td>
<td>743.97 ± 366.58</td>
<td>0.15 ± 0.08</td>
<td>53.53 ± 6.08</td>
<td>134.12 ± 21.51</td>
<td>375.29 ± 116.32</td>
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<tr>
<td>Corcorax melanorhamphos</td>
<td>4.0</td>
<td>1259.96 ± 860.38</td>
<td>2788.40 ± 1132.59</td>
<td>-</td>
<td>248.87 ± 30.70</td>
<td>435.81 ± 202.21</td>
<td>980.63 ± 266.54</td>
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<tr>
<td>C ractis torquatus</td>
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<td>289.78 ± 14.77</td>
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<td>0.11 ± 0.02</td>
<td>81.78 ± 9.42</td>
<td>168.23 ± 5.40</td>
<td>422.35 ± 96.68</td>
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<tr>
<td>Daphoenositta chrysoptera</td>
<td>3.2</td>
<td>57.90 ± 19.44</td>
<td>96.14 ± 28.54</td>
<td>0.18 ± 0.01</td>
<td>27.92 ± 2.44</td>
<td>61.30 ± 4.53</td>
<td>144.10 ± 26.29</td>
</tr>
<tr>
<td>Grallina cyanoleuca</td>
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<td>419.28 ± 46.53</td>
<td>615.45 ± 180.96</td>
<td>-</td>
<td>91.93 ± 7.38</td>
<td>216.57 ± 15.67</td>
<td>402.27 ± 57.87</td>
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<td>59.27 ± 5.29</td>
<td>62.76 ± 24.76</td>
<td>0.06 ± 0.01</td>
<td>25.23 ± 5.09</td>
<td>59.86 ± 3.76</td>
<td>95.76 ± 13.85</td>
</tr>
<tr>
<td>Lichenostomus cratilis</td>
<td>6.3</td>
<td>72.23 ± 4.98</td>
<td>116.65 ± 30.08</td>
<td>0.09 ± 0.03</td>
<td>25.08 ± 3.58</td>
<td>68.92 ± 2.55</td>
<td>129.76 ± 15.91</td>
</tr>
<tr>
<td>Lichenostomus leucotis</td>
<td>4.1*</td>
<td>87.83 ± 16.35</td>
<td>117.56 ± 61.40</td>
<td>0.11</td>
<td>23.57 ± 1.74</td>
<td>81.92 ± 12.32</td>
<td>143.03 ± 32.68</td>
</tr>
<tr>
<td>Lichenostomus ornatus</td>
<td>1*,1*</td>
<td>50.29</td>
<td>33.36</td>
<td>0.08</td>
<td>18.86</td>
<td>54.36</td>
<td>75.02</td>
</tr>
<tr>
<td>Lichenostomus penicillatus</td>
<td>6.1*</td>
<td>61.22 ± 9.28</td>
<td>91.82 ± 42.79</td>
<td>0.05</td>
<td>22.38 ± 1.73</td>
<td>61.46 ± 7.09</td>
<td>111.28 ± 24.82</td>
</tr>
<tr>
<td>Lichenostomus plumulos</td>
<td>1*,0</td>
<td>59.55</td>
<td>163.41</td>
<td>-</td>
<td>22.90</td>
<td>59.86</td>
<td>142.06</td>
</tr>
<tr>
<td>Lichenostomus virescens</td>
<td>7.6</td>
<td>82.56 ± 23.85</td>
<td>119.90 ± 22.57</td>
<td>0.06 ± 0.02</td>
<td>29.64 ± 5.71</td>
<td>73.08 ± 13.81</td>
<td>132.65 ± 18.24</td>
</tr>
<tr>
<td>Lichmera indistincta</td>
<td>5*,1</td>
<td>37.00 ± 4.09</td>
<td>54.63 ± 6.75</td>
<td>0.05</td>
<td>17.76 ± 2.27</td>
<td>43.40 ± 3.55</td>
<td>78.60 ± 3.80</td>
</tr>
<tr>
<td>Manorina flavigula</td>
<td>7.7</td>
<td>259.84 ± 26.31</td>
<td>804.75 ± 167.18</td>
<td>0.05 ± 0.01</td>
<td>67.40 ± 7.30</td>
<td>157.66 ± 10.61</td>
<td>399.11 ± 48.00</td>
</tr>
<tr>
<td>Melanodryas cucullata</td>
<td>5.2</td>
<td>72.20 ± 7.13</td>
<td>136.42 ± 45.18</td>
<td>0.14 ± 0.08</td>
<td>28.29 ± 1.41</td>
<td>67.17 ± 4.64</td>
<td>136.17 ± 18.43</td>
</tr>
<tr>
<td>Melanodryas vitattata</td>
<td>1*,1</td>
<td>89.74</td>
<td>116.33</td>
<td>0.09</td>
<td>37.39</td>
<td>76.96</td>
<td>133.92</td>
</tr>
<tr>
<td>Microeca fascinans</td>
<td>2.0</td>
<td>20.86 ± 6.80</td>
<td>39.49 ± 42.73</td>
<td>-</td>
<td>17.36 ± 1.45</td>
<td>29.10 ± 6.22</td>
<td>58.01 ± 33.00</td>
</tr>
<tr>
<td>Oriolus sagittatus</td>
<td>2.0</td>
<td>321.32 ± 127.68</td>
<td>388.44 ± 174.91</td>
<td>-</td>
<td>84.47 ± 20.71</td>
<td>179.49 ± 48.09</td>
<td>305.76 ± 14.14</td>
</tr>
<tr>
<td>Pachycephala inornata</td>
<td>7.7</td>
<td>113.84 ± 26.50</td>
<td>306.66 ± 149.60</td>
<td>0.12 ± 0.06</td>
<td>42.78 ± 5.45</td>
<td>90.85 ± 14.54</td>
<td>210.09 ± 58.93</td>
</tr>
<tr>
<td>Pachycephala olivacea</td>
<td>1*,1</td>
<td>124.86</td>
<td>747.89</td>
<td>0.10</td>
<td>40.72</td>
<td>96.87</td>
<td>389.43</td>
</tr>
<tr>
<td>bird species</td>
<td>N^</td>
<td>nest cup volume ($V_{\text{cup}}$, cm³)</td>
<td>nest wall volume ($V_{\text{w}}$, cm³)</td>
<td>nest wall density ($\rho$, g cm⁻³)</td>
<td>nest opening surface area ($A_{\text{LID}}$, cm²)</td>
<td>internal nest surface area ($A_{\text{I}}$, cm²)</td>
<td>external nest surface area ($A_{\text{E}}$, cm²)</td>
</tr>
<tr>
<td>---------------------------</td>
<td>----</td>
<td>----------------------------------------</td>
<td>----------------------------------------</td>
<td>-------------------------------------</td>
<td>-----------------------------------------------</td>
<td>-----------------------------------------------</td>
<td>-----------------------------------------------</td>
</tr>
<tr>
<td><em>Pachycephala pectoralis</em></td>
<td>19,19</td>
<td>74.95 ± 8.93</td>
<td>145.96 ± 19.81</td>
<td>0.07 ± 0.01</td>
<td>32.44 ± 1.30</td>
<td>68.14 ± 5.82</td>
<td>140.49 ± 10.81</td>
</tr>
<tr>
<td><em>Pachycephala rufiventris</em></td>
<td>7,6</td>
<td>67.33 ± 16.38</td>
<td>106.21 ± 28.54</td>
<td>0.08 ± 0.02</td>
<td>34.24 ± 4.35</td>
<td>63.33 ± 10.74</td>
<td>118.52 ± 19.93</td>
</tr>
<tr>
<td><em>Pachycephala rufogularis</em></td>
<td>6,6</td>
<td>134.52 ± 22.65</td>
<td>423.15 ± 142.44</td>
<td>0.12 ± 0.02</td>
<td>39.12 ± 5.48</td>
<td>103.15 ± 12.09</td>
<td>259.81 ± 47.49</td>
</tr>
<tr>
<td><em>Petroica goodenovii</em></td>
<td>3,0</td>
<td>31.48 ± 6.17</td>
<td>54.78 ± 31.12</td>
<td>-</td>
<td>15.68 ± 0.92</td>
<td>38.79 ± 5.44</td>
<td>77.20 ± 23.92</td>
</tr>
<tr>
<td><em>Petroica multicolor</em></td>
<td>3,2</td>
<td>46.83 ± 12.71</td>
<td>64.62 ± 21.98</td>
<td>0.23 ± 0.03</td>
<td>18.67 ± 2.88</td>
<td>51.07 ± 9.17</td>
<td>89.96 ± 14.22</td>
</tr>
<tr>
<td><em>Psophodes nigrogularis</em></td>
<td>5,5</td>
<td>155.41 ± 53.59</td>
<td>541.95 ± 262.23</td>
<td>0.10 ± 0.02</td>
<td>50.15 ± 5.04</td>
<td>110.90 ± 27.17</td>
<td>309.44 ± 103.92</td>
</tr>
<tr>
<td><em>Rhipidura albiscapa</em></td>
<td>14,0</td>
<td>29.01 ± 4.41</td>
<td>57.20 ± 6.84</td>
<td>-</td>
<td>14.97 ± 1.15</td>
<td>36.67 ± 4.06</td>
<td>80.13 ± 5.21</td>
</tr>
<tr>
<td><em>Rhipidura leucophrys</em></td>
<td>9,4</td>
<td>52.01 ± 5.91</td>
<td>70.12 ± 14.36</td>
<td>0.22 ± 0.12</td>
<td>26.10 ± 2.39</td>
<td>53.38 ± 4.09</td>
<td>94.48 ± 8.45</td>
</tr>
<tr>
<td><em>Strepera versicolor</em></td>
<td>1*,0</td>
<td>827.63</td>
<td>6681.11</td>
<td>-</td>
<td>216.42</td>
<td>340.34</td>
<td>1484.58</td>
</tr>
<tr>
<td><em>Struthidea cinerea</em></td>
<td>2,0</td>
<td>599.52 ± 63.19</td>
<td>761.07 ± 252.72</td>
<td>-</td>
<td>116.14 ± 2.25</td>
<td>275.61 ± 21.06</td>
<td>482.36 ± 83.73</td>
</tr>
<tr>
<td><em>Turdus merula</em></td>
<td>8,8</td>
<td>262.21 ± 32.58</td>
<td>848.53 ± 104.33</td>
<td>0.26 ± 0.05</td>
<td>70.06 ± 8.17</td>
<td>158.26 ± 13.67</td>
<td>416.23 ± 31.30</td>
</tr>
<tr>
<td><em>Zosterops lateralis</em></td>
<td>21,14</td>
<td>44.11 ± 8.08</td>
<td>50.66 ± 8.15</td>
<td>0.08 ± 0.03</td>
<td>23.65 ± 3.44</td>
<td>47.89 ± 5.26</td>
<td>79.48 ± 7.49</td>
</tr>
</tbody>
</table>

Values represent the mean ± 95 % C.I. for a species of bird.

* Values that do not have a listed confidence interval were not measured with significant replication to enable calculation of a confidence interval.

^ Replicate values (N) separated by commas indicate the replicate for the nest dimensions, followed by the replicate for the nest density measurements. Multiple nests and species could not be included in nest density analysis due to the attachment of supporting branches contributing to the mass component.
Figure A5.1. Egg of Acanthorhynchus tenuirostris.
Figure A5.2. Egg of Anthochaera carunculata.
Figure A5.3. Egg of *Anthochara chrysoptera*.
Figure A5.4. Egg of *Colluricincla harmonica*.
The structural and thermal properties of avian cup-shaped nests

Figure A5.5. Egg of *Corcorax melanorhamphos*. 
Figure A5.6. Egg of *Cracticus torquatus*. 
The structural and thermal properties of avian cup-shaped nests

Figure A5.7. Egg of *Daphoenositta chrysoptera*. 
Figure A5.8. Egg of *Eopsaltria australis*.
**Figure A5.9.** Egg of *Grallina cyanoleuca.*
Figure A5.10. Egg of *Lichenostomus chrysops*.
Figure A5.11. Egg of Lichenostomus cratitius.
Figure A5.12. Egg of *Lichenostomus leucotis*.
The structural and thermal properties of avian cup-shaped nests

Figure A5.13. Egg of *Lichenostomus ornatus*. 
Figure A5.14. Egg of *Lichenostomus penicillatus*. 
Figure A5.15. Egg of *Lichenostomus plumulus*. 
Figure A5.16. Egg of *Lichenostomus virescens.*
The structural and thermal properties of avian cup-shaped nests

Figure A5.17. Egg of Lichmera indistincta.
Figure A5.18. Egg of *Manorina flavigula*.
Figure A5.19. Egg of *Melanodryas cucullata*. 
Figure A5.20. Egg of *Melanodryas vittata*.
Figure A5.21. Egg of *Microeca fascinans*. 
Figure A5.22. Egg of Oriolus sagittatus.
Figure A5.23. Egg of *Pachycephala inornata*. 
Figure A5.24. Egg of Pachycephala olivacea.
Figure A5.25. Egg of *Pachycephala pectoralis*. 
Figure A5.26. Egg of Pachycephala rufiventris.
The structural and thermal properties of avian cup-shaped nests

Figure A5.27. Egg of *Pachycephala rufogularis*. 

![Figure A5.27. Egg of *Pachycephala rufogularis*.](image-url)
Figure A5.28. Egg of Petroica goodenovii.
Figure A5.29. Egg of *Petroica multicolour.*
Figure A5.30. Egg of *Psophodes nigrogularis*. 
Figure A5.31. Egg of *Rhipidura albiscapa*. 
Figure A5.32. Egg of *Rhipidura leucophrys*. 
The structural and thermal properties of avian cup-shaped nests

Figure A5.33. Egg of *Strepera versicolor*. 
Figure A5.34. Egg of *Struthidea cinerea*. 

*Struthidea cinerea* is a species of flightless bird native to New Zealand. The egg shown in the figure is characteristic of this species, with its distinctive pattern of dark blotches on a white background.
Figure A5.35. Egg of *Turdus merula*.
Figure A5.36. Egg of Zosterops lateralis.
APPENDIX 6: OOMORPHOLOGY MACRO

This Appendix is replicated in digital form on the attached compact disc (Electronic Supplementary Material, Appendix 7)

Quick Instructions

Open raw egg image in Corel

Encase egg with vector, red hairline outline and white fill

Export image as a .JPG file

Open file in ImageJ

Select rectangle around egg then Image > Crop [Or Cntrl+Shft+X]

To get a smaller file (macro will run faster), Image > Scale... set both x and y to .5 or .25 [Or Cntrl+E]

Image > Colour > Split Channels [use green file and delete the rest]

Image > Adjust > Brightness/contrast... [set top slider to 254] [Or Cntrl+Shft+C]

Process > Find Edges

Process > Smooth [Or Cntrl+Shft+S]

Repeat Find Edges & Smoothing if required

Edit > Invert [Or Cntrl+Shft+I]

Image > Transform > Rotate 90 degrees right (To prevent the macro rotating the image the wrong way)

File > Save as [FileName.xxx]

Plugins > New > Macro [paste in the text below only]

Run("Select All");

function BBtop()
{
    w = getWidth();
    h = getHeight();

    found=false;
    for(i=1;i<h && !found;i++)
    {
        for(j=1;j<w+1;j++)
        {
            p = getPixel(j,i);
            if(p>0)
                found=true;
        }
    }
    if(found)
        return(i);
    else
        return(0);
}
function BBbot()
{
    w = getWidth();
    h = getHeight();

    found=false;
    for(i=1;i<h && !found;i++)
    {
        for(j=1;j<w+1;j++)
        {
            p = getPixel(j,h-i+1);
            if(p>0)
                found=true;
        }
    }
    if(found)
        return(h+1-i);
    else
        return(0);
}

function BBleft()
{
    w = getWidth();
    h = getHeight();

    found=false;
    for(i=1;i<w+1 && !found;i++)
    {
        for(j=1;j<h+1;j++)
        {
            p = getPixel(i,j);
            if(p>0)
                found=true;
        }
    }
    if(found)
        return(i);
    else
        return(0);
}

function BBright()
{
    w = getWidth();
    h = getHeight();

    found=false;
    for(i=1;i<w+1 && !found;i++)
    {
        for(j=1;j<h+1;j++)
        {
            p = getPixel(i,j);
            if(p>0)
                found=true;
        }
    }
    if(found)
        return(h+1-i);
    else
        return(0);
The structural and thermal properties of avian cup-shaped nests

$$p = \text{getPixel}(w-i+1,j);$$
$$\text{if}(p>0)$$
$$\text{found} = \text{true};$$

$$\}\}
$$\text{if}(\text{found})$$
$$\text{return}(w-i+1);$$
$$\text{else}$$
$$\text{return}(0);$$

$$\}\}
$$\text{function CoMv(row,bot,top) \{}$$
$$\text{m} = 0;$$
$$\text{pos} = 0;$$
$$\text{for}(i=\text{bot};i<\text{top}+1;i++)$$
$$\{$$
$$p = \text{getPixel}(\text{row},i);$$
$$\text{m} += p;$$
$$\text{pos} += i*p;$$
$$\}\}
$$\text{if}(\text{m}>0)$$
$$\text{return}(\text{pos}/\text{m});$$
$$\text{else}$$
$$\text{return}(0);$$

$$\}\}
$$\text{function CoMh(col,left,right) \{}$$
$$\text{m} = 0;$$
$$\text{pos} = 0;$$
$$\text{for}(i=\text{left};i<\text{right}+1;i++)$$
$$\{$$
$$p = \text{getPixel}(i,\text{col});$$
$$\text{m} += p;$$
$$\text{pos} += i*p;$$
$$\}\}
$$\text{if}(\text{m}>0)$$
$$\text{return}(\text{pos}/\text{m});$$
$$\text{else}$$
$$\text{return}(0);$$

$$\}\}
$$\text{function sa(b2,c2,d2,e2) \{}$$
$$\text{w} = \sqrt{1-b2*b2};$$
$$\text{P1} = 9-16*w*w+8*\text{pow}(w,4);$$
$$\text{P2} = 15-21*w*w+8*\text{pow}(w,4);$$
$$\text{P3} = 3*(140-255*w*w+144*\text{pow}(w,4)-24*\text{pow}(w,6));$$
$$\text{P4} = 315-600*w*w+360*\text{pow}(w,4)-64*\text{pow}(w,6);$$
$$\text{P5} = 3*(210-455*w*w+320*\text{pow}(w,4)-72*\text{pow}(w,6));$$
$$\text{Q1} = 9-10*w*w;$$
$$\text{Q2} = 15-11*w*w+2*\text{pow}(w,4);$$

$$\}$$
\begin{verbatim}
Q3 = 420 - 485*w*w + 146*\text{pow}(w, 4);
Q4 = 315 - 390*w*w + 128*\text{pow}(w, 4);
Q5 = 630 - 945*w*w + 386*\text{pow}(w, 4) - 16*\text{pow}(w, 6);
T1 = b2/w*(\text{asin}(w) + b2*w) + d2*b2*(\text{asin}(w) * P1 - b2*w*Q1)/(4*\text{pow}(w, 5));
T1 = T1 + c2*c2*\text{pow}(b2, 3) * (\text{asin}(w) * P2 - b2*w*Q2)/(2*\text{pow}(w, 7));
T1 = T1 + c2*e2*\text{pow}(b2, 3) * (\text{asin}(w) * P3 - b2*w*Q3)/(12*\text{pow}(w, 9));
T1 = T1 + d2*d2*\text{pow}(b2, 3) * (\text{asin}(w) * P4 - b2*w*Q4)/(16*\text{pow}(w, 9));
T1 = T1 + e2*e2*\text{pow}(b2, 3) * (\text{asin}(w) * P5 - b2*w*Q5)/(16*\text{pow}(w, 11));
return(T1);
\}

\begin{verbatim}
function vol(c2,d2,e2)
{ 
    return(1+2*d2/5+6*c2*e2/35+3*d2*d2/35+e2*e2/21);
}
\end{verbatim}

//function D0(a,b0,c0,x,y)
//{
//    r = (y/(b0*sqrt(a*a-x*x)) - 1-c0*x/a)/(x*x);
//    return(r);
//}

\begin{verbatim}
function q1(a,x1,x2,x3,x4)
{ 
    return(sqrt(1-(x1/a)*(x1/a))*(x1-x2)*(x1-x3)*(x1-x4));
}
\end{verbatim}

\begin{verbatim}
function pp1(x1,x2,x3,x4)
{ 
    return(-x2*x3*x4);
}
\end{verbatim}

\begin{verbatim}
function pp2(x1,x2,x3,x4)
{ 
    return(x2*x3+x3*x4+x4*x2);
}
\end{verbatim}

\begin{verbatim}
function pp3(x1,x2,x3,x4)
{ 
    return(-(x2+x3+x4));
}
\end{verbatim}

\begin{verbatim}
function B0(a,x1,x2,x3,x4,y1,y2,y3,y4)
{ 
    s = y1*pp1(x1,x2,x3,x4)/q1(a,x1,x2,x3,x4);
    s = s+y2*pp1(x2,x3,x4,x1)/q1(a,x2,x3,x4,x1);
    s = s+y3*pp1(x3,x4,x1,x2)/q1(a,x3,x4,x1,x2);
    s = s+y4*pp1(x4,x1,x2,x3)/q1(a,x4,x1,x2,x3);
    return(s);
}
\end{verbatim}
\end{verbatim}
The structural and thermal properties of avian cup-shaped nests

function C0(a,x1,x2,x3,x4,y1,y2,y3,y4)
{
  s = y1*pp2(x1,x2,x3,x4)/q1(a,x1,x2,x3,x4);
  s = s+y2*pp2(x2,x3,x4,x1)/q1(a,x2,x3,x4,x1);
  s = s+y3*pp2(x3,x4,x1,x2)/q1(a,x3,x4,x1,x2);
  s = s+y4*pp2(x4,x1,x2,x3)/q1(a,x4,x1,x2,x3);
  return(s);
}

function D0(a,x1,x2,x3,x4,y1,y2,y3,y4)
{
  s = y1*pp3(x1,x2,x3,x4)/q1(a,x1,x2,x3,x4);
  s = s+y2*pp3(x2,x3,x4,x1)/q1(a,x2,x3,x4,x1);
  s = s+y3*pp3(x3,x4,x1,x2)/q1(a,x3,x4,x1,x2);
  s = s+y4*pp3(x4,x1,x2,x3)/q1(a,x4,x1,x2,x3);
  return(s);
}

function E0(a,x1,x2,x3,x4,y1,y2,y3,y4)
{
  s = y1/q1(a,x1,x2,x3,x4);
  s = s+y2/q1(a,x2,x3,x4,x1);
  s = s+y3/q1(a,x3,x4,x1,x2);
  s = s+y4/q1(a,x4,x1,x2,x3);
  return(s);
}

macro "eggShape"
{
  length = getString("Enter the length of the egg:","5.00");
  name0=getTitle();
  name1=split(name0,".");
  name=name1[0];
  run("Make Binary");
  H = getHeight();
  W = getWidth();
  if(H>W)
  {
    run("Rotate 90 Degrees Right");
    H = getWidth();
    W = getHeight();
  }
  L = BBleft();
  R = BBright();
  T = BBtop();
  B = BBbot();
eggLength=0;
for(i=1;i<H+1;i++)
{
  lft = CoMh(i,1,mT);
  rght = CoMh(i,mT,W);
  if(rght-lft+1>eggLength)
  {
    eggLength=rght-lft+1;
  }
}

scale = eggLength/length;

rot=0;

if(abs(mR-mL)>2)
{
  dist = 0;
  locX = 0;
  locY = 0;
  for(i=1;i<W+1;i++)
  {
    t = CoMv(i,1,mL+(mR-mL)*(i/W));
    dl = sqrt((i-(mT+mB)/2)*(i-(mT+mB)/2)+(t-(mL+mR)/2)*(t-(mL+mR)/2));
    if(dl>dist && t>0)
    {
      locX = i;
      locY = t;
      dist = dl;
    }
  }

  rot = -atan((locY-(mL+mR)/2)/(locX-(mT+mB)/2))*180/PI;

  print("The image is rotated by ",rot," degrees");

  run("Select All");
  run("Rotate... ", "angle=rot grid=1 interpolation=Bicubic background");
}

L = BBleft();
R = BBright();
T = BBtop();
B = BBbot();
The structural and thermal properties of avian cup-shaped nests

$mL = \frac{(CoMv(L+10,1,H) + CoMv(L+5,1,H) + CoMv(L+15,1,H))}{3};$

$mR = \frac{(CoMv(R-10,1,H) + CoMv(R-5,1,H) + CoMv(R-15,1,H))}{3};$

$mT = \frac{(CoMh(T+10,1,W) + CoMh(T+5,1,W) + CoMh(T+15,1,W))}{3};$

$mB = \frac{(CoMh(B-10,1,W) + CoMh(B-5,1,W) + CoMh(B-15,1,W))}{3};$

eggLength=0;
for(i=1;i<H+1;i++)
{
    lft = CoMh(i,1,mT);
    rght = CoMh(i,mT,W);
    if(rght-lft+1>eggLength)
    {
        eggLength=rght-lft+1;
    }
}

scale = eggLength/length;
}

eggWidth=0;
for(i=1;i<W+1;i++)
{
    top = CoMv(i,1,mL);
    bot = CoMv(i,mL,H);
    if(bot-top>eggWidth)
    {
        eggWidth=bot-top;
    }
}

maxLoc=(CoMh(T,1,W)+CoMh(B,1,W))/2;

N = floor(eggLength/4)+1;
V = 0;
A = 0;
ia = 0;

h=(R-L)/N;
y1 = 0;
x1 = L;

for(i=0;i<N;i++)
{
    x0 = x1;
    x1 = x0+h;

    y0 = y1;
y1 = mL+(mR-mL)*i/N-CoMv(x1,1,mL+(mR-mL)*i/N);

dV = (y0+y1)*(y0+y1)*h/4;

\[ dA = (y_0 + y_1) \sqrt{(h^2 + (y_1 - y_0)^2)} / 2; \]

\[ V = V + dV; \]
\[ A = A + dA; \]
\[ i_a = i_a + (y_0 + y_1)h; \]

\}

\[ A = 2\pi A; \]
\[ V = \pi V; \]

print("Number of slices: ",N);
print("Scale: ",scale, " (pixels per cm)");
print("Egg length=", eggLength/scale);
print("Egg width=", eggWidth/scale);
print("Distortion from circular: ", eggLength/eggWidth," (circle=1)" );
print("Max width at position ",maxLoc/scale," on the screen");
print("Distortion from elliptical: ",(R-maxLoc+1)/(maxLoc-L+1)," (ellipse=1) ");
print("Egg volume [Ve] = ",V/(scale*scale*scale));
print("Egg surface area [SAe] = ",A/(scale*scale*scale));
print("Egg profile area [PAe] = ",i_a/(scale*scale));

yVals= newArray(eggLength+2);
for(i=0;i<eggLength;i++)
    yVals[i]=mL+(mR-mL)*i/eggLength-CoMv(L-1+i,1,mL+(mR-mL)*i/eggLength);
yVals[0]=0;
yVals[eggLength]=0;
Plot.create("","","",yVals);
Plot.setColor("blue");

a=eggLength/2;
M = maxLoc-(L+a);

if(M<0)
{
    x1=(M-a)/2;
    x2=M;
    x3=(a-M)/3;
    x4=2*(a-M)/3;
}
else
{
    x1=(M-2*a)/3;
    x2=(2*M-a)/3;
    x3=M;
    x4=(a+M)/2;
}
The structural and thermal properties of avian cup-shaped nests

```javascript

y1 = yVals[x1+a];
y2 = yVals[x2+a];
y3 = yVals[x3+a];
y4 = yVals[x4+a];

b0 = B0(a,x1,x2,x3,x4,y1,y2,y3,y4)/a;
c0 = C0(a,x1,x2,x3,x4,y1,y2,y3,y4)/b0;
d0 = a*D0(a,x1,x2,x3,x4,y1,y2,y3,y4)/b0;
e0 = a*a*E0(a,x1,x2,x3,x4,y1,y2,y3,y4)/b0;

b = a*b0;
c = c0/a;
d = d0/(a*a);
e = e0/(a*a*a);

tm = M/a;

znNVals = newArray(eggLength+2);
for(i=1;i<eggLength+1;i++)
{
    x = i-1-a;
    znNVals[i] = b0*sqrt(a*a-x*x)*(1+c*x+d*x*x+e*x*x*x);
}
znNVals[0] = 0;
znNVals[eggLength]=0;
Plot.setColor("blue");
Plot.add("line",znNVals);

znnVals = newArray(eggLength+2);
for(i=1;i<eggLength+1;i++)
{
    x = i-1-a;
    znnVals[i] = b0*sqrt(a*a-x*x)*(1+c*x);
}
znnVals[0] = 0;
znnVals[eggLength]=0;
Plot.setColor("green");
Plot.add("line",znnVals);

Plot.setColor("black");
Plot.addText("Red=measured",1/4,21/50);
Plot.addText("Blue=calculated",1/4,24/50);
Plot.addText("green=calculated with d=0=e",1/4,27/50);

Plot.setColor("red");

SA = 2*PI*a*a*sa(b0,c0,d0,e0);
VOL = 4*PI*a*b*b*vol(c0,d0,e0)/3;

print("");
print("Based on measured length, width and deviations,");`
print("Egg volume should be approximately ", VOL/(scale*scale*scale));
print("Egg surface area should be approximately ", SA/(scale*scale));
print("Egg image area should be approximately ", PI*a*b*(1+d0/4)/(scale*scale));

print("\n\n");
print("a = ",a);
print("b = ",b);
print("c = ",c);
print("d = ",d);
print("e = ",e);
print("\n\n");
print("Rescaled: ");
print("\n\n");
print("b0 = ",b0);
print("c0 = ",c0);
print("d0 = ",d0);
print("e0 = ",e0);

print("xm = ",M," tm = ",tm," 1-2*tm^2 = ",1-2*tm*tm);
print("\n\n");

print("\n\n");
print("Headers for data fields represented at end of output: ");
print("\n\n");
print("Rotation");
print("Number of slices");
print("Scale, pixels per cm");
print("Egg length");
print("Egg width");
print("Distortion from circular");
print("Distortion from elliptical");
print("Egg volume [Ve]");
print("Egg area [SAe]");
print("Egg profile area [PAe]");
print("a");
print("b");
print("c");
print("d");
print("e");
print("a0");
print("b0");
print("c0");
print("d0");
print("e0");

print("\n\n");
print("Data as vertical arrangement for copy/paste:");
print("\n\n");
The structural and thermal properties of avian cup-shaped nests

```c

print(rot);
print(N);
print(scale);
print(eggLength/scale);
print(eggWidth/scale);
print(eggLength/eggWidth);
print((R-maxLoc+1)/(maxLoc-L+1));
print(V/(scale*scale*scale));
print(A/(scale*scale));
print(ia/(scale*scale));
print(a);
print(b);
print(c);
print(d);
print(e);
print(l);
print(b);
print(c*a);
print(d*a*a);
print(e*a*a*a);

print("");
print("Data as horizontal arrangement for copy/paste:");
print(""');
print(name,"\t",rot,"\t",N,"\t",scale,"\t",eggLength/scale,"\t",eggLength/eggWidth,"\t",(R-maxLoc+1)/(maxLoc-L+1),"\t",V/(scale*scale*scale),"\t",A/(scale*scale),"\t",ia/(scale*scale),"\t",a,"\t",b,"\t",c,"\t",d,"\t",e,"\t",l,"\t",d*a*a,"\t",e*a*a*a);```
APPENDIX 7: ELECTRONIC SUPPLEMENTARY MATERIAL
APPENDIX 8: SHAPE PARAMETERS OF AVIAN EGGS

<table>
<thead>
<tr>
<th>bird species</th>
<th>( b_0 )</th>
<th>( c_0 )</th>
<th>( d_0 )</th>
<th>( e_0 )</th>
<th>( t_m )</th>
<th>( D_C )</th>
<th>( D_E )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthorhynchus tenuirostris</td>
<td>0.7368 ± 0.03</td>
<td>-0.1717 ± 0.02</td>
<td>-0.0391 ± 0.01</td>
<td>0.0351 ± 0.04</td>
<td>-0.1622 ± 0.01</td>
<td>1.37 ± 0.06</td>
<td>1.40 ± 0.04</td>
</tr>
<tr>
<td>Anthochaera carunculata</td>
<td>0.7286 ± 0.02</td>
<td>-0.1323 ± 0.03</td>
<td>-0.0580 ± 0.03</td>
<td>0.0284 ± 0.02</td>
<td>-0.1265 ± 0.03</td>
<td>1.36 ± 0.03</td>
<td>1.30 ± 0.08</td>
</tr>
<tr>
<td>Anthochaera chrysoptera</td>
<td>0.6926 ± 0.02</td>
<td>-0.1200 ± 0.02</td>
<td>-0.0347 ± 0.02</td>
<td>0.0388 ± 0.03</td>
<td>-0.1160 ± 0.02</td>
<td>1.43 ± 0.03</td>
<td>1.27 ± 0.05</td>
</tr>
<tr>
<td>Colluricincla harmonica</td>
<td>0.6950 ± 0.02</td>
<td>-0.1301 ± 0.02</td>
<td>-0.0582 ± 0.03</td>
<td>0.0511 ± 0.04</td>
<td>-0.1253 ± 0.02</td>
<td>1.43 ± 0.05</td>
<td>1.29 ± 0.05</td>
</tr>
<tr>
<td>Corcorax melanorhamphos</td>
<td>0.7030 ± 0.03</td>
<td>-0.0806 ± 0.03</td>
<td>-0.0936 ± 0.04</td>
<td>0.0214 ± 0.02</td>
<td>-0.0784 ± 0.03</td>
<td>1.43 ± 0.06</td>
<td>1.18 ± 0.08</td>
</tr>
<tr>
<td>Cracticus torquatus</td>
<td>0.7310 ± 0.02</td>
<td>-0.1200 ± 0.02</td>
<td>-0.0608 ± 0.01</td>
<td>0.0340 ± 0.04</td>
<td>-0.1162 ± 0.02</td>
<td>1.37 ± 0.04</td>
<td>1.28 ± 0.04</td>
</tr>
<tr>
<td>Daphoenositta chrysoptera</td>
<td>0.7649 ± 0.03</td>
<td>-0.1013 ± 0.02</td>
<td>-0.0840 ± 0.02</td>
<td>0.0152 ± 0.03</td>
<td>-0.0988 ± 0.02</td>
<td>1.30 ± 0.05</td>
<td>1.23 ± 0.05</td>
</tr>
<tr>
<td>Eopsaltria australis</td>
<td>0.7872 ± 0.02</td>
<td>-0.1061 ± 0.02</td>
<td>-0.0543 ± 0.02</td>
<td>0.0227 ± 0.03</td>
<td>-0.1035 ± 0.02</td>
<td>1.26 ± 0.03</td>
<td>1.24 ± 0.04</td>
</tr>
<tr>
<td>Grallina cyanoleuca</td>
<td>0.7345 ± 0.02</td>
<td>-0.1491 ± 0.02</td>
<td>-0.0655 ± 0.03</td>
<td>0.0411 ± 0.02</td>
<td>-0.1425 ± 0.02</td>
<td>1.35 ± 0.04</td>
<td>1.35 ± 0.04</td>
</tr>
<tr>
<td>Lichenostomus chrysops</td>
<td>0.7197 ± 0.02</td>
<td>-0.1272 ± 0.02</td>
<td>-0.0377 ± 0.02</td>
<td>0.0788 ± 0.03</td>
<td>-0.1226 ± 0.02</td>
<td>1.39 ± 0.04</td>
<td>1.29 ± 0.05</td>
</tr>
<tr>
<td>Lichenostomus cratittus</td>
<td>0.7264 ± 0.02</td>
<td>-0.1378 ± 0.02</td>
<td>-0.0440 ± 0.01</td>
<td>0.0430 ± 0.04</td>
<td>-0.1323 ± 0.02</td>
<td>1.37 ± 0.03</td>
<td>1.31 ± 0.05</td>
</tr>
<tr>
<td>Lichenostomus leucotis</td>
<td>0.7443 ± 0.01</td>
<td>-0.0875 ± 0.02</td>
<td>-0.0433 ± 0.02</td>
<td>0.0015 ± 0.03</td>
<td>-0.0857 ± 0.02</td>
<td>1.34 ± 0.02</td>
<td>1.19 ± 0.05</td>
</tr>
<tr>
<td>Lichenostomus ornatus</td>
<td>0.7341 ± 0.02</td>
<td>-0.1409 ± 0.02</td>
<td>-0.0231 ± 0.03</td>
<td>0.0353 ± 0.04</td>
<td>-0.1351 ± 0.02</td>
<td>1.35 ± 0.04</td>
<td>1.32 ± 0.05</td>
</tr>
<tr>
<td>Lichenostomus penicillatus</td>
<td>0.7154 ± 0.03</td>
<td>-0.1409 ± 0.02</td>
<td>-0.0422 ± 0.02</td>
<td>0.0473 ± 0.03</td>
<td>-0.1348 ± 0.02</td>
<td>1.37 ± 0.05</td>
<td>1.32 ± 0.06</td>
</tr>
<tr>
<td>Lichenostomus plumulus</td>
<td>0.7331 ± 0.02</td>
<td>-0.1204 ± 0.03</td>
<td>-0.0317 ± 0.03</td>
<td>0.0601 ± 0.03</td>
<td>-0.1156 ± 0.03</td>
<td>1.35 ± 0.03</td>
<td>1.28 ± 0.08</td>
</tr>
<tr>
<td>Lichenostomus virescens</td>
<td>0.7322 ± 0.03</td>
<td>-0.1326 ± 0.02</td>
<td>-0.0544 ± 0.02</td>
<td>0.0330 ± 0.04</td>
<td>-0.1278 ± 0.02</td>
<td>1.37 ± 0.05</td>
<td>1.30 ± 0.04</td>
</tr>
<tr>
<td>Lichmera indistincta</td>
<td>0.7522 ± 0.03</td>
<td>-0.1368 ± 0.02</td>
<td>-0.0436 ± 0.02</td>
<td>0.0392 ± 0.03</td>
<td>-0.1312 ± 0.02</td>
<td>1.32 ± 0.04</td>
<td>1.32 ± 0.06</td>
</tr>
<tr>
<td>Manorina flavigula</td>
<td>0.7232 ± 0.03</td>
<td>-0.1183 ± 0.02</td>
<td>-0.0605 ± 0.03</td>
<td>0.0565 ± 0.02</td>
<td>-0.1146 ± 0.02</td>
<td>1.39 ± 0.06</td>
<td>1.27 ± 0.05</td>
</tr>
<tr>
<td>Melanodryas cucullata</td>
<td>0.7444 ± 0.02</td>
<td>-0.1411 ± 0.02</td>
<td>-0.0729 ± 0.03</td>
<td>0.0251 ± 0.02</td>
<td>-0.1349 ± 0.02</td>
<td>1.34 ± 0.03</td>
<td>1.32 ± 0.06</td>
</tr>
<tr>
<td>Melanodryas vittata</td>
<td>0.7449 ± 0.01</td>
<td>-0.1119 ± 0.03</td>
<td>-0.0661 ± 0.02</td>
<td>0.0225 ± 0.03</td>
<td>-0.1082 ± 0.03</td>
<td>1.34 ± 0.02</td>
<td>1.26 ± 0.06</td>
</tr>
<tr>
<td>Microeca fascinans</td>
<td>0.7603 ± 0.02</td>
<td>-0.1244 ± 0.02</td>
<td>-0.0526 ± 0.02</td>
<td>0.0165 ± 0.03</td>
<td>-0.1201 ± 0.02</td>
<td>1.31 ± 0.03</td>
<td>1.28 ± 0.05</td>
</tr>
<tr>
<td>bird species</td>
<td>$b_0$</td>
<td>$c_0$</td>
<td>$d_0$</td>
<td>$e_0$</td>
<td>$tm$</td>
<td>circular distortion ($D_c$)</td>
<td>elliptical distortion ($D_e$)</td>
</tr>
<tr>
<td>--------------------------</td>
<td>------------</td>
<td>------------</td>
<td>------------</td>
<td>------------</td>
<td>------------</td>
<td>-----------------------------</td>
<td>-------------------------------</td>
</tr>
<tr>
<td><em>Oriolus sagittatus</em></td>
<td>0.6742 ± 0.01</td>
<td>-0.1470 ± 0.02</td>
<td>-0.0343 ± 0.03</td>
<td>0.0431 ± 0.02</td>
<td>-0.1407 ± 0.01</td>
<td>1.47 ± 0.03</td>
<td>1.34 ± 0.04</td>
</tr>
<tr>
<td><em>Pachycephala inornata</em></td>
<td>0.7129 ± 0.02</td>
<td>-0.1119 ± 0.02</td>
<td>-0.0841 ± 0.03</td>
<td>0.0181 ± 0.04</td>
<td>-0.1089 ± 0.02</td>
<td>1.40 ± 0.03</td>
<td>1.25 ± 0.04</td>
</tr>
<tr>
<td><em>Pachycephala olivacea</em></td>
<td>0.7108 ± 0.02</td>
<td>-0.0887 ± 0.02</td>
<td>-0.1132 ± 0.02</td>
<td>0.0175 ± 0.02</td>
<td>-0.0867 ± 0.02</td>
<td>1.41 ± 0.04</td>
<td>1.20 ± 0.05</td>
</tr>
<tr>
<td><em>Pachycephala pectoralis</em></td>
<td>0.7378 ± 0.02</td>
<td>-0.1026 ± 0.01</td>
<td>-0.0801 ± 0.03</td>
<td>0.0347 ± 0.02</td>
<td>-0.1004 ± 0.01</td>
<td>1.36 ± 0.04</td>
<td>1.23 ± 0.03</td>
</tr>
<tr>
<td><em>Pachycephala rufiventris</em></td>
<td>0.7289 ± 0.03</td>
<td>-0.1647 ± 0.03</td>
<td>-0.0328 ± 0.04</td>
<td>0.0386 ± 0.04</td>
<td>-0.1550 ± 0.02</td>
<td>1.37 ± 0.05</td>
<td>1.38 ± 0.07</td>
</tr>
<tr>
<td><em>Pachycephala rufogularis</em></td>
<td>0.7130 ± 0.01</td>
<td>-0.1321 ± 0.01</td>
<td>-0.0835 ± 0.03</td>
<td>0.0697 ± 0.02</td>
<td>-0.1276 ± 0.01</td>
<td>1.39 ± 0.02</td>
<td>1.30 ± 0.03</td>
</tr>
<tr>
<td><em>Petroica goodenovii</em></td>
<td>0.8056 ± 0.03</td>
<td>-0.0745 ± 0.02</td>
<td>-0.0559 ± 0.02</td>
<td>0.0164 ± 0.01</td>
<td>-0.0730 ± 0.02</td>
<td>1.24 ± 0.04</td>
<td>1.17 ± 0.06</td>
</tr>
<tr>
<td><em>Petroica multicolor</em></td>
<td>0.7845 ± 0.02</td>
<td>-0.0727 ± 0.02</td>
<td>-0.1057 ± 0.02</td>
<td>0.0380 ± 0.05</td>
<td>-0.0715 ± 0.02</td>
<td>1.28 ± 0.01</td>
<td>1.16 ± 0.05</td>
</tr>
<tr>
<td><em>Psophodes nigrogularis</em></td>
<td>0.7147 ± 0.02</td>
<td>-0.1266 ± 0.02</td>
<td>-0.0239 ± 0.02</td>
<td>0.0378 ± 0.02</td>
<td>-0.1221 ± 0.02</td>
<td>1.40 ± 0.05</td>
<td>1.29 ± 0.05</td>
</tr>
<tr>
<td><em>Rhipidura albiscapa</em></td>
<td>0.7621 ± 0.03</td>
<td>-0.1144 ± 0.02</td>
<td>-0.0498 ± 0.02</td>
<td>0.0630 ± 0.03</td>
<td>-0.1110 ± 0.02</td>
<td>1.30 ± 0.04</td>
<td>1.26 ± 0.05</td>
</tr>
<tr>
<td><em>Rhapidura leucophrys</em></td>
<td>0.7500 ± 0.03</td>
<td>-0.1420 ± 0.02</td>
<td>-0.0868 ± 0.02</td>
<td>0.0203 ± 0.03</td>
<td>-0.1362 ± 0.02</td>
<td>1.34 ± 0.05</td>
<td>1.32 ± 0.04</td>
</tr>
<tr>
<td><em>Strepera versicolor</em></td>
<td>0.6833 ± 0.03</td>
<td>-0.1607 ± 0.03</td>
<td>-0.0409 ± 0.02</td>
<td>0.0188 ± 0.04</td>
<td>-0.1515 ± 0.03</td>
<td>1.45 ± 0.05</td>
<td>1.37 ± 0.08</td>
</tr>
<tr>
<td><em>Struthidea cinerea</em></td>
<td>0.7412 ± 0.02</td>
<td>-0.1140 ± 0.01</td>
<td>-0.0731 ± 0.03</td>
<td>0.0664 ± 0.04</td>
<td>-0.1111 ± 0.01</td>
<td>1.34 ± 0.04</td>
<td>1.25 ± 0.02</td>
</tr>
<tr>
<td><em>Turdus merula</em></td>
<td>0.7255 ± 0.02</td>
<td>-0.1253 ± 0.02</td>
<td>-0.0391 ± 0.03</td>
<td>0.0361 ± 0.04</td>
<td>-0.1207 ± 0.02</td>
<td>1.37 ± 0.04</td>
<td>1.28 ± 0.06</td>
</tr>
<tr>
<td><em>Zosterops lateralis</em></td>
<td>0.7231 ± 0.03</td>
<td>-0.1462 ± 0.02</td>
<td>-0.0535 ± 0.02</td>
<td>0.0451 ± 0.02</td>
<td>-0.1395 ± 0.02</td>
<td>1.36 ± 0.04</td>
<td>1.33 ± 0.06</td>
</tr>
</tbody>
</table>

Values are expressed as mean ± 95 % C.I. (N = 10).
## APPENDIX 9: AVIAN EGG SIZE

<table>
<thead>
<tr>
<th>bird species</th>
<th>N</th>
<th>female mass (Mf, g)</th>
<th>egg length (L, cm)</th>
<th>egg width (W, cm)</th>
<th>egg profile area (PAE, cm²)</th>
<th>egg surface area (SAE, cm²)</th>
<th>egg volume (VE, cm³)</th>
<th>clutch size (E)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthorhynchus tenuirostris</td>
<td>10, 29</td>
<td>10.5</td>
<td>1.80 ± 0.06</td>
<td>1.31 ± 0.04</td>
<td>1.84 ± 0.09</td>
<td>7.23 ± 0.38</td>
<td>1.62 ± 0.11</td>
<td>2.2 ± 0.26</td>
</tr>
<tr>
<td>Anthochaera carunculata</td>
<td>10, 76</td>
<td>98.7</td>
<td>2.99 ± 0.07</td>
<td>2.20 ± 0.04</td>
<td>5.04 ± 0.20</td>
<td>19.14 ± 0.73</td>
<td>7.30 ± 0.44</td>
<td>2.0 ± 0.41</td>
</tr>
<tr>
<td>Anthochaera chrysoptera</td>
<td>10, 33</td>
<td>59.7</td>
<td>2.82 ± 0.06</td>
<td>1.97 ± 0.04</td>
<td>4.27 ± 0.16</td>
<td>16.12 ± 0.65</td>
<td>5.55 ± 0.32</td>
<td>2.0 ± 0.29</td>
</tr>
<tr>
<td>Colluricinclina harmonica</td>
<td>10, 59</td>
<td>63.9</td>
<td>2.96 ± 0.07</td>
<td>2.08 ± 0.05</td>
<td>4.71 ± 0.20</td>
<td>17.49 ± 0.76</td>
<td>6.44 ± 0.43</td>
<td>2.6 ± 0.32</td>
</tr>
<tr>
<td>Corcorax melanorhamphos</td>
<td>10, 41</td>
<td>380.1</td>
<td>4.06 ± 0.11</td>
<td>2.82 ± 0.06</td>
<td>8.84 ± 0.27</td>
<td>32.72 ± 0.96</td>
<td>16.56 ± 0.72</td>
<td>3.7 ± 0.66</td>
</tr>
<tr>
<td>Cracticus torquatus</td>
<td>10, 30</td>
<td>82.0</td>
<td>3.06 ± 0.05</td>
<td>2.24 ± 0.05</td>
<td>5.28 ± 0.17</td>
<td>19.83 ± 0.74</td>
<td>7.83 ± 0.47</td>
<td>3.2 ± 0.39</td>
</tr>
<tr>
<td>Daphoenositta chrysoptera</td>
<td>10, 36</td>
<td>11.4</td>
<td>1.74 ± 0.06</td>
<td>1.34 ± 0.03</td>
<td>1.76 ± 0.09</td>
<td>6.68 ± 0.31</td>
<td>1.54 ± 0.11</td>
<td>2.8 ± 0.39</td>
</tr>
<tr>
<td>Eopsaltria australis</td>
<td>10, 37</td>
<td>18.3</td>
<td>2.01 ± 0.03</td>
<td>1.60 ± 0.03</td>
<td>2.47 ± 0.07</td>
<td>9.46 ± 0.29</td>
<td>2.60 ± 0.12</td>
<td>2.4 ± 0.32</td>
</tr>
<tr>
<td>Grallina cyanoleuca</td>
<td>10, 40</td>
<td>81.3</td>
<td>2.84 ± 0.09</td>
<td>2.09 ± 0.03</td>
<td>4.55 ± 0.18</td>
<td>17.03 ± 0.55</td>
<td>6.27 ± 0.29</td>
<td>3.8 ± 0.57</td>
</tr>
<tr>
<td>Lichenostomus chrysops</td>
<td>10, 32</td>
<td>16.6</td>
<td>2.03 ± 0.04</td>
<td>1.46 ± 0.03</td>
<td>2.29 ± 0.08</td>
<td>8.58 ± 0.28</td>
<td>2.22 ± 0.11</td>
<td>2.4 ± 0.32</td>
</tr>
<tr>
<td>Lichenostomus cratitius</td>
<td>10, 10</td>
<td>18.0</td>
<td>2.07 ± 0.07</td>
<td>1.51 ± 0.05</td>
<td>2.41 ± 0.16</td>
<td>9.05 ± 0.63</td>
<td>2.42 ± 0.25</td>
<td>2.1 ± 0.20</td>
</tr>
<tr>
<td>Lichenostomus leucotis</td>
<td>10, 15</td>
<td>21.5</td>
<td>2.11 ± 0.07</td>
<td>1.58 ± 0.03</td>
<td>2.57 ± 0.15</td>
<td>9.67 ± 0.53</td>
<td>2.68 ± 0.22</td>
<td>2.1 ± 0.20</td>
</tr>
<tr>
<td>Lichenostomus ornatus</td>
<td>10, 20</td>
<td>16.9</td>
<td>1.91 ± 0.06</td>
<td>1.41 ± 0.04</td>
<td>2.07 ± 0.10</td>
<td>7.81 ± 0.37</td>
<td>1.94 ± 0.14</td>
<td>2.1 ± 0.20</td>
</tr>
<tr>
<td>Lichenostomus penicillatus</td>
<td>10, 46</td>
<td>18.0</td>
<td>2.01 ± 0.11</td>
<td>1.47 ± 0.05</td>
<td>2.25 ± 0.17</td>
<td>8.47 ± 0.65</td>
<td>2.17 ± 0.22</td>
<td>2.4 ± 0.32</td>
</tr>
<tr>
<td>Lichenostomus plumulites</td>
<td>10, 3</td>
<td>15.6</td>
<td>1.89 ± 0.03</td>
<td>1.40 ± 0.03</td>
<td>2.04 ± 0.07</td>
<td>7.66 ± 0.28</td>
<td>1.88 ± 0.11</td>
<td>2.0 ± 0.26</td>
</tr>
<tr>
<td>Lichenostomus virescens</td>
<td>10, 44</td>
<td>20.0</td>
<td>2.19 ± 0.09</td>
<td>1.61 ± 0.04</td>
<td>2.71 ± 0.17</td>
<td>10.22 ± 0.59</td>
<td>2.89 ± 0.26</td>
<td>2.2 ± 0.26</td>
</tr>
<tr>
<td>Lichnera indistincta</td>
<td>10, 11</td>
<td>9.0</td>
<td>1.68 ± 0.05</td>
<td>1.26 ± 0.02</td>
<td>1.65 ± 0.06</td>
<td>6.24 ± 0.20</td>
<td>1.39 ± 0.07</td>
<td>2.0 ± 0.26</td>
</tr>
<tr>
<td>Manorina flavigula</td>
<td>10, 28</td>
<td>55.8</td>
<td>2.58 ± 0.09</td>
<td>1.87 ± 0.04</td>
<td>3.72 ± 0.16</td>
<td>13.92 ± 0.57</td>
<td>4.60 ± 0.28</td>
<td>2.9 ± 0.68</td>
</tr>
<tr>
<td>Melanodryas cucullata</td>
<td>10, 40</td>
<td>24.0</td>
<td>2.11 ± 0.04</td>
<td>1.59 ± 0.03</td>
<td>2.56 ± 0.07</td>
<td>9.64 ± 0.30</td>
<td>2.66 ± 0.13</td>
<td>1.8 ± 0.39</td>
</tr>
<tr>
<td>Melanodryas vittata</td>
<td>10, 15</td>
<td>25.6</td>
<td>2.21 ± 0.05</td>
<td>1.66 ± 0.02</td>
<td>2.79 ± 0.11</td>
<td>10.83 ± 0.55</td>
<td>3.03 ± 0.17</td>
<td>2.6 ± 0.43</td>
</tr>
<tr>
<td>Microeca fascinans</td>
<td>10, 3</td>
<td>16.2</td>
<td>1.85 ± 0.06</td>
<td>1.41 ± 0.04</td>
<td>2.01 ± 0.10</td>
<td>7.64 ± 0.37</td>
<td>1.89 ± 0.13</td>
<td>2.0 ± 0.26</td>
</tr>
<tr>
<td>bird species</td>
<td>N *</td>
<td>female mass (M_f, g)</td>
<td>egg length (L, cm)</td>
<td>egg width (W, cm)</td>
<td>egg profile area (PA, cm²)</td>
<td>egg surface area (SA, cm²)</td>
<td>egg volume (V, cm³)</td>
<td>clutch size (E)</td>
</tr>
<tr>
<td>----------------------------------</td>
<td>-----</td>
<td>---------------------</td>
<td>-------------------</td>
<td>------------------</td>
<td>----------------------------</td>
<td>----------------------------</td>
<td>-------------------</td>
<td>----------------</td>
</tr>
<tr>
<td>Oriolus sagittatus</td>
<td>10, 18</td>
<td>94.4</td>
<td>3.37 ± 0.13</td>
<td>2.29 ± 0.05</td>
<td>5.95 ± 0.37</td>
<td>21.88 ± 1.32</td>
<td>9.03 ± 0.78</td>
<td>2.3 ± 0.42</td>
</tr>
<tr>
<td>Pachycephala inornata</td>
<td>10, 10</td>
<td>32.2</td>
<td>2.48 ± 0.06</td>
<td>1.77 ± 0.02</td>
<td>3.34 ± 0.12</td>
<td>12.45 ± 0.42</td>
<td>3.88 ± 0.19</td>
<td>2.7 ± 0.42</td>
</tr>
<tr>
<td>Pachycephala olivacea</td>
<td>10, 9</td>
<td>39.3</td>
<td>2.71 ± 0.08</td>
<td>1.92 ± 0.04</td>
<td>3.99 ± 0.19</td>
<td>14.87 ± 0.71</td>
<td>5.08 ± 0.36</td>
<td>2.2 ± 0.26</td>
</tr>
<tr>
<td>Pachycephala pectoralis</td>
<td>10, 15</td>
<td>24.8</td>
<td>2.32 ± 0.06</td>
<td>1.71 ± 0.05</td>
<td>3.06 ± 0.13</td>
<td>11.91 ± 0.92</td>
<td>3.46 ± 0.23</td>
<td>2.2 ± 0.39</td>
</tr>
<tr>
<td>Pachycephala rufiventris</td>
<td>10, 39</td>
<td>23.9</td>
<td>2.29 ± 0.05</td>
<td>1.68 ± 0.03</td>
<td>2.97 ± 0.07</td>
<td>11.13 ± 0.30</td>
<td>3.30 ± 0.14</td>
<td>2.3 ± 0.42</td>
</tr>
<tr>
<td>Pachycephala rufogularis</td>
<td>10, 8</td>
<td>36.5</td>
<td>2.51 ± 0.04</td>
<td>1.81 ± 0.03</td>
<td>3.45 ± 0.11</td>
<td>12.87 ± 0.42</td>
<td>4.08 ± 0.20</td>
<td>2.2 ± 0.26</td>
</tr>
<tr>
<td>Petroica goodenovii</td>
<td>10, 40</td>
<td>9.1</td>
<td>1.57 ± 0.04</td>
<td>1.25 ± 0.03</td>
<td>1.54 ± 0.05</td>
<td>5.92 ± 0.22</td>
<td>1.29 ± 0.08</td>
<td>2.6 ± 0.32</td>
</tr>
<tr>
<td>Petroica multicolor</td>
<td>10, 23</td>
<td>15.8</td>
<td>1.85 ± 0.03</td>
<td>1.44 ± 0.02</td>
<td>2.04 ± 0.07</td>
<td>7.77 ± 0.26</td>
<td>1.95 ± 0.10</td>
<td>2.8 ± 0.39</td>
</tr>
<tr>
<td>Psophodes nigrogularis</td>
<td>10, 7</td>
<td>43.1</td>
<td>2.67 ± 0.06</td>
<td>1.90 ± 0.05</td>
<td>3.97 ± 0.12</td>
<td>14.81 ± 0.47</td>
<td>5.05 ± 0.23</td>
<td>1.9 ± 0.20</td>
</tr>
<tr>
<td>Rhipidura albiscapa</td>
<td>10, 37</td>
<td>7.7</td>
<td>1.61 ± 0.05</td>
<td>1.22 ± 0.02</td>
<td>1.52 ± 0.07</td>
<td>6.06 ± 0.43</td>
<td>1.23 ± 0.09</td>
<td>2.6 ± 0.32</td>
</tr>
<tr>
<td>Rhipidura leucophrys</td>
<td>10, 51</td>
<td>21.3</td>
<td>1.95 ± 0.05</td>
<td>1.46 ± 0.04</td>
<td>2.18 ± 0.09</td>
<td>8.25 ± 0.38</td>
<td>2.11 ± 0.14</td>
<td>2.9 ± 0.35</td>
</tr>
<tr>
<td>Strepera versicolor</td>
<td>10, 13</td>
<td>367.7</td>
<td>4.35 ± 0.11</td>
<td>2.99 ± 0.07</td>
<td>9.99 ± 0.31</td>
<td>36.95 ± 1.25</td>
<td>19.73 ± 1.07</td>
<td>2.4 ± 0.51</td>
</tr>
<tr>
<td>Struthidea cinerea</td>
<td>10, 17</td>
<td>133.4</td>
<td>2.93 ± 0.07</td>
<td>2.18 ± 0.05</td>
<td>4.90 ± 0.20</td>
<td>18.49 ± 0.76</td>
<td>7.07 ± 0.44</td>
<td>3.1 ± 0.80</td>
</tr>
<tr>
<td>Turdus merula</td>
<td>10, 17</td>
<td>96.9</td>
<td>2.90 ± 0.06</td>
<td>2.11 ± 0.03</td>
<td>4.74 ± 0.15</td>
<td>17.81 ± 0.53</td>
<td>6.64 ± 0.31</td>
<td>3.3 ± 0.78</td>
</tr>
<tr>
<td>Zosterops lateralis</td>
<td>10, 16</td>
<td>12.6</td>
<td>1.65 ± 0.04</td>
<td>1.21 ± 0.02</td>
<td>1.52 ± 0.05</td>
<td>5.63 ± 0.18</td>
<td>1.20 ± 0.06</td>
<td>2.8 ± 0.57</td>
</tr>
</tbody>
</table>

Values are expressed as mean ± 95 % C.I.

* Replicate values are those for the digital image analysis that apply to the overall study, followed by the replicate for Hoyt's (1979) equation methods (Chapter 3 § 2(h)). Some of the replicates for the latter are lower, as additional eggs were used (i.e. eggs not used in duplicate for both methods) to avoid pseudoreplication.

^ Indicates that there is no variation in the data and hence a 95 % confidence interval could not be calculated.
APPENDIX 10: MATERIAL USE IN AVIAN CUP-SHAPED NESTS

The types of materials used in nest construction can influence a nest through changes to the material conductivity, strength and water-holding capacity. Of interest are the thermal properties of nests and it is therefore important to have an understanding of the types of materials used in nests. In addition, we report collection location information, as this may influence the availability of certain materials. We also report the method of nest attachment and the density of weave, where known.

Nests used in this study were borrowed from the South Australian Museum and Queensland Museum ornithology collections. A total of 213 nests (from 36 species) were included in the study (see Chapter 2 for replicates). Nests were measured from species that construct cup-shaped nests over a range of parent sizes from 8 to 360 g. Nests were photographed to provide a visual record of construction materials and nest design (Figures A2.1 to A2.36).

The method of attachment was determined for nests that had branches supporting the nest structure. Attachment was classified as single, double, forked, or multiple attachments to the top lip, side or base, with either horizontal or vertical arrangement of branches (Appendix 11). Collection location information was obtained from the museum databases. Nest weave density was assessed qualitatively as loose, medium or dense for the outer and inner layers, respectively.

The types of materials used for construction in the outer and inner layers were recorded; however, the quantity of each material could not be determined, as destructive methods could not be employed. Materials were classed as tough plant, grass, leaves, soft plant, keratin, amino acid, organic or anthropogenic. ‘Tough plant’ matter includes sticks, twigs, vines, rootlets, tendrils and bark. ‘Grass’ includes grass blades and runners or sedges. ‘Soft plant’ matter includes flowers, seed pods, plant-down, cotton, moss and lichen. ‘Keratin’ includes animal-derived fibres such as fur, hair, wool and feathers. ‘Amino acid’ includes silk products such as spider silk, egg sacks and cocoons. ‘Organic’ materials include faeces, mud and other unidentifiable organic debris. ‘Anthropogenic’ materials include processed cottons, cloth, paper, plastic and nylon.

An indicator species analysis was performed in PC-Ord (McCune and Mefford (1999), version 5.0) to test whether the materials used in nest construction differed between species. An indicator species is the characteristic species of a group; thus a species with a high indicator value occurs frequently in one group and not in other groups (Dufrene and Legendre 1997). In this test, the materials used in construction are the indicator species and the nest species are groups. The analysis was based on indicator values (percent of perfect indication, based on combining relative abundance values and relative frequency) calculated with the methods of Dufrene and Legendre (1997) and a Monte Carlo one-sided test of significance of the observed maximum indicator value for materials found in nests. The Monte Carlo test yields a P-value, which is the proportion of randomised trials with an indicator value equal to or exceeding the observed indicator value, based on 1000 permutations.
The common nest materials used in each of the 36 cup-shaped passerine nests is listed in Appendix 12, as well as information regarding collection location, nest attachment and weave of the outer and inner layers of the nest. Based on the indicator species analysis (Table A10.1), only leaves, plant down and anthropogenic materials differ significantly between nests. Leaves are used most often in nests of *Psophodes nigrogularis* (Figure A1.30, Table A10.1), while *Lichenostomus chrysops* uses plant down more than other species (Figure A1.10a, Figure A1.10b and Table A10.1). Anthropogenic materials are found in nests of *Daphoenositta chrysoptera* more than any other nests (Figure A1.7, Table A10.1). Organic material use in nests of *Turdus merula* (Figure A1.35, Table A10.1) only approaches significance ($P = 0.064$). Tough plant matter, grass and animal derived materials are used commonly among nests of most species in the present study.

Material use differs between species, as expected, but materials such as sticks, grass, feathers and silk are used commonly and do not differ significantly between species. These are materials that birds would have easy access to and are known to keep the nest warm (in the case of feathers) and provide good structural support (in the case of tough plant materials and spider silk).

**Table A10.1. Indicator species analysis output for materials found in nests**

<table>
<thead>
<tr>
<th>material #</th>
<th>observed indicator value</th>
<th>indicator value from randomised groups mean</th>
<th>standard deviation</th>
<th>P-value</th>
<th>'max' species</th>
</tr>
</thead>
<tbody>
<tr>
<td>plant</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>tough plant</td>
<td>4.1</td>
<td>4.4</td>
<td>0.14</td>
<td>1.00</td>
<td><em>Anthochaera carunculata</em></td>
</tr>
<tr>
<td>grass</td>
<td>3.8</td>
<td>3.8</td>
<td>0.09</td>
<td>0.22</td>
<td><em>Rhipidura albiscapa</em></td>
</tr>
<tr>
<td>leaves</td>
<td>10.2</td>
<td>7.1</td>
<td>2.16</td>
<td>0.013 *</td>
<td><em>Psophodes nigrogularis</em></td>
</tr>
<tr>
<td>soft plant</td>
<td>10.3</td>
<td>7.2</td>
<td>2.16</td>
<td>0.013 *</td>
<td><em>Lichenostomus chrysops</em></td>
</tr>
<tr>
<td>animal</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>keratin</td>
<td>5.5</td>
<td>5.7</td>
<td>0.41</td>
<td>0.82</td>
<td><em>Lichenostomus virescens</em></td>
</tr>
<tr>
<td>amino acid</td>
<td>7.4</td>
<td>6.6</td>
<td>1.19</td>
<td>0.32</td>
<td><em>Rhipidura albiscapa</em></td>
</tr>
<tr>
<td>miscellaneous</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>organic</td>
<td>19.9</td>
<td>8.0</td>
<td>4.55</td>
<td>0.064</td>
<td><em>Turdus merula</em></td>
</tr>
<tr>
<td>anthropogenic</td>
<td>17.8</td>
<td>7.6</td>
<td>4.13</td>
<td>0.036 *</td>
<td><em>Daphoenositta chrysoptera</em></td>
</tr>
</tbody>
</table>

The indicator species analysis output includes the indicator values and Monte Carlo test of significance of observed maximum indicator values for materials found in nests.

* Indicates that there is a significant correlation between the material type used in the nest and the species with the greater observed indicator value, or ‘max’ species ($\alpha = 0.05$).

Statistics include the observed indicator values (percent of perfect indication, based on combining relative abundance values and relative frequency) for nests of each species, mean and standard deviation for the indicator value from randomised groups, as well as the P-value. The P-value is the proportion of randomized trials with an indicator value equal to or exceeding the observed indicator value.

* ‘Tough plant’ matter includes sticks, twigs, vines, rootlets, tendrils and bark. ‘Grass’ includes grass blades and runners or sedges.

‘Soft plant’ matter includes flowers, seed pods, plant-down, cotton, moss and lichen. ‘Keratin’ includes animal-derived fibres such as fur, hair, wool and feathers. ‘Amino acid’ includes silk products such as spider silk, egg sacks and cocoons. ‘Organic’ materials include faeces, mud and other unidentifiable organic debris. ‘Anthropogenic’ materials include processed cottons, cloth, paper, plastic and nylon.
### APPENDIX 11: METHODS OF ATTACHMENT BETWEEN CUP-SHAPED NESTS AND HOST BRANCH

<table>
<thead>
<tr>
<th></th>
<th>Single attachment</th>
<th>Double attachment</th>
<th>Forked attachment</th>
<th>Multiple attachments</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Top lip</strong></td>
<td><strong>Top lip single (TLS):</strong> Attached on the top lip by one branch</td>
<td><strong>Top lip double (TLD):</strong> Attached on the top lip</td>
<td><strong>Top lip fork (TLF):</strong> Attached on the top lip</td>
<td><strong>Top lip multiple (TLM):</strong> Attached on the top lip</td>
</tr>
<tr>
<td></td>
<td></td>
<td>between two adjacent branches</td>
<td>between the fork of a branch</td>
<td>between more than two unattached branches</td>
</tr>
<tr>
<td><strong>Side</strong></td>
<td><strong>Side single (SS):</strong> Attached part way down the nest wall by one branch</td>
<td><strong>Side double (SD):</strong> Attached part way down the</td>
<td><strong>Side fork (SF):</strong> Attached part way down the</td>
<td><strong>Side multiple (SM):</strong> Attached part way down</td>
</tr>
<tr>
<td></td>
<td></td>
<td>nest wall between two adjacent branches</td>
<td>nest wall between the fork of a branch</td>
<td>the nest wall between more than two unattached branches</td>
</tr>
<tr>
<td></td>
<td>Single attachment</td>
<td>Double attachment</td>
<td>Forked attachment</td>
<td>Multiple attachments</td>
</tr>
<tr>
<td>---------------------</td>
<td>-------------------</td>
<td>-------------------</td>
<td>-------------------</td>
<td>---------------------</td>
</tr>
<tr>
<td><strong>Base</strong></td>
<td><img src="image_base_single.png" alt="Single Attachment" /></td>
<td><img src="image_base_double.png" alt="Double Attachment" /></td>
<td><img src="image_base_forked.png" alt="Forked Attachment" /></td>
<td><img src="image_base_multiple.png" alt="Multiple Attachment" /></td>
</tr>
<tr>
<td><strong>Base single (BS)</strong>:</td>
<td>Attached at the base of the nest by one branch</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Base double (BD)</strong>:</td>
<td>N/A</td>
<td></td>
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<tr>
<td><strong>Base fork horizontal (BFH)</strong>:</td>
<td>Attached at the base of the nest between the fork of a horizontal branch</td>
<td></td>
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</tr>
<tr>
<td><strong>Base fork vertical (BFV)</strong>:</td>
<td>Attached at the base of the nest between the fork of a vertical branch</td>
<td></td>
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</tr>
<tr>
<td><strong>Base multiple (BM)</strong>:</td>
<td>Attached at the base of the nest between more than two unattached branches</td>
<td></td>
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</tr>
</tbody>
</table>
### APPENDIX 12: COLLECTION LOCATION, ATTACHMENT METHOD, WEAVE AND NEST MATERIAL USE FOR CUP-SHAPED NESTS OF AUSTRALIAN PASSERINES

<table>
<thead>
<tr>
<th>species</th>
<th>breeding season</th>
<th>collection location</th>
<th>attachment</th>
<th>outer layer weave</th>
<th>inner layer weave</th>
<th>outer layer materials</th>
<th>inner layer materials</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthorhynchus tenuirostris</td>
<td>August to April</td>
<td>Mount Lofty Ranges, SA (4) South-East, SA (1)</td>
<td>TLF (1)</td>
<td>Medium (6)</td>
<td>Medium (6)</td>
<td>bark, feathers, grass, grass seed heads, hair, nylon, plastic strips, wool</td>
<td>feathers, hair, moss</td>
</tr>
<tr>
<td>Anthochaera carunculata</td>
<td>May to March</td>
<td>Murray Mallee, SA (4) Adelaide District, SA (2) Mount Lofty Ranges, SA (1) South-East, SA (1) Flinders Ranges, SA (1)</td>
<td>BFV (1)</td>
<td>Loose (9)</td>
<td>Dense (9)</td>
<td>bark, fruits (Eucalyptus sp.), sticks, vines/rootlets</td>
<td>algae, bark, cotton, feathers, flowers or bracts, fur, grass, plant down, plastic twine, tissue paper, wool</td>
</tr>
<tr>
<td>Anthochaera chrysoptera</td>
<td>All year</td>
<td>Mount Lofty Ranges, SA (4) South-East, SA (4)</td>
<td>TLS (1)</td>
<td>Loose (8)</td>
<td>Medium (3)</td>
<td>feathers, grass, hair, leaves, plastic, spider silk, sticks, vines/rootlets, wool</td>
<td>bark, elastic, feathers, foam, grass, grass seed heads, nylon, sticks, wool, yarn</td>
</tr>
<tr>
<td>Colluricinclia harmonica</td>
<td>July to March</td>
<td>South-East, QLD (1) South-East, SA (1) Mount Lofty Ranges, SA (1)</td>
<td>Loose (2)</td>
<td>Medium (2)</td>
<td>Medium (3)</td>
<td>algae, bark, cotton cloth strips, cotton thread, grass, leaves, mud, newspaper, plastic sheets, sticks, tissue paper, vines/rootlets, wool</td>
<td>bark, fruits (Eucalyptus sp.), grass, sticks, vines/rootlets</td>
</tr>
<tr>
<td>Corcorax melanorhamphos</td>
<td>June to April</td>
<td>Murray Mallee, SA (1) Mount Lofty Ranges, SA (1) Flinders Ranges, SA (1) Eyre Peninsula, SA (1)</td>
<td>BS (3)</td>
<td>Dense (4)</td>
<td>Dense (4)</td>
<td>algae, bark, grass, mud,</td>
<td>bark, feathers, grass, leaves, mud, sticks</td>
</tr>
<tr>
<td>species</td>
<td>breeding season</td>
<td>collection location</td>
<td>attachment</td>
<td>outer layer weave</td>
<td>inner layer weave</td>
<td>outer layer materials</td>
<td>inner layer materials</td>
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<tr>
<td><em>Cracticus torquatus</em></td>
<td>July to January</td>
<td>Murray Mallee, SA (2)</td>
<td>Loose (2)</td>
<td>Medium (2)</td>
<td>sticks</td>
<td>grass, vines/rootlets</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Murray Mallee, SA (1)</td>
<td>BFV (3)</td>
<td>Dense (3)</td>
<td>bark strips, bracts (Banksia sp.), spider silk, tissue paper</td>
<td>algea, bark, general debris, grass, leaves, lichen, spider silk, tissue paper</td>
<td></td>
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<tr>
<td><em>Daphenositta chrysoptera</em></td>
<td>June to April</td>
<td>Murray Mallee, SA (1) Mount Lofty Ranges, SA (1) Flinders Ranges, SA (1)</td>
<td>BFV (3)</td>
<td>Dense (3)</td>
<td>bark, fur, grass, hair, leaves, lichen, spider silk</td>
<td>bark, grass, leaves, plant stems (Casuarina sp., Pinus sp. Needles), sticks, vines/rootlets</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>South-East, SA (6) South-East, QLD (2) Vic (1)</td>
<td>BS (1) SF (1) BMV (1) BFV (1)</td>
<td>Medium (9)</td>
<td>Medium (6) Dense (3)</td>
<td>bark, feathers, grass, hair, mud</td>
<td>cloth, feathers, fur, grass, hair, leaves, mud, nylon, sticks, straw, vines/rootlets, women's hosiery</td>
</tr>
<tr>
<td><em>Eopsaltria australis</em></td>
<td>June to January</td>
<td>South-East, QLD (5) South-East, SA (2) Flinders Ranges, SA (1) Lake Alexandrina, SA (1)</td>
<td>BS (6) BFH (2)</td>
<td>Dense (8)</td>
<td>Medium (6) Dense (2)</td>
<td>bark, feathers, grass, hair, mud</td>
<td>cloth, feathers, fur, grass, hair, leaves, mud, nylon, sticks, straw, vines/rootlets, women's hosiery</td>
</tr>
<tr>
<td><em>Grallina cyanoleuca</em></td>
<td>All year</td>
<td>South-East, QLD (5) Flinders Ranges, SA (2) Lake Alexandrina, SA (1)</td>
<td>BS (6) BFH (2)</td>
<td>Dense (8)</td>
<td>Medium (6) Dense (2)</td>
<td>bark, feathers, grass, hair, mud</td>
<td>cloth, feathers, fur, grass, hair, leaves, mud, nylon, sticks, straw, vines/rootlets, women's hosiery</td>
</tr>
<tr>
<td><em>Lichenostomus chrysops</em></td>
<td>July to March</td>
<td>Mount Lofty Ranges, SA (7)</td>
<td>TLD (2) TLF (2) TLS (2)</td>
<td>Loose (1)</td>
<td>Loose (1) Medium (6)</td>
<td>grass, grass seed heads, hair, moss, spider silk, wool</td>
<td>grass, hair, plant matter</td>
</tr>
<tr>
<td><em>Lichenostomus cratitius</em></td>
<td>August to April</td>
<td>Murray Mallee, SA (5) South-East, SA (1)</td>
<td>TLD (1) TLF (1) TLS (1) BFV (1)</td>
<td>Loose (1)</td>
<td>Medium (3) Dense (3)</td>
<td>bark, cotton thread, grass, leaves, newspaper, spider egg sacks, spider silk, sticks, tissue paper, wool</td>
<td>feathers, fur, grass, plant stems (Pinus sp. needles), wool</td>
</tr>
<tr>
<td><em>Lichenostomus leucotis</em></td>
<td>All year</td>
<td>Murray Mallee, SA (3) Kangaroo Island, SA (1)</td>
<td>BFV (2) BMV (1)</td>
<td>Medium (3)</td>
<td>Medium (2) Dense (2)</td>
<td>algae, bark, flowers, grass, leaves, spider silk, wool</td>
<td>algae, bark, feathers, grass, wool</td>
</tr>
<tr>
<td>species</td>
<td>breeding season</td>
<td>collection location</td>
<td>attachment</td>
<td>outer layer weave</td>
<td>inner layer weave</td>
<td>outer layer materials</td>
<td>inner layer materials</td>
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<tr>
<td><em>Lichenostomus ornatus</em></td>
<td>July to April</td>
<td>River Murray, SA (1)</td>
<td>Loose (1)</td>
<td>Medium (1)</td>
<td>grass, wool</td>
<td>grass, wool</td>
<td></td>
</tr>
<tr>
<td><em>Lichenostomus penicillatus</em></td>
<td>All year</td>
<td>Adelaide District, SA (4)</td>
<td>TLD (2)</td>
<td>Medium (5)</td>
<td>Medium (1)</td>
<td>algae, cotton, feathers, fur, grass, leaves, nylon, spider silk, tissue paper, twine, vines/rootlets, wool</td>
<td>feathers, fur, grass, hair, nylon twine, plant down, wool</td>
</tr>
<tr>
<td><em>Lichenostomus plumulus</em></td>
<td>All year</td>
<td>Flinders Ranges, SA (1)</td>
<td>SMH (1)</td>
<td>Loose (2)</td>
<td>Medium (4)</td>
<td>algae, cotton, feathers, fur, grass, grass seed heads, leaves, moss, sticks, tissue paper, vines/rootlets, wool</td>
<td>grass, wool, wool</td>
</tr>
<tr>
<td><em>Lichenostomus virescens</em></td>
<td>All year</td>
<td>Flinders Ranges, SA (5)</td>
<td>TLD (4)</td>
<td>Medium (2)</td>
<td>Medium (4)</td>
<td>algae, bark, grass, hair, leaves, spider egg sacks, spider silk, wool</td>
<td>bark, grass, leaves, plant down, wool, yarn</td>
</tr>
<tr>
<td><em>Lichmera indistincta</em></td>
<td>All year</td>
<td>NT (3)</td>
<td>TLF (1)</td>
<td>Medium (5)</td>
<td>Medium (1)</td>
<td>algae, bark, grass, hair, leaves, spider egg sacks, spider silk, wool</td>
<td>bark, grass, leaves, plant down, wool, yarn</td>
</tr>
<tr>
<td><em>Manorina flavigula</em></td>
<td>All year</td>
<td>North-East, SA (4)</td>
<td>Loose (7)</td>
<td>Medium (3)</td>
<td>Dense (4)</td>
<td>cocoons, egg sacks, grass, leaves, spider silk, sticks, vines/rootlets, wool</td>
<td>bark, feathers, fur, grass, hair, nylon, plant down, sticks, vines/rootlets, wool, yarn</td>
</tr>
<tr>
<td>species</td>
<td>breeding season</td>
<td>collection location</td>
<td>attachment</td>
<td>outer layer weave</td>
<td>inner layer weave</td>
<td>outer layer materials</td>
<td>inner layer materials</td>
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<tr>
<td>Melanodryas cucullata</td>
<td>August to January</td>
<td>Murray Mallee, SA (3) River Murray, SA (1) Flinders Ranges, SA (1)</td>
<td>BS (2) Imbedded in top of tree hollow (2) Attached to inside of a large strip of bark (1)</td>
<td>Medium (4) Dense (1) Dense (3)</td>
<td>bark, feathers, grass, spider silk, sticks, vines/rootlets</td>
<td>bark, feathers, fur, grass, sticks, vines/rootlets, wool</td>
<td></td>
</tr>
<tr>
<td>Melanodryas vittata</td>
<td>July to January</td>
<td>TAS (1)</td>
<td>Medium (1) Dense (1)</td>
<td>bark, grass, vines/rootlets</td>
<td>grass seed heads, vines/rootlets</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Microeca fascinans</td>
<td>August to January</td>
<td>Murray Mallee, SA (1) South-East, SA (1)</td>
<td>BFH (2)</td>
<td>Medium (1) Dense (1) Dense (2)</td>
<td>bark, feathers, grass, spider silk, wool</td>
<td>fur, grass, hair, vines/rootlets, wool</td>
<td></td>
</tr>
<tr>
<td>Oriolus sagittatus</td>
<td>August to March</td>
<td>South-East, NSW (1) Mount Lofty Ranges, SA (1)</td>
<td>TLF (2)</td>
<td>Medium (2) Dense (2)</td>
<td>bark, grass, hair, leaves, spider egg sacks, sticks, wool</td>
<td>bark, grass, spider egg sacks, wool</td>
<td></td>
</tr>
<tr>
<td>Pachycephala inornata</td>
<td>July to December</td>
<td>Flinders Ranges, SA (3) Mount Lofty Ranges, SA (2) Murray Mallee, SA (2)</td>
<td>Loose (5) Medium (2)</td>
<td>bark, cocoon, grass, insect carapace, leaves, plant debris, spider egg sack, spider silk, sticks, wool, yarn</td>
<td>grass, hair, vines/rootlets, wool</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pachycephala olivacea</td>
<td>September to January</td>
<td>South-East, SA (1)</td>
<td>Loose (1)</td>
<td>bark, sticks, vines/rootlets</td>
<td>vines/rootlets</td>
<td></td>
<td></td>
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<tr>
<td>species</td>
<td>breeding season</td>
<td>collection location</td>
<td>attachment</td>
<td>outer layer weave</td>
<td>inner layer weave</td>
<td>outer layer materials</td>
<td>inner layer materials</td>
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<tr>
<td><em>Pachycephala pectoralis</em></td>
<td>August to February</td>
<td>Fleurieu Peninsula, SA (7) Mount Lofty Ranges, SA (5) Murray Mallee, SA (3) Adelaide District, SA (2) South-East, SA (2)</td>
<td>TLS (5)</td>
<td>Loose (6) Medium (13)</td>
<td>Loose (1) Medium (11) Dense (7)</td>
<td>animal faeces, bark, catkin ('pussy willow grass'), feathers, flowers, fur, grass, grass seed heads, insect carapace, leaves, nylon, plant stems (<em>Casuarina</em> sp.), spider silk, sticks, vines/rootlets, wool, yarn</td>
<td>grass, leaves, plant material, plant stems, sticks, vines/rootlets, yarn</td>
</tr>
<tr>
<td><em>Pachycephala rufiventris</em></td>
<td>July to February</td>
<td>Mount Lofty Ranges, SA (3) Fleurieu Peninsula, SA (1) River Murray, SA (1) Adelaide District, SA (1) QLD (1)</td>
<td>BFV (1)</td>
<td>Loose (7)</td>
<td>Loose (7)</td>
<td>bark, grass, grass seed heads, plant stems (<em>Casuarina</em> sp.), spider silk, sticks, vines/rootlets</td>
<td>grass, sticks, vines/rootlets</td>
</tr>
<tr>
<td><em>Pachycephala rufogularis</em></td>
<td>August to November</td>
<td>Murray Mallee, SA (5) Fleurieu Peninsula, SA (1)</td>
<td>Loose (5) Medium (1) Dense (6)</td>
<td>bark, leaves, plant stems, sticks, thorns</td>
<td>bark, leaves, plant down, plant stems, sticks, vines/rootlets</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Petroica goodenovii</em></td>
<td>June to January</td>
<td>Murray Mallee, SA (2) SA (1)</td>
<td>BFH (2) BFV (1)</td>
<td>Dense (3)</td>
<td>Dense (3)</td>
<td>bark, fur, grass, lichen, moss, spider egg sacks, spider silk</td>
<td>feathers, fur, leaves, moss</td>
</tr>
<tr>
<td><em>Petroica multicolor</em></td>
<td>July to January</td>
<td>Kangaroo Island, SA (1) Mount Lofty Ranges, SA (1) South-East, SA (1)</td>
<td>BFV (1)</td>
<td>Medium (3) Medium (1) Dense (2)</td>
<td>medium (1) Dense (2)</td>
<td>bark, fur, grass, lichen, spider silk, wool</td>
<td>bark, feathers, fur, grass</td>
</tr>
<tr>
<td><em>Psophodes nigrogularis</em></td>
<td>July to October</td>
<td>Murray Mallee, SA (5)</td>
<td>Loose (5) Medium (4) Dense (1)</td>
<td>bark, leaves, sticks</td>
<td>flowers (<em>Eucalyptus</em> sp.), grass, leaves, sticks</td>
<td></td>
<td></td>
</tr>
<tr>
<td>species</td>
<td>breeding season</td>
<td>collection location</td>
<td>attachment</td>
<td>outer layer weave</td>
<td>inner layer weave</td>
<td>outer layer materials</td>
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<tr>
<td><em>Rhipidura albiscapa</em></td>
<td>August to January</td>
<td>Mount Lofty Ranges, SA (6)</td>
<td>BFH (14)</td>
<td>Dense (14)</td>
<td>Medium (9)</td>
<td>Dense (5)</td>
<td>grass, spider silk</td>
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<td></td>
<td></td>
<td>Fleurieu Peninsula, SA (2)</td>
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<td>South-East, SA (3)</td>
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<td>VIC (1)</td>
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<td>Yorke Peninsula, SA (1)</td>
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<td>Fleurieu Peninsula, SA (2)</td>
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<tr>
<td><em>Rhipidura leucophrys</em></td>
<td>July to February</td>
<td>South-East, QLD (3)</td>
<td>BFH (4)</td>
<td>Medium (1)</td>
<td>Medium (3)</td>
<td>Dense (8)</td>
<td>bark, cloth, feathers, fur,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Adelaide District, SA (2)</td>
<td>SF (1)</td>
<td>Medium (8)</td>
<td>Dense (6)</td>
<td></td>
<td>grass, grass seed heads,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Murray Mallee, SA (2)</td>
<td>BS (1)</td>
<td></td>
<td></td>
<td></td>
<td>hair, moss, spider silk</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fleurieu Peninsula, SA (2)</td>
<td>TLF (1)</td>
<td></td>
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<tr>
<td><em>Strepera versicolor</em></td>
<td>July to March</td>
<td>Mount Lofty Ranges, SA (1)</td>
<td></td>
<td>Loose (1)</td>
<td>Dense (1)</td>
<td>sticks</td>
<td>grass, leaves, sticks</td>
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<tr>
<td><em>Struthidea cinerea</em></td>
<td>August to April</td>
<td>Olary Plains, SA (1)</td>
<td>BFH (1)</td>
<td>Dense (2)</td>
<td>Medium (2)</td>
<td>grass, mud</td>
<td>grass, mud, sticks</td>
</tr>
<tr>
<td></td>
<td></td>
<td>North-East, QLD (1)</td>
<td>SSV (1)</td>
<td>Medium (2)</td>
<td>Dense (2)</td>
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<tr>
<td><em>Turdus merula</em></td>
<td>August to April</td>
<td>South-East, SA (3)</td>
<td></td>
<td>Medium (4)</td>
<td>Dense (4)</td>
<td>Dense (8)</td>
<td>bark, feather, grass,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Adelaide District, SA (3)</td>
<td></td>
<td>Medium (4)</td>
<td>Dense (4)</td>
<td></td>
<td>leaves, mud, nylon string,</td>
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<tr>
<td></td>
<td></td>
<td>Lake Alexandrina District, SA (1)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>onion skin, reeds, sticks,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mount Lofty Ranges, SA (1)</td>
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<td></td>
<td></td>
<td></td>
<td>vines/rootlets</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td>feathers, flower petals,</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>grass, leaves, plant stems</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>(Pinus sp. needles), seed</td>
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<td></td>
<td></td>
<td></td>
<td>pods, vines/rootlets</td>
</tr>
<tr>
<td>species</td>
<td>breeding season</td>
<td>collection location</td>
<td>attachment</td>
<td>outer layer weave</td>
<td>inner layer weave</td>
<td>outer layer materials</td>
<td>inner layer materials</td>
</tr>
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<td>--------------------</td>
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</tr>
<tr>
<td>Zosterops lateralis</td>
<td>All year</td>
<td>South-East, QLD (8) Fleurieu Peninsula, SA (5) South-East, SA (5) Mount Lofty Ranges, SA (1) Kangaroo Island, SA (1) Heron Island, QLD (1)</td>
<td>TLD (7)</td>
<td>Medium (18)</td>
<td>Medium (10)</td>
<td>algae, bark, cocoon, cotton thread, fern fronds, fur, grass, grass seed heads, leaves, lichen, moss, nylon, spider egg sacks, spider silk, sticks, tissue paper, vines/rootlets, wool, yarn</td>
<td>feathers, fur, grass, grass seed heads, hair, leaves, lichen, moss, nylon, plant down, seed pods, spider silk, sticks, vines/rootlets, wool, yarn</td>
</tr>
</tbody>
</table>

Breeding seasons obtained from the Handbook of Australian, New Zealand and Antarctic Birds resource series (Marchant and Higgins 2001; 2002; 2006). Numbers in brackets represent the number of nests that fit each category. Total nest replicates can be found in Appendix 2. Summed replicates from each category may not be equal to the total nest replicates in all cases, as collection location and attachment information for some nests could not be obtained.
Figure A13.1. Lateral view of a nest of Gliciphilla melanops, showing the medium weave of the outer layer.
Figure A13.2. Arial view of a nest of *Gliciphilla melanops*, showing the dense inner lining.
Figure A13.3. Nest of *Gliciphilla melanops*. Photo courtesy of Lydia Paton.
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