A Comparative Study of the Energetics of Avian Reproduction

by

James Todd Pearson
B.Sc (Hons) Adelaide

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Summary

The growth and development of precocial king quail (='chinese painted quail'; *Coturnix chinensis*) and altricial cockatiel (*Nymphicus hollandicus*) is examined during embryonic and posthatching periods up until fledging.

Both species lay relatively small eggs (4.9 and 5.9 g respectively), which hatch after 16.5 and 19-21 days respectively. After hatching, the quail is independent of the parents, except for parental brooding, but the cockatiel is totally dependent on the parents for food and brooding. The male quail does not incubate the eggs, whereas the male cockatiel incubates, and both quail and cockatiel parents brood chicks. However, the patterns of parental attentiveness during the brooding period is different between the two species. Quail chicks must forage in order to feed, and return to parents for brooding when body temperature decreases, which is dependent on ambient temperature. In contrast, cockatiel chicks are brooded continuously for 10 days after hatching, then intermittently for 2-3 days, after which the chicks are no longer brooded during the day.

Aims of this thesis

Quail and cockatiel are non-passerines which hatch with a similar body mass (about 4 g). Little information exists for the patterns of growth and development in avian species with small hatchlings other than altricial passerines. The incubation time of all embryos is inversely related to fresh egg mass and the degree of precocity at hatching. Altricial hatchlings are believed to hatch earlier in the developmental sequence at an immature state, whereas precocial hatchlings are mature. As fresh egg mass decreases the developmental time for embryonic growth and maturation decreases, and because maturation occurs late in the incubation period, it is suggested that there is a minimum incubation period for precocial hatchlings. This question is examined in this study by comparing the embryonic development of metabolism of king quail with larger precocial hatchlings.

Posthatching growth rates increase with decreasing asymptotic body mass and decrease with increasing degree of precocity at hatching. The early onset of homeothermy in precocial hatchlings is thought to limit the available energy that can be allocated to converting chemical potential energy to living tissues, and therefore resulting in lower relative growth rates at any given body mass. However, possible limitations of foraging time and ambient temperature on the relative growth rates of small precocial hatchlings have not been considered in other studies. Foraging time of precocial hatchlings is likely to decrease with body mass, because of unfavourable heat production to heat loss ratios. Growth may be further limited by low ambient temperatures due to increased thermogenic costs whilst foraging. This study examines if the relative growth rate of king quail is lower than allometric predictions because of the limiting factors of foraging time and low ambient temperatures.

The relative growth rates of parrots are lower than those of open-nesting altricial land birds. This is thought to be related to the absence of the selective pressures of predation on cavity-nesting parrots. However, part of the explanation may be that parrots develop homeothermy earlier in their posthatching development than other altricial land birds. Therefore the relationship between relative growth rate and the timing of homeothermy in cockatiel is examined to consider if this alternative explanation for the low growth rates of parrots exists.

Findings

Egg composition and energy invested in eggs

Quails eggs are a smaller fraction of adult body mass, and total investment in clutches is less than in other galliform birds. However, the composition of egg contents and water content is similar to predictions based on fresh egg mass. The energy density of quail egg contents is within the reported range of other precocial eggs. Cockatiel eggs are a similar fraction of adult body mass to the predictions for parrots of the same mass, but total investment in clutches is less than predicted. The fraction of yolk in cockatiel eggs is similar to other parrots, but is higher than other altricial birds. Water content of cockatiel eggs is also similar to predictions. The energy density of cockatiel egg contents is similar to other altricial and semi-altricial eggs. On the basis of hatchling developmental type quail eggs are similar to larger precocial eggs, but cockatiel eggs contain more yolk and therefore more energy than other altricial eggs.

Embryonic respiration and development

The oxygen consumption rate of quail embryos increases exponentially throughout incubation, without the typical plateau of the precocial pattern of development. The oxygen consumption rate of cockatiel embryos also increases exponentially as typical of altricial development. The pre-internal pipping rate of oxygen consumption is similar to predictions based on fresh egg mass of all hatchling types. The water vapour conductance of cockatiel eggs is similar to predictions, but is significantly higher than predicted for quail eggs based on fresh egg mass. The estimated partial pressures of O_2 and CO_2 in the aircells of quail eggs reach 100 and 37 torr respectively at internal pipping. In cockatiel eggs the partial pressures reach 120 and 30 torr respectively at internal pipping, but reverse shortly after to 130 and 15 torr due to star-fracturing of eggshell before external pipping commences.

Growth of quail and cockatiel embryos increases exponentially throughout incubation, but in the quail growth slows late in the incubation period without ever reaching a plateau. The total energy used by both embryos during incubation is a similar fraction of the total available energy in eggs. The energy contents of internal yolk and yolk-free quail hatchlings is identical to predicted values based on fresh egg contents. The energy content of internal yolk and cockatiel hatchlings is similar to that of quail, but the energy remaining in the internal yolk is greater than predicted for altricial eggs.

Based on fresh egg mass and energy content of eggs, the incubation period of quail is shorter than predicted for a precocial bird and the incubation period of cockatiel is longer than predicted for an altricial bird. However, the incubation period of cockatiel is similar to predictions for parrots, which are characteristically longer than other altricial birds. It is concluded that embryos of quail and cockatiel develop in a manner similar to all other species. Despite the earlier than predicted hatching of quail embryos, there is no obvious indication of reduced maturity in the small precocial hatchlings. It is possible that the relatively poor muscle coordination of hatchlings and weak thermogenic responses reflects some degree of muscle immaturity at hatchling.

Hatchling metabolism and degree of precocity

The mean resting metabolic rates at thermoneutrality of quail and cockatiel hatchlings are higher than allometric predictions for all hatchling types. Quail resting metabolism is 60% higher, and that of the cockatiel is about 50% higher, than predictions for galliforms and parrots respectively. The higher resting metabolism of both species reflects a higher degree of homeothermy at hatching than expected, but this capacity is nevertheless low, due to the small hatchling masses. In response to short-term gradual cooling, oxygen consumption rates of hatchling quail and cockatiel are elevated initially in some individuals, but not in others. In all hatchlings the oxygen consumption rate is at least maintained at resting levels during cooling, and does not decline with ambient temperature as typical of passerine hatchlings. Thus it is concluded that quail are variable in their thermogenic responses to cold after hatching, unlike larger precocial hatchlings, and cockatiel resting metabolism reflects a higher degree of precocity than previously recognised.

Posthatching growth of chicks

The relative growth rates of quail at ambient temperatures > 30 °C during the first 20 days after hatching was almost double the growth rates of quail at 15-20 °C. The highest growth rates of quail are lower than predicted by previous allometric relationships between growth rate and asymptotic mass for precocial land birds. The relative growth rate of cockatiel during summer is similar to allometric predictions for parrots, but is significantly lower than other altricial land birds. Similarly the growth rate of cockatiel hatched in winter is significantly lower than those hatched in summer.

Development of homeothermy in chicks

Hatchlings and chicks less than 10 days of age in both quail and cockatiel are poikilothermic, but between 10-13 days of age chicks of both species are able to maintain high body temperature (33-40 °C) at constant levels dependent on their body mass at ambient temperatures above 20 °C, but not at colder temperatures. With increases in body mass, chicks of both species are eventually able to regulate body temperature at adult levels. It is concluded that cockatiel chicks develop homeothermic abilities earlier in their nestling period than any other altricial species reported so far, and that the timing of homeothermy is not coordinated with the acquisition of plumage as has been suggested for altricial passerines.

The resting metabolism of quail chicks at thermoneutrality increases to a maximum of double the hatchling resting metabolism after small increases in body mass (at 5-7 g), and then declines to adult levels as body mass increases. Peak metabolic rate of quail chicks during cold exposure is identical to resting metabolism initially, but increases to double resting metabolism at 7-10 g body mass, and then declines in parallel to resting metabolism as body mass increases. The resting metabolism of cockatiel chicks increases at 2-3 days of age, and is maximal at a body mass of 13 g, and then declines to adult levels as body mass increases. Peak metabolic rate of cockatiel chicks is higher than resting metabolic rate when body mass is 20 g at the end of the brooding period, and is maintained at maximal levels throughout the nestling period, until the feathers are unsheathed prior to fledging. Thus the resting metabolic rate exceeds that of an adult bird of the same mass early in the development of both species. This pattern is typical of precocial development. However, the early development of thermogenic responses in cockatiel is unlike the pattern of development in altricial passerine nestlings.

Metabolism of chicks and adults during brooding

Brooded quail chicks maintain oxygen consumption rates at rates similar to that of unbrooded chicks at thermoneutrality at ambient temperatures between 10-37 °C. Quail chicks are brooded intermittently during the day until 17-18 days of age when they generally become homeothermic. It is concluded that periods of brooding represent an energy saving to quail chicks, but chicks expend energy during activity and thermoregulation whilst foraging. The oxygen consumption rates of adult quail whilst brooding 1-5 chicks at ambient temperatures above thermoneutrality are not significantly different from non-brooding quail. However, at ambient temperatures below thermoneutrality, the oxygen consumption rates of brooding quail are significantly elevated above non-brooding rates. Oxygen consumption rates remain elevated at night, which indicates that the circadian rhythm of metabolism is temporarily suppressed. The time quail spend brooding chicks decreases when chicks are 5 days old, but brooding continues intermittently until chicks reach 17-20 days of age.

Brooded cockatiel chicks (less than 8-9 days of age) maintain oxygen consumption rates at half the thermoneutral rates of unbrooded chicks when ambient temperature is between 10-37 °C. At 9-13 days of age, cockatiel chicks are 20-30g body mass and are no longer brooded effectively by parents, and oxygen consumption rates of brooded chicks increases as T_a decreases, but remain lower than unbrooded chicks of the same age. Brood huddling during parental absences in combination with their thermogenic powers allows chicks to achieve effective homeothermy. Continuous brooding also represents an energy saving to cockatiel chicks, but as chick body mass approaches 20 g the energetic savings to the chick diminishes. At the end of the brooding period cockatiel chicks incur significant thermoregulatory costs dependent on ambient temperature. Thermoregulatory costs for cockatiel chicks are higher during winter than summer due to low daily ambient temperatures, and as a result cockatiel growth rates are lower. The oxygen consumption rates of adult cockatiel brooding 1-4 chicks increases as ambient temperature decreases, but is not significantly higher than non-brooding cockatiel at any ambient temperature. It is suggested here that brooding oxygen consumption rate is not elevated because a large thermal gradient in body temperature exists between the adult and chick, and the chick is essentially naked, which makes parental heat transfer more efficient. Therefore it is concluded that the brooding period is an energetic burden to parent quail when ambient temperature decreases below thermoneutrality, but it is not an energetic burden to brooding cockatiel.

Conclusions

Embryonic Development

The results of this study indicate that the embryonic development of king quail is similar to larger precocial birds, except that the incubation period of king quail is shorter than predicted. Two correlates with the shorter incubation are that embryonic metabolism never becomes constrained by shell gas conductance, nor does embryo growth reach a plateau before hatching. The cockatiel embryo development is like the typical altricial pattern, but embryos achieve a higher degree of homeothermy at hatching than other altricial passerines.

Growth of small precocial birds

After hatching, quail chicks rapidly increase their thermogenic powers with little increase in body mass, which is similar to the precocial pattern of development. The amount of time chicks spend foraging is a function of the cooling rate and the degree of homeothermy at hatching. Quail hatchlings are a smaller than expected fraction of adult mass, and have higher than expected hatchling resting metabolic rates which increases their degree of homeothermy at hatching, thereby reducing brooding time. However, king quail hatchlings' degree of homeothermy is lower than other galliform species in general, and as a result the relative growth rate of quail is lower than predicted for precocial land birds of similar asymptotic body mass, because whilst chicks are brooded they can not forage.

Growth of parrots

On the other hand, the thermogenic powers of cockatiel chicks increases disproportionately as body mass increases early in their posthatching development, which is more like the precocial pattern of development. But the relative growth rates of cockatiel are lower than predicted for altricial land birds of similar asymptotic body mass. The lower growth rate is attributed to the early achievement of homeothermy in comparison to passerines, but unlike the precocial quail, cockatiel benefit from parental feeding, reduced activity and continuous brooding to achieve a growth rate intermediate between precocial and altricial birds.

Declaration

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 had been made in the text.

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Signed [signature]   Date 17/2/95.

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