

**RESOLVING CONCEPTUAL CONFUSION AND
QUANTIFYING CROSS-TAXA PATTERNS OF
'DENSITY DEPENDENCE' IN POPULATION ECOLOGY**

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ABSTRACT

Density dependence represents a causal relationship between the size of a population and at least one of its measurable demographic rates. It encapsulates the demographic and evolutionary role of a range of social and trophic mechanisms (e.g., cannibalism, competition, cooperation, parasitism, predation), whose effects on crowding and extinction are themselves modified by the population's abundance (**density feedback**). The concept is applied in conservation and management to assess critical matters such as harvest quotas, pest/invasion control and thresholds of extinction. I review the use of density dependence in ecology.

I quantify a temporal increase in the number of ecological papers examining this concept across an augmenting number of study taxa, and little consensus around the meaning of density dependence and associated concepts in a questionnaire survey among 136 ecologists (**Chapter 1**). Next, I revise the vocabulary of density dependence in a historical context, finding more than 60 terms, many of which are polysemous, synonymous, or grounded in opinionated statements; I name five unequivocal qualifiers of density feedback (compensatory, delayed compensatory, overcompensatory, dependant/Allee effect) linked to known population phenomena (stability, cycles, chaos, decline), and dissect the semantic differences between density dependence and population regulation (**Chapter 2**).

Using empirical methods, I show that the strength of density feedback increases with the pace of species' life histories (**Chapter 3**), yet is only negligibly correlated with coarse climatic gradients (**Chapter 4**). These results suggest that broad life-history information can assist management and conservation actions when detailed demographic data are unavailable; and that many demographic processes might operate at spatial scales specific to populations, not species. Subsequently, I provide the first empirical cross-taxa demonstration that density effects on single fertility/survival rates (components) have weak association with feedback at the population level — a phenomenon I call 'ensemble' density feedback (**Chapter 5**). The major implication is that population processes can buffer variation in demographic rates, and management/conservation can be misled when based only on component density feedbacks.

In my corollary discussion (**Chapter 6**), I advocate for phenomenological models to characterise long-term population trends, argue that better integration of temporal and spatial demography could circumvent ongoing semantic conundrums, and highlight the need for a code of ecological nomenclature. Stronger emphasis on the comprehension, mathematical description and application of density feedback through ecological disciplines, from students to seasoned academics, is absolutely necessary for ecology to become one of the most influential branches of modern science, a tool of knowledge for improving societal and environmental well-being.

STATEMENT OF ORIGINALITY

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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Salvador Herrando-Pérez

Adelaide, 10 June 2012

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The financial difficulty that I have experienced during the course of my PhD forced me into a nomadic lifestyle, following short-term rentals and house-sitting in numerous suburbs as follows: [Northern Territory] North Flinders International House, Wanguri, Nightcliff; [South Australia] Plympton, Unley, North Adelaide, Saint Peters, Adelaide (South West), Mile End, West Lakes, Wayville, Stirling, Adelaide (South), Urrbrae, Adelaide (South East), Mansfield Park, Modbury, Largs Bay, Waterfall Gully, Coromandel Valley, Glandore, Bellevue Heights, Athelston, and Ashton. Along the way, I am fondly grateful to those who generously offered their homes at no cost, namely: **Clive McMahon, Derek Hamer, Donna Harris and Stephen Gregory, Judith Giraldo, Karah Wertz and Corey Bradshaw, Karen Smagala, Karen Wood and Brian Rayner, Lochran Traill, Nerissa Haby, Nunung Lehmann, Phill Cassey, Rubby Frittmann and Victor Burt, and Rosa Ana Jaco.**

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FOREWORD

*“At school he [Albert Einstein] was bored, intimidated, shy, and withdrawn...”
The science class you wish you ever had (Brody & Brody 1998)*

I have bolstered my research skills through a PhD with a strong mathematical component, and the challenge has been of such magnitude that I feel compelled to reflect on how I managed to succeed.

From the time I did my undergraduate degree in Spain in the 1980s, universities have transformed into a form of business enterprise, where money is attracted not only through student recruitment, but also by benchmarking other universities, nationally and globally. In the growth of such capitalisation of education, I would like to think that one day someone will forge an indicator to measure the extent to which the delivery of education unleashes (or constraints) creativity, and this indicator become a universal beacon of education quality.

Standards come to mind. It is appalling that, since their earliest training, students are encouraged into a learning method that encourages storing information, and their academic merit is scored on how well they regurgitate that information in an exam. More than a century ago, Chamberlain (1890) made the cogent distinction between an ‘acquisitive study’ “...to follow by close imitation the processes of previous thinkers, or to acquire by memorising the results of their investigations”; and a ‘creative study’ “...to discover new truth, or to make new combinations of truth, or at least to develop an individualised aggregation of truth. The endeavour is to think for one’s self, whether the thinking lies wholly in the fields of previous thought or not”. The acquisitive style of education pervades primary, secondary, and tertiary education — I have seen or experienced it in Australia, Colombia, England, Mexico, Peru and Spain. Along the way, teachers and venues change, but students keep memorising theoretical content that will sooner or later fall into oblivion, with no benefit to individuals or society: a colossal waste of resources! This vicious machinery is sustained by reward and punishment in convoluted manners, denouncing the pedagogical void to inspire creative thinking. For instance, one of my primary-school teachers had boys seated in class by a ‘ranking of intelligence’. So one could lose the first seat if the classmate in the second seat answered a question correctly, which the up-to-then ‘most intelligent’ had failed to hit. The competition to occupy the first seat and shame to sit in the last one are metaphors for our atrocious modern societies and academic institutions. How many Beethovens, Christies, Einsteins or Van Goghs

(all documented dyslexic geniuses) might have been mocked and ruined in the rear seats of their classes.

One aftermath of the acquisitive style of education within the biological sciences relates to statistics. Numerical skills, to measure quantities and their uncertainty, have become the cornerstone of modern science. And statistics are intimately linked to creativity because analysing data is one of the core activities to think, construct, evidence and communicate new ideas. Regrettably, mathematical training is in a precarious state in our field, due to a disconnection between the quantitative nature of ecology and the skills of mentors and students (Ellison & Dennis 2010). Johnson *et al.* (2001) have eloquently argued that ‘wildlifera’ who either lack or master statistical knowledge always walk on safe ground; because the former rely on experts to do their analyses, whilst the latter work out their numerical riddles by themselves (**Figure 1**). In contrast, the vast majority of scholars, across all levels of expertise, dwells in a statistical limbo prone to ill application, inference and/or reporting. Poor statistical training explains why most biologists that reach a postgraduate level are faced by a stunning contradiction: **Their hosting institutions expect them to have a solid mathematical background which, nonetheless, they most often never received.** I say ‘expect’ because, upon postgraduate enrolment, no procedure is generally in place to directly gauge an individual’s practical skills with the methodological requirements of their intended projects.

Figure 1. Relationship between how well biologists use statistical methods (performance) relative to how much statistical expertise they have (knowledge). Performance is understood as one minus the probability of making a fatal statistical mistake (modified from Johnson *et al.* 2001).

NOTE:

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Foreword

When the postgraduate researcher has had little statistical training, his/her study is doomed to drift into a do-it-yourself crusade. Some postgraduates will pretend to oversee their statistical weakness until they have collected their very final datum before entering into a state of acute concern when the time has come for wrestling with understanding and analysing their data. For others (I am one of them), such concern is chronic and they combat it by allocating resources and time to fill their statistical gap (e.g., courses, books), which can only ever be filled minimally given the demanding workload of a Masters or PhD. Fortunately, many postgraduates will survive the malady of numbers and get their degrees, although their struggle will simply perpetuate the demise of numerical training through the chain of education providers. I think that **a student can be intellectually dull or brilliant but, if he/she works hard, an adequate provision of statistical training and mentorship is the sole responsibility of the education providers.** Universities could have stringent criteria to accept only students with top statistical proficiency — but, as mentioned before, there would be too few who fitted the bill. The alternative, and most humane option, is *simply* delivering the training that is missing through the entire process of education. Excellent universities and excellent schools can only provide the best of their societal services, not in isolation but as parts of an excellent holistic education; that is a system that integrates all the phases of academic formation since the child sees a number or a letter for the first time until the adult might become a Nobel laureate.

As I finalise this foreword, my mind pounds ‘science is a point of view’, so we are not born with it and it requires dedicated learning... and teaching.

Salvador Herrando-Pérez
Mawson Building, room G39

CHAPTER 1

— BACKGROUND

“... the search for density dependence has become a holy grail” (Krebs 1995)

To some unfamiliar with the term ‘density dependence’ (‘DD’ hereafter), a key-word search in the *Science Citation Index* would cast the profile of this concept in the field of ecology: popular, strongly mathematised, and controversial. It is ‘popular’ because thousands of publications in all environmental sciences juggle with it, ‘mathematised’ because a large component of published work lies within biostatistical journals, and a closer look into ecological journals features the same numerical pedigree, and ‘controversial’ because some of the most cited works portrait polemics on a gamut of terminological, semantic, mathematical, and philosophical aspects. Shortly after I had embarked on the content proposal of my PhD, my supervisors were adamant that, by the end of it, I would be the world’s DD authority. Of course, I cannot become so in five years, but the expectation set the standards fairly high.

With hindsight, the final structure of my PhD research has pivoted on the results from an extensive literature review, and a questionnaire survey among ecologists. Before delving into such preliminary work, and as a matter of setting the scene, I simply outline that DD embraces the idea that the pace with which a population grows or declines is a function of its own density. A giant shoal of herrings zigzagging protectively in response to a predator, a swarm of social bees tending the multitudinous offspring of their queen, a dense pine forest depriving its own seedlings from light, an overharvested population of lobsters where individuals can hardly find reproductive mates, the pioneering strands of a seaweed colonising a foreign sea after a transoceanic trip attached to the hulk of boat, the respiratory parasites spreading in a herd of caribou, or malaria protozoans making their way between mosquitoes and humans, are all examples of population processes that operate under a density check. Any DD measure in those populations would relate population size to temporal or spatial variation in the magnitude of survival, fertility or dispersal of the involved individuals, populations and species.

In the rest of this introductory chapter, I present a brief history of DD mathematical development and applications in ecology (much expanded throughout the thesis), and the

results of my literature and questionnaire surveys. Based on the former information, I will describe my PhD research plan and aims.

1.1 History in short

The history of DD is certainly one of mathematical development. In **Table 17 (Appendix A1)**, I list the sequence of primary-literature publications that I regard as milestones of debates, developments and updating reviews. Initially, as a means of confirming population regulation [process by which a population tends to return to its equilibrium density (Murdoch 1970)], a battery of tests for DD in time series of abundance was developed from the 1970s to the 1990s, covering simple correlation (Eberhardt 1970), key factors (Sibly & Smith 1998), and computer-intensive procedures (Fox & Ridsdillsmith 1995; Brook & Bradshaw 2006; Freckleton *et al.* 2006). Superseding the assumption of linear responses in DD relationships, nonlinearity was injected into demographic studies in the 1970s. Thus, May (1974, 1976) eloquently portrayed that the simplest single-species nonlinear difference equations exhibited a suite of dynamical behaviours from stability, through cycles of expanding lag to chaos. From the late 1990s up to now, the word ‘test’ has been gradually replaced by the word ‘model’ in the main title of publications. The research focus has shifted from DD detection to quantification of DD strength and shape via estimation of parameters, effect sizes, and residual variance as a potential composite of process and observation errors. Parameter estimation features strongly in the analyses of time series (Royama 1981; Bjørnstad & Grenfell 2001; Dennis *et al.* 2006), and has also incorporated a spatial component which manifests in concepts such as the ‘Moran effect’ (spatially auto-correlated noise) (Lundberg *et al.* 2000). Recent developments have also plugged density feedbacks in models of elasticities (Grant 1997; Grant & Benton 2000), as well as life history, population structure (ages, stages) and evolutionary change (Coulson *et al.* 2001; Lande *et al.* 2002; Reznick *et al.* 2002; Hairston *et al.* 2005; Kokko & López-Sepulcre 2007).

Along with the physical environment, life history and evolutionary change, DD factors determine the growth of a population as its size increases or decreases in time or space, with obvious implications for ecosystem management and conservation. Visualisation of those implications is straightforward at the highest and lowest end of the spectrum of population abundances. At high numbers, if a fraction of a population dies off naturally due to limited food resources, killing the surplus of individuals should have a minor impact on a target population’s growth rate, and estimates of that surplus (= quotas) can guide strategies of predator protection, hunting (Boyce *et al.* 1999) and fishery limits (Rose *et al.* 2001). At low

numbers, populations can fall into a vortex of extinction due to factors like inbreeding depression or disruption of aggregative interactions, so measuring minimum populations sizes at which deaths outnumber births can be critical to establish protected areas, harvest moratoria, programs of release of predators for pest control, or thresholds of establishment of invaders (Courchamp *et al.* 1999; Stephens & Sutherland 1999). As a whole, it is this link between the mathematical description of DD and a number of mechanisms driving population persistence and extinction that has rendered this concept prominent in applied research such as conservation biology (Henle *et al.* 2004; Sabo *et al.* 2004), biological control (Fagan *et al.* 2002; Tobin *et al.* 2011), management of fisheries (Jennings 2000; Lorenzen 2008) and harvesting (Fowler 1981; Eberhardt *et al.* 2008), as well as a crucial element to take into account in assessing the combined impacts of climate and biotic processes (Stenseth *et al.* 2002). The legacy of the past fifty years of research has endowed contemporary ecologists with models which can now aspire to track the ‘noisy clockwork’ (Bjørnstad & Grenfell 2001) of nature by accounting for (linear and nonlinear) deterministic and stochastic forces simultaneously shaping the state and fate of (meta)populations within a changing environment, over ecological and evolutionary time scales.

1.2 Trends of use

In my literature review, I compiled information on publication trends for DD. The review focused on population-level demographic studies in the primary literature of ecology as obtained from the *Science Citation Index* (SCI) over the period 1980-2008. I targeted seven ‘core journals’ (*The American Naturalist*, *Canadian Journal of Fisheries and Aquatic Sciences*, *Ecology*, *Journal of Animal Ecology*, *Marine Ecology Progress Series*, *Oecologia* and *Oikos*), because they were the only ones to have published at least one paper on DD annually within the study period. I also added 11 journals that had 2008 SCI impact factors greater than the core journals (*Annual Review of Ecology Evolution and Systematics*, *Biological Reviews*, *Ecological Monographs*, *Ecology Letters*, *Nature*, *PLoS Biology*, *Philosophical Transactions of the Royal Society B-Biological Sciences*, *Proceedings of the National Academy of Sciences of the USA*, *Science*, *The Quarterly Review of Biology*, and *Trends in Ecology and Evolution*). To retrieve records I did two key-word searches, namely (i) in the title of publications to guarantee that DD had not been merely cited but estimated in some way, and (ii) in the abstract for additional papers in which regulatory or nonregulatory dynamics was specified with regard to DD. Key-word strings were:

Chapter 1

- TITLE=(‘density dependance’ OR ‘density dependence’ OR ‘density-dependent’ OR ‘density dependant’ OR ‘density-dependence’ OR ‘density-dependance’ OR ‘Allee’ OR ‘depensatio7n’)
- ABSTRACT=((‘density dependance’ OR ‘density dependence’ OR ‘density-dependent’ OR ‘density dependant’ OR ‘density-dependence’ OR ‘density-dependance’ OR ‘Allee’ OR ‘depensation’) OR (regulation OR compensation)) AND ((‘population growth’ OR ‘population’s growth’) AND (density OR ‘population size’ OR ‘population’s size’ OR ‘population abundance’ OR ‘population’s abundance’ OR demograph*))

From each selected paper, I collated three fields of information: (i) bibliographical (author, affiliation, journal and volume), (ii) taxonomic (species identity and IUCN Red List threatened status), (iii) and geographical (biogeographic region, biome and country of study sites). I then compared the temporal trend of DD publications in core journals (DD trend) to the temporal trend of the total number of publications issued by those same journals (overall trend). I assessed the hypothesis that the DD trend had increased at a higher rate than the overall trend with a model set accounting for linear and nonlinear (quadratic) trends in the number of publications over time, differences in the slopes between DD and overall trends, and a null (intercept-only) model with no trend (**Table 1**). Lastly, I contrasted models using Akaike’s information criterion corrected for small sample size, AIC_c (Sugiura 1978), and assessed assumptions and structural goodness-of-fit (normality, heteroscedasticity, outliers, variance explained) for the most-complex and best-supported models by means of standard diagnostic tests.

The cumulative number of species investigated for DD has augmented nearly exponentially over time and has featured 693 species (excluding species counts from meta-analyses) (**Figure 2**). Nearly 80 % of the reviewed papers focused on one (60 %) or two (20 %) taxa only. Species belonged to 559 genera, 347 families, 153 orders, 44 classes and 27 phyla. Across papers, I recorded 85 % animal and 11 % plant taxa — from **Chapter 2**, I reason that the paucity of DD plant studies is only apparent, due to the terminological jargon used by botanists, especially *self-thinning*. Insects led DD research until 1995, after which time mammals became the most favoured study group. The study of DD on bird and fish species has also showed a relatively pronounced increase in the last decade (**Figure 2**). About 85 % of the taxa citations were of the Nearctic (45 %) or Palearctic (39 %) regions (Northern Hemisphere), with forest (32 %) and marine (28 %) biomes dominating over freshwater (19 %), grasslands (18 %) and, particularly, desert (3 %) biomes (**Figure 2**).

The core journals published a total of 44,785 papers from 1980 to 2008 (mean = 1,600 papers/year), of which 658 addressed DD (1.5 %; mean = 24 papers/year) (**Figure 2**). The higher impact-factor journals contributed a further 96 DD papers. Only the model representing a different linear change (slope) in publication rate between DD and overall papers was substantively supported and explained 94 % of total variation (**Table 1**). That model indicated that, over the last three decades, the linear rate of increase in DD studies in the core journals was 2.3 times higher than that of the overall publication trend (**Figure 3**).

Figure 2. Cumulative number of species investigated for density dependence according to 658 papers from seven core ecological journals (listed in **Figure 3** caption) reviewed in the *Science Citation Index* between 1980 and 2007 (ie., full years for which data had been collected). Histograms show relative numbers of papers by biomes (black bars) and taxonomical groups (grey bars) for consecutive 5-year periods from 1980 onwards.

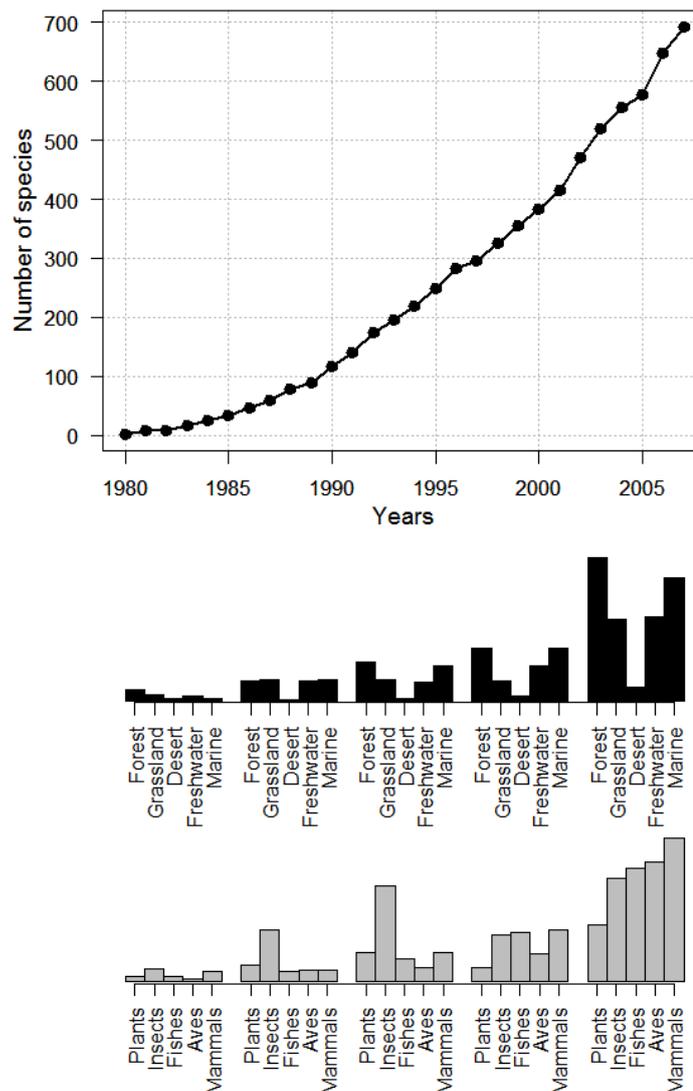


Figure 3. Annual overall number of peer-reviewed scientific papers (●, OVERALL, $n = 44,785$), and the subset number of papers on density dependence (■, DD, $n = 658$), published between 1980 and 2007 (*Science Citation Index*) in the journals *Ecology* ($n = 145$), *Oecologia* ($n = 119$), *Oikos* ($n = 116$), *Journal of Animal Ecology* ($n = 111$), *American Naturalist* ($n = 38$), *Canadian Journal of Fisheries and Aquatic Sciences* ($n = 57$) and *Marine Ecology Progress Series* ($n = 42$). Numbers standardised to a [0,1] scale. Linear trends (bolded lines) are fitted through least squares. See trend model support in **Table 1**.

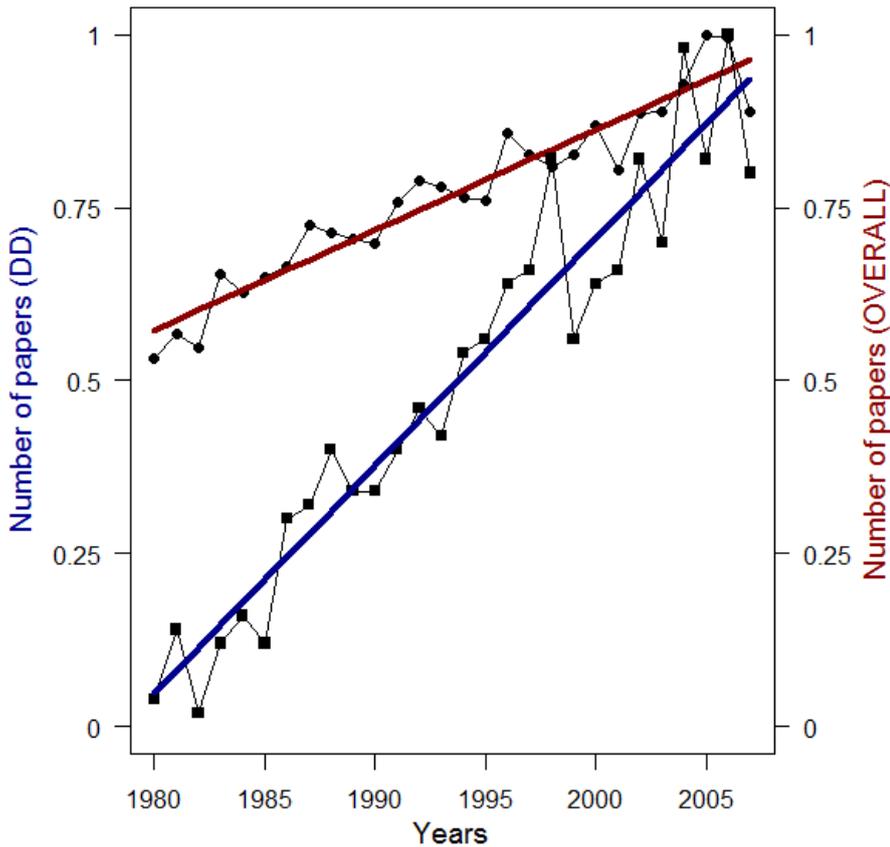


Table 1. Comparison of models examining temporal trends in total number of papers, and only those addressing density dependence, published from 1980 to 2007 by seven core ecological journals. Models ranked by relative Akaike information criterion weights ($wAIC_c$) and regression coefficients (R^2), both adjusted for finite sample size. Prior to model fitting, paper numbers for both time series were standardised to a [0,1] scale and centred on the median year (1993). Variables include: ‘#’ = number of papers, ‘publication’ = categorical predictor coding for density-dependence or overall publication trends, and ‘year’ = year of publication. See journals and trends in **Figure 3** caption.

Model	$wAIC_c$	Adjusted R^2
# ~ year + publication + year*publication	> 0.999	0.94
# ~ year + publication	< 0.001	0.85
# ~ publication + year + year ²	< 0.001	0.85
# ~ publication + year + year ² + year ² *publication	< 0.001	0.85
# ~ publication	< 0.001	0.28
# ~ 1	< 0.001	0.00

The importance of DD in population dynamics has been qualitatively described only in association with the concept of *regulation* in two major reviews (Sinclair 1989; Turchin 1995), with one quantitative assessment restricted to Allee effects (Kramer *et al.* 2009). My review gives the first quantitative evidence that DD research effort has increased considerably in the last thirty years, and this concept has now a profound establishment in ecology. It also indicates that the latest predominance of DD studies in homeotherms would be a bounty of long-term datasets for the empirical chapters of my PhD research.

1.3 A survey of experts

A direct way of assessing agreement on concepts amidst authorities and of pinpointing key areas of new research is to approach them personally. Thus, I invited 183 ecologists to answer a questionnaire survey with 58 closed statements on concepts, statistics and terminology in three different sections regarding DD, DD and population regulation, and regulation and limitation — I present the set of statements in **Table 18** and the list of respondents in **Table 19 (Appendix A2)**. In one way or another, the inter-relationships between the former three concepts have attracted most debates on DD to the present (Sinclair and Pech 1996; Krebs 2002b; Berryman 2004; White 2004) — I explain those debates in **Chapter 6**. The statements of my survey mostly originated from my literature review above, and included literal quotations from papers, or personal sentences capturing expert opinion. The emphasis of the questionnaire was on demography, with a specific focus on patterns and processes related to population growth, mortality, reproduction and dispersal. I grouped statements *a priori* by theme, e.g., four statements dealt with the DD terminology, namely “depensation and Allee effects are forms of inverse density dependence”, “density dependence is a negative feedback of density on population growth rate”, “overcompensation is a type of density dependence”, and “direct density dependence and negative density dependence represent the same type of density feedback”. Authors also had a space to write comments relevant to the themes under study.

For each statement, respondents had to tick a box along a ‘Likert’ scale [1-5] from strong agreement to strong disagreement. The scale midpoint [3] indicated neither agreement nor disagreement (neutral response). I invited authors to participate via email, as obtained from my literature review, and through several long-standing ecological/biological mailing lists. Prior to distribution, three colleagues (see **Acknowledgements**) piloted the questionnaire for clarity and to minimise ambiguities. Considering all their responses, I ordinated authors by a covariance-based principal component analysis (PCA, Jolliffe 2004). The dispersion of

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respondents in the PCA space was proportional to disagreement on the 58 statements, while principal coefficients (loads) were largest for those statements most disagreed upon across respondents. Five respondents who answered < 75 % of the statements were left out of the analysis, while I imputed no-responses with the middle value (i.e., 3).

A total of 136 respondents (74 %) replied by the due date. Over 90 % of respondents worked in USA, Canada or one of 17 European countries. PCA explained 14 and 28 % of the variation in agreement among authors in the first two and five principal axes, respectively. Three of the four statements on DD terminology were among the 10 most loaded in PC1, PC2, PC3 and PC5, and those four statements were overall the main source of no-response across authors. The statement “density dependence can never drive a population extinct” scored the largest average (absolute) principal coefficient over the first five PCA axes [indicating strong discrepancy in the association between DD and regulation], while top-loaded statements per axis were as follows:

- “Demographic Allee effects contribute to population regulation” (PC1)
- “Limitation has to do with the primary factor determining population size, while regulation is a population response to limitation” (PC1)
- “Density dependence is a negative feedback of density on population growth rate” (PC2)
- “A positive relationship between mortality and population size is indicative of regulation” (PC2)
- “A long-term growth rate of zero need not indicate that population numbers are regulated” (PC3)
- “Regulation involves the processes that prevent population growth” (PC4)
- “The term density-dependent regulation is a tautology (i.e. redundant)” (PC5)

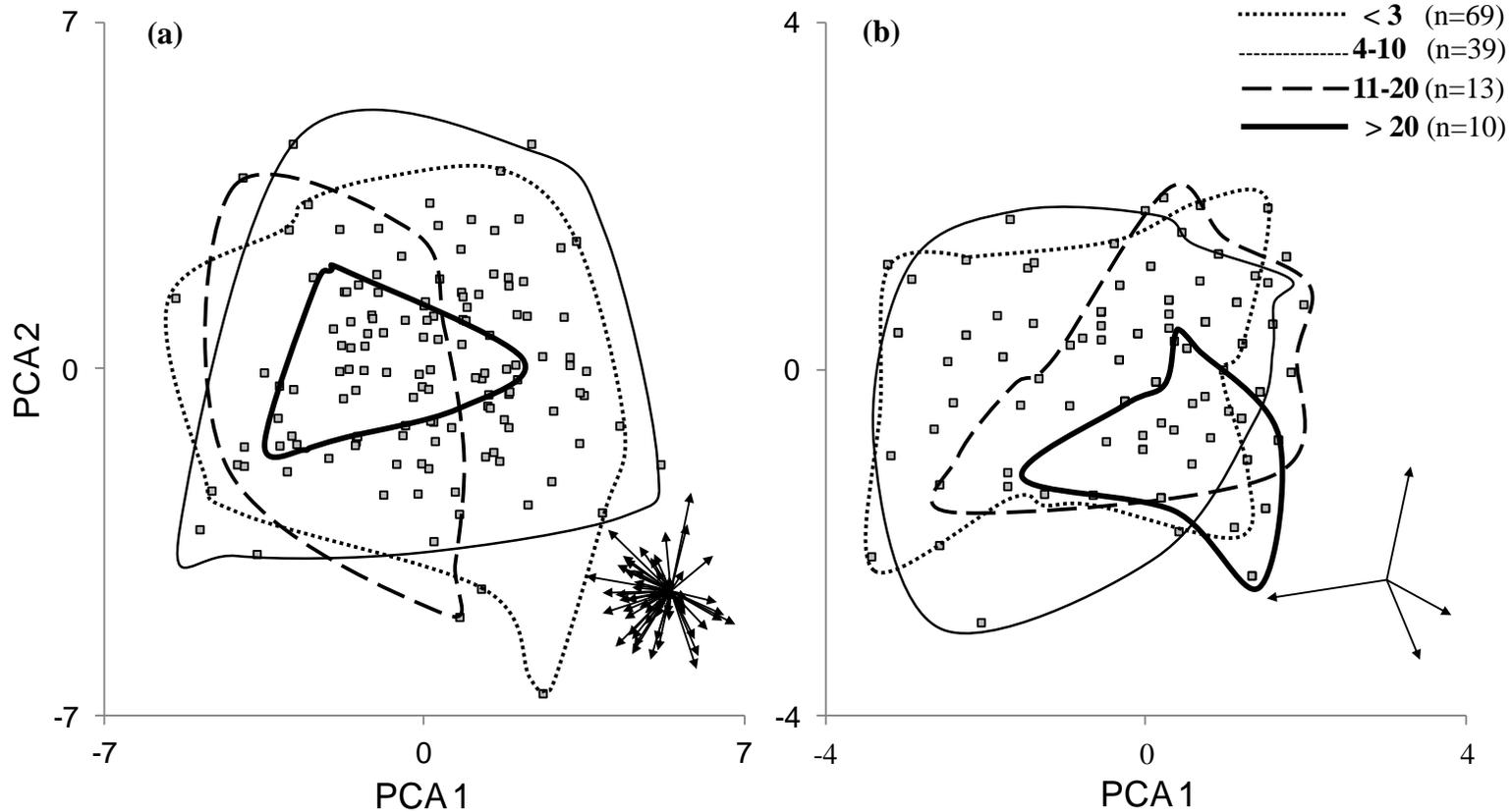
When I grouped respondents by their level of expertise, measured as the number of papers they had published on DD by 2008, I observed a similar disagreement across groups, although group dispersion tended to be lower in those authors having published > 20 DD papers (**Figure 4**). I found the same pattern of disagreement across levels of expertise when the PCA was done only with the four DD terminological statements (**Figure 4**). However, > 90 % of the questionnaire respondents agreed with Murdoch and Walde’s (1989) classical definition “...a dependence of per capita population growth rate on present and/or past population densities”. Therefore, authors seem to perceive the statistical relationship involved in the DD concept, but have contrasting views as to how to relate types of those relationships with habitually cited DD jargon.

Six statements gathering views confronting the concepts of regulation and limitation yielded the highest number of neutral responses. In **Table 20 (Appendix A2)**, I provide a

sample of incisive comments given by respondents on limitation, e.g., “limitation is certainly not neglected in the literature; people just don’t necessarily know that they study limitation” (L. Witting, pers. com.). Some of these discrepancies might be strengthened by different uses and misuses of the same concepts in different areas of research, e.g., “... what I found most interesting was that my answers to many questions could be dependent on whether I was thinking from an empirical or theoretical perspective, and if from a theoretical perspective which model framework I was thinking in” (T. Coulson, pers. com.), or “... my problems are twofold: I am a modeller, not a field ecologist, and therefore I have no overview over the species-oriented literature. And my work is exclusively concentrated on plant populations. However, your questions are mostly concentrated on the demands of animal ecologists” (E. Winkler, pers. com.).

The questionnaire survey served to emphasise that DD terminology causes important signs of disagreement or non-response among respondents. Likewise, conceptual, statistical and terminological aspects, all embroidered with population regulation (see quotes from the ecological literature on regulation in **Appendix A2; Table 21**) and its relation with population limitation, appear to be unresolved.

Figure 4. Covariance-based PCA ordination of 136 questionnaire respondents (grey squares) based on their degree of agreement, from 1 = strong agreement to 5 = strong disagreement, on a set of 58 closed statements dealing with aspects of density dependence, and population regulation and limitation (a), and only a subset of four statements dealing with terminology of density dependence (b). Vectors represent loading of statements in the direction of highest variance. Curves circumscribe groups of authors according to their number of papers published on density dependence in the ecological literature. A total of 14 % (a) and 65 % (b) of the variation were explained by the two first principal axes of each ordination, respectively.



1.4 Research plan

My PhD research is embedded in the work of the Global Change Ecology Group at the Environmental Institute (The University of Adelaide), looking at DD in mathematical modelling for conservation biology (Bradshaw *et al.* 2006; Brook & Bradshaw 2006; Brook *et al.* 2006; Traill *et al.* 2007; Clark *et al.* 2010; Gregory *et al.* 2010). Building on those previous studies, and considering the results of my literature review and questionnaire survey, I have undertaken in my PhD a broad revision on the application of DD in ecology, addressing both conceptual issues, and cross-taxa patterns by means of long-term population data. The wide taxonomical approach made sense from the logic of seeking generalities in a concept-reviewing piece of research; and in turn established that I was not to collect field data myself, the data would all come from the literature, the Earth being my sampling site! The former rationale also determined my statistical approach, so I foresaw to use simple models that could be compared unambiguously across species and ecosystems, and avoided black-or-white hypothesis testing in favour of a multi-model inference approach.

Given the terminological inconsistencies of DD revealed by my questionnaire survey, I reviewed in **Chapter 2** the conceptual origin and vocabulary of DD in a historical context. **Chapters 3, 4** and **5** incorporate data analyses. My main focus was on macroecological patterns of variation in density feedback across taxa and, where possible, assessing situations where long-term change in population growth rate could be, or could be not, inferred from population data other than censuses of abundance. Firstly, my literature review highlighted the recently overwhelming impact that evolutionary research is having on the study of demography, based on the seminal Darwinian principle that evolution shapes and is shaped by how density feedbacks mould survival and fertility rates; so I devoted **Chapter 3** to examining the proneness with which different life-history tactics can determine the magnitude of density feedbacks in vertebrates, invertebrates and plants. Secondly, climate change is one of the main drivers of modern extinctions of wildlife and, clearly, contemporaneous ecologists and the leading ecological journals are strongly engaged in understanding the interaction between density feedbacks and external forcing such as climate; I therefore directed **Chapter 4** to exploring the magnitude of density feedbacks along large climatic gradients for homeotherms. Thirdly, **Chapter 5** was a natural extension of one key elaboration from **Chapter 2**, whereby [‘ensemble’] density feedbacks on a population’s growth rate (fitness) need to be investigated (hence named) as a composite of [‘component’] density feedbacks on single demographic rates — therein I correlate strength of *ensemble* and *component* density

Chapter 1

feedbacks in birds and mammals. Throughout the thesis, I have indicated how single-species population models accounting for density feedback can inform conservation and management actions, and suggest ways of extending the analyses I have done. In **Chapter 6**, I advocate the use of phenomenological models to assess long-term population trends, a better integration of spatial and temporal demography to circumvent ongoing semantic conundrums, and a code of ecological nomenclature for ecology. As a whole, by linking density feedback to its conceptual history, and to population-level fitness, evolution and climate across hundreds of taxa, my PhD research is transversal to all ecological disciplines and taxa, and should illuminate the sound application of this concept in my discipline.

A chief part of my training has had to do with data manipulation and analyses. On one hand, I have done the compilation and manipulation of data from three of the main sources of information available for macroecological research, including re-evaluation of available datasets (**Chapter 3**), downloading of public datasets (**Chapter 4**), and direct acquisition of data from individual researchers and published papers (**Chapter 5** and this chapter). I have undertaken the majority of statistical analyses in *R* v2.14 (R Development Core Team 2011), and principal component analyses in *Primer* v.6 (Clarke & Gorley 2006). Furthermore, I have submitted **Chapter 2** (*Oecologia*, In press), **Chapter 3** (*Ecology*, In press), **Chapter 4** (*Ecology and Evolution*, In press) and **Chapter 5** (*Oikos*, In review) as self-contained manuscripts to different ecological journals; whereas I gave a talk on the core findings of **Chapter 2** at the ‘10th International Congress of Ecology’ organised by the ‘International Association for Ecology’ in Brisbane (Australia, August 2009). To avoid repetition of basic background information, in the PhD thesis I have slightly modified the introductory sections of the peer-reviewed manuscripts, and substituted all plural possessive adjectives and pronouns (‘we’, ‘our’) by singulars (‘I’, ‘my’). Lastly, all submitted manuscripts had appendices for online publication, so I have merged with the main text of the thesis only those appendices that directly reinforce the main arguments under consideration. At the end of the thesis, I list the set of references for the entire thesis and collate a total of seven appendices.

1.5 Aims

General

1. Re-statement of the biological meaning of ‘density dependence’ in ecological studies
2. Examination of patterns of density feedback in long-term data of population abundance across taxa
3. Emphasis on the usefulness of single-species population models accounting for density feedback in conservation and management

Specific

4. Provision of unambiguous terminological rules for density dependence, based on the history of the concept
5. Evaluation of the use of broad life-history and climate information to explain variation in the strength of density feedback
6. Evaluation of situations in which the magnitude of density feedback on demographic rates can or cannot drive measurable shifts in overall population growth

CHAPTER 2

— TERMINOLOGY

1.6 Title

Density dependence: an ecological Tower of Babel

1.7 Abstract:

The concept of density dependence represents the effect of changing population size on demographic rates, and captures the demographic role of social and trophic mechanisms (e.g., cooperation, competition, parasitism, predation). Ecologists have coined more than 60 terms to name different statistical and semantic properties of this concept, resulting in a formidable lexicon of synonymies and polysemies. I examined the vocabulary of density dependence used in the modern ecological literature from the foundational lexicon developed by Smith, Allee, Haldane, Neave and Varley. A few simple rules suffice to abate terminological inconsistency and to enhance the biological meaning of this important concept. Correct citation of original references by ecologists and research journals could ameliorate terminological standards in our discipline, and avoid linguistic confusion of mathematically and theoretically complex patterns.

1.8 Key words: Allee effect; Demographic rate; Density feedback; Population dynamics; Regulation; Terminology

STATEMENT OF AUTHORSHIP

Published in *Oecologia*, by Herrando-Pérez, Delean, Brook & Bradshaw

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Lead author Herrando-Pérez conceived the work, reviewed the literature, did the statistical analyses, and wrote the first draft of the paper (score of 0.80). Bradshaw (0.10), Brook (0.05) and Delean (0.05) contributed substantially to revisions.

All co-authors certify that the statement of contribution is accurate, and give permission for the inclusion of the paper in the thesis.

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Steven Delean (Supervisor)

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Date: 10 June 2012

Corey J. A. Bradshaw (Principal supervisor)

Date: 10 June 2012

Biologists do not apply the term 'chromosome' to any coloured body (Varley 1958)

1.9 Introduction

Most ecologists would agree with a definition of density dependence (DD hereafter) as “...a dependence of per capita population growth rate on present and/or past population densities” (Murdoch & Walde 1989). Behind such a *simple* definition lies a long history of debates that has ramified into a colourful body of jargon. Inconsistencies in the lexicon used to name statistical and semantic DD properties, and associated population phenomena and mechanisms (Murray 1982; Sale & Tolimieri 2000; Cooper 2001; Berryman et al. 2002), have nourished an old debate through ecology’s infancy (Andrewartha 1958; Nicholson 1958a; Andrewartha 1959; Nicholson 1959; Varley 1959), maturation (Slobodkin *et al.* 1967; den Boer 1968; Reddingius 1971; Strong 1986a; Hanski *et al.* 1993; Krebs 1995; Wolda 1995) and modern sophistication (Bjørnstad & Grenfell 2001; Murray 2001; Krebs 2002a; Berryman 2004; White 2008). This debate has contrasted (in simple terms) the demographic roles of biotic interactions (as inferred from DD) and stochastic and abiotic factors, and has focussed on how to provide quantitative evidence for those roles in the single-most important theme of ecology: what determines population numbers? (Elton 1927; May 1999).

The heated and recurring bouts of scientific confrontation have been themselves one of the main reasons for diversification of the lexicon by authors massaging an array of terms to ground their views. As early as the 1950s, entomologists were striving to tidy up the large jargon concerning DD (Solomon 1949; Milne & Solomon 1958; Solomon 1958; Varley 1958; Milne 1962). Since then, this lexicon has kept expanding into an imposing collection of synonymies and polysemies, driving a pervasive inconsistency in the literature, and potentially threatening communication across authors, publications and disciplines. Far from dissuading authors from using DD, the polemics have emboldened this concept, likely boosting its currently wide cross-taxa and -discipline usage — at the expense of terminological standards and ecological clarity.

Through the first historical examination of the DD terminology, I herein track the genesis of the term (*density dependence*), related lexicon (*Allee effect*, *density feedback*, *self-thinning*), and currently used qualifiers (*compensatory*, *direct*, *delayed*, *depensatory*, *inverse*, *negative*, *positive*). I show that simple rules of nomenclature suffice to abate pervading terminological inconsistency and to affirm the biological meaning of the concept. I expect this

study to become a reference tool for early-career researchers as they become confronted with the voluminous DD literature, as well as for scholars and experts who might consider making a conscious selection of terms with respect to the foundational studies. My overarching aim is to emphasise that a more precise terminology is required for any discipline with solid and unified foundations, which can facilitate communication between ecologists in different fields of research and degrees of expertise and, ultimately, contribute to drawing generalities around the complex dynamics of populations across taxa, ecosystems, methods and disciplines.

1.10 The concept, not the term

Historically, the concept substantiating *density dependence* is distilled from Malthus' thinking on limits to growth in human demography (Malthus 1798), Darwin's views on natural selection and the struggle for existence (Darwin 1859), the popularisation of the logistic curve (Verhulst 1838; Pearl 1925; Kingsland 1995), some of the earliest and most influential treatises of ecology (Elton 1927; Fisher 1930), and from among the precursors of general systems theory where individuals are treated as molecules exchanging matter and energy in a dynamic matrix (Adams 1918).

Harper (1974) attributes the first conceptualisation of DD into a mathematical model to the Swiss botanist Karl Wilhelm von Nägeli (1874). Botanists had certainly founded the study of competition and population dynamics through the 19th (e.g., DeCandolle, Sachs, Wollny) and early 20th (e.g., Clements, Sukatschew, Tansley) centuries, addressing DD questions in field observations and experimental manipulations of plant densities (reviewed in Clements *et al.* 1929): "There are certain points of resemblance between communities of plants and those of human beings or animals; one of these is the competition for food which takes place between similar individuals and causes the weaker to be more or less suppressed" (Warming 1909). Over the first third of the 20th Century, zoologists embraced DD in the study of animal demography within two main fields, namely the biological control of insect pests (Howard & Fiske 1911; Thompson 1928; Smith 1935), and the physiology and demography of protozoans in laboratory cultures (Woodruff 1911; Robertson 1924; Johnson 1933). Entomologists emphasised the prevention of population growth rates by crowding due to increased predation/parasitism on outbreaking insects, while protozoologists did so with increased mortality resulting from accumulation of toxins of thriving protozoa. Warder Allee married the advances of the two disciplines in the promotion of DD, and amplified its semantics with those cases where population growth rates were measured in groups of living beings benefitting from some degree of *aggregation* (Allee 1927) or *cooperation* (Allee 1931a).

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Allee borrowed the principles of cooperation from the earliest scientists who studied animal societies systematically (e.g., Éspinas, Kropotkin and Wheeler whom Allee cited frequently), and adopted terminology from fellow botanists (Clements & Shelford 1939) to apply it to animal demography (Allee 1927, 1931b, a). Due to his pioneering broad view of DD, I believe that Allee could claim fatherhood of this concept in ecology.

Mathematically, DD is a statistical signal of a (causal) relationship between the size of a population and at least one of its measurable demographic rates. Thus, the demographic rate represents the response variable, and population size functions as the predictor. DD can be measured by three statistical properties: (i) evidence [i.e., relative statistical support for the DD relationship through estimates of Type I error probability (Fox & Ridsdillsmith 1995), model probabilities (Brook & Bradshaw 2006) or parameter goodness-of-fit (Dennis *et al.* 2006)], (ii) strength [slope of a linear relationship (May 1974; May *et al.* 1974)], and (iii) shape [degree of nonlinearity (Gilpin & Ayala 1973; Fowler 1981)]. Strength measures changes in a demographic rate in response to unit (raw scale) or order-of-magnitude (proportional scale, e.g., logarithmic) changes in population size. The effects of population size on overall population growth rates are popularly gauged through ‘population growth curves’, like logistic equations (Eberhardt *et al.* 2008). As to shape, upwardly curved DD growth responses imply that most DD (i.e., the highest rate of change in a demographic rate) happens at relatively high population size, and downwardly curved DD growth responses imply that most DD takes place at low population size.

In most demographic studies, population size is estimated as the number of individuals per unit area or volume (density), but DD applies equally to absolute numbers or biomass where the entire or a consistent fraction of the population is surveyed. On the other hand, demographic rates encompass fertility, survival, dispersal, or their compound interplay in an overall population rate of change generically known as ‘population growth rate’ – i.e., change in population size between two consecutive time steps due to losses (mortality, emigration) and gains (fertility, immigration) of individuals (Sibly & Hone 2002) (**Chapter 5**).

Ecologically, DD studies ultimately investigate the demographic role of social and trophic interactions (cannibalism, competition, cooperation, disease, herbivory, mutualism, parasitism, parasitoidism, predation, reproductive behaviour and the like) between individuals within a population (Sinclair 1989; Turchin 1995; Courchamp *et al.* 1999; Stephens & Sutherland 1999), because the intensity of these mechanisms varies with population size. Social and trophic interactions affect demographic rates; in turn, the change in demographic rates alters population size, looping back to modify the intensity of social and trophic interactions (**Figure 5**). Such loops constitute a ‘density feedback’ (Berryman 1989;

Berryman *et al.* 2002). In tests, models, experiments and surveys accounting for this feedback (**Figure 6** and **Figure 7**), ecologists use the statistical relationship between population size and a demographic rate as a signal for the ecological relationship between social or trophic interactions and that demographic rate, hypothesising that the latter will follow the former. In reality, population size is used as a statistical surrogate for how organisms interact at different density ranges.

Figure 5. Variables involved in the study of density feedbacks driven by social and trophic interactions among the individuals of a population (mechanisms such as aggression, cannibalism, competition, cooperation, disease, mutualism, parasitism, parasitoidism, predation, etc). Over time, those interactions alter demographic rates, in turn resulting in changes in population size, which subsequently alter the intensity of trophic/social interactions, and so on (hence, the feedback). The causal statistical relationship between population size and demographic rates is taken as a surrogate for the causal ecological relationship between trophic/social interactions and those demographic rates. The density feedback and emerging phenomena (population dampening, cycles, chaos, decline) will be modified by stochasticity, and complex interactions between stochastic and deterministic factors, whereas feedbacks can be seen in a spatial context with dispersal taking a primary demographic role.

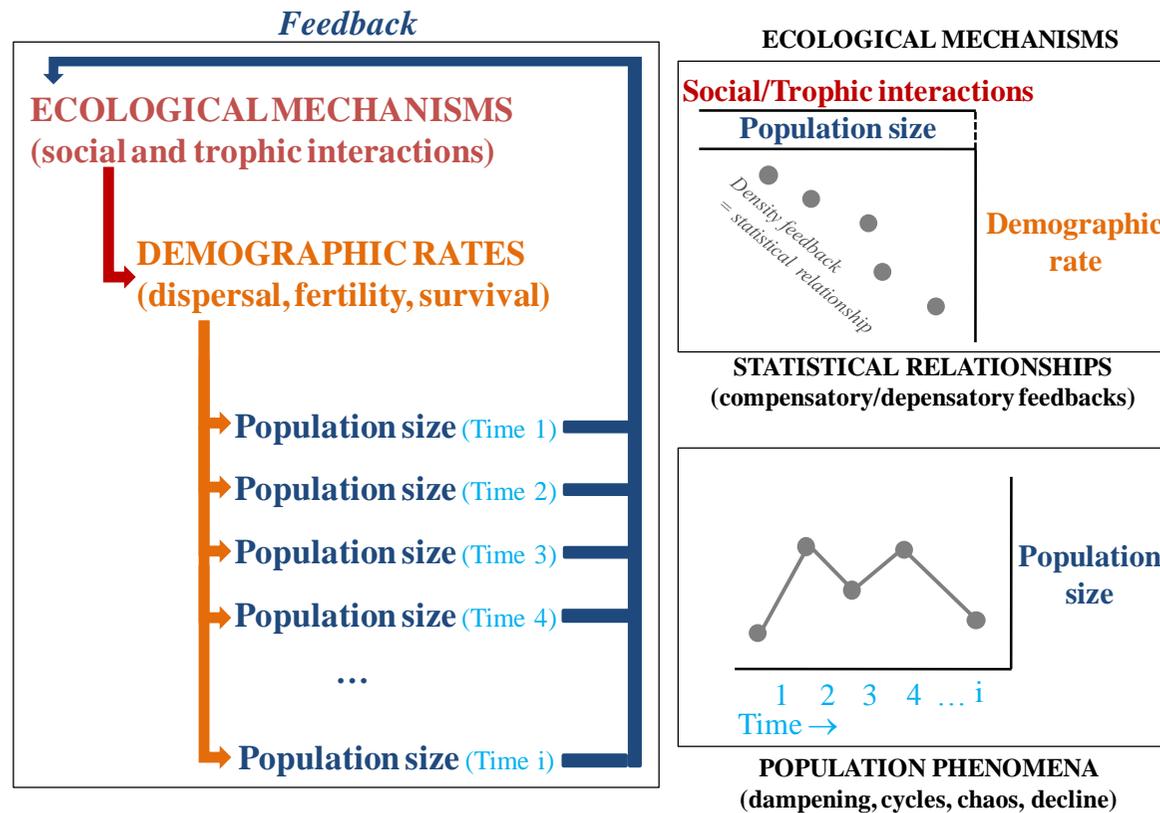


Figure 6. Examples of studies of density feedback. (a) Year-round (1978-2002) population growth curves for densities (number per river km) of saltwater crocodiles (*Crocodylus porosus*) from the Daly River (Northern Territory, Australia) (Bradshaw *et al.* 2006): following population recovery from skin-trade, harvesting proportional to annual recruitment minimises population depletion as opposed to fixed-quota based on top-ranked Ricker-logistic model-derived carrying capacity (K) (compensatory density feedback; ensemble density feedback) [Photo: Bigwave TV, UK]; (b) Percentage of yellow-tailed damselfish (*Dascyllus flavicaudus*) lost to predation (mean % \pm 1SE, $n = 6$) at two densities in net-caged and uncaged coral heads transplanted in Maharepa Lagoon (Moorea, French Polynesia) (Holbrook & Schmitt 2002): extrinsic predation enhanced by increased competition for coral shelter from low to high fish density (compensatory density feedback; component density feedback) [Photo: Melissa Holbrook Schmitt]; (c) Fertility rates (seed number per m²) as a function of fragmentation (shrub area per m²) of the endangered shrub *Banksia goodii* in Albany (Western Australia) (Lamont *et al.* 1993): number of seeds produced per unit area decreased from large to small fragments of the only 16 known populations (depensatory density feedback; component density feedback) [Photo: Byron Lamont]; (d) Year-round (1986-2005) Montagu's harrier (*Circus pygargus*) numerical response to prey (density per 100 traps) in two localities of central-western France (Millon & Bretagnolle 2008): harrier population growth rates tended to increase in years where summer densities of common voles (*Microtus arvalis*) were highest [Photo: Alain Balthazard]. r = overall population growth rate.

See figure in the next page

(a) Salt crocodile harvest assessment**(b) Damselfish competition and predation**

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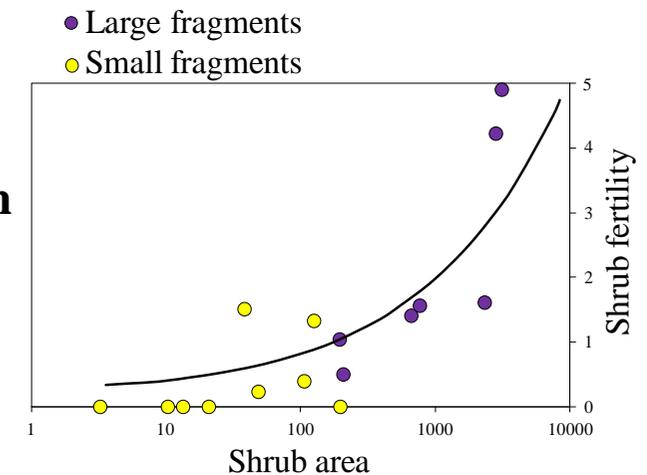
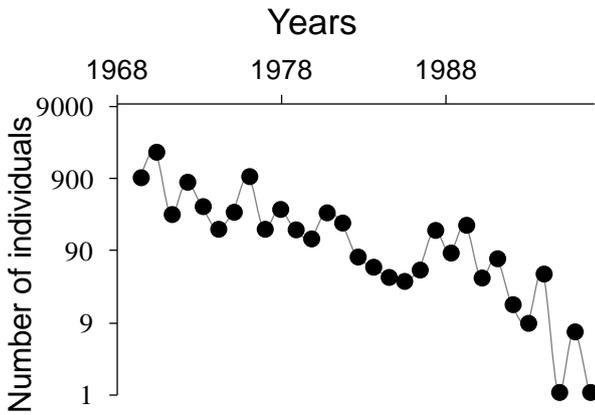
(c) Banksia fragmentation**(d) Harrier-vole predator-prey interaction**

Figure 7. Year-round time series of population size from four species' populations experiencing hypothesised phenomena of decline, chaos, cycles and stability/instability driven by density feedback. They include: (a) the butterfly *Euphydryas editha bayensis* (Data: McLaughlin *et al.* 2002; Photo: Richard A. Arnold) [Allee effect statistically supported but ecologically discarded], (b) the crab *Cancer magister* (Data: Higgins *et al.* 1997a; Higgins *et al.* 1997b; Photo: Gregory C. Jensen) [overcompensatory feedback unsupported], (c) the stoat *Mustela erminea* and the lemming *Dicrostonyx gorenlandicus* (Data: Gilg *et al.* 2003; Photo: Olivier Gilg and Brigitte Sabard/GREA) [delayed density feedback supported], and (d) the eagle *Aquila adalberti* (Data: Ferrer & Penteriani 2008; Photo: Vincenzo Penteriani) [compensatory and depensatory feedbacks supported]. Detailed description of results is given in **Appendix A3**.

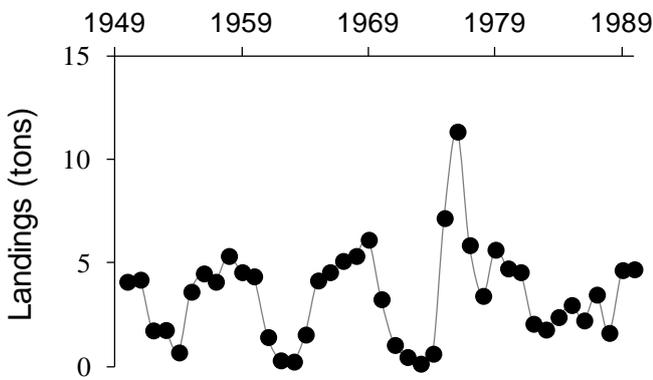
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Figure 7. Continuation.



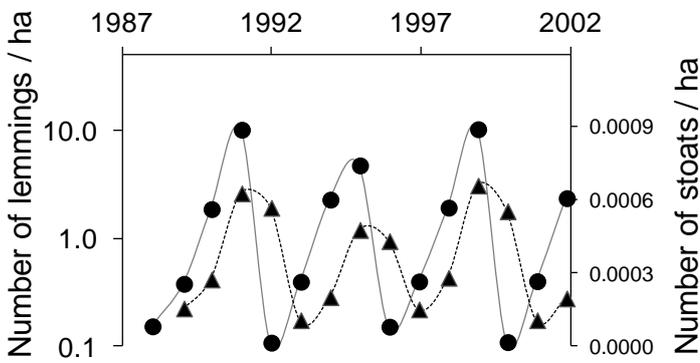
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Checkerspot butterfly
California, USA



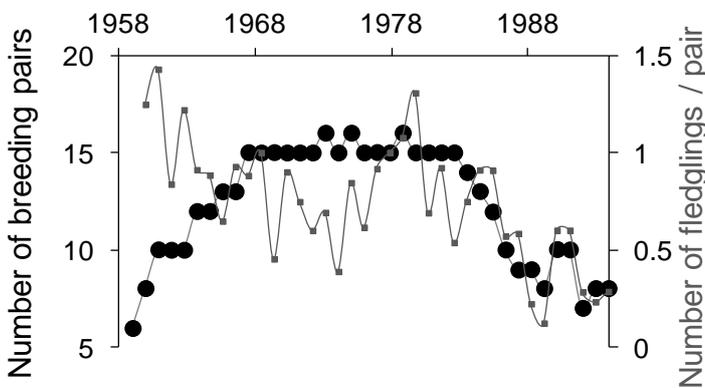
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Dungeness crab
California, USA



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Stoat (▲)
Collared lemming (●)
Tunu, Greenland



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Spanish imperial eagle
Andalucía, Spain

1.11 Genesis of the modern vocabulary

From the beginning of the 20th Century, ecologists have coined more than 60 different DD terms, often in relation to population stability or instability (variance of population size) known to be (at least partly) driven by social/tropic interactions in wild populations (**Table 2** and **Table 3**). Throughout, the DD terminology has mainly adopted the formula ‘qualifier + density-dependent’, with other peculiar terms such as *centripetality* (Caughley & Sinclair 1994), *depensatory* (Neave 1953), *disoperation* (Allee *et al.* 1949) or *self-thinning* (Shinozaki & Kira 1956). A total of 12 of those terms persist across all disciplines in the modern ecological literature from their genesis, mostly by the 1950s. Below I review the biography of those foundational terms and identify their synonymies and polysemies.

Density-dependent

Botanists initially branded a variety of generic terms, e.g., *priority*, *dependence*, *mutuality* (Yapp 1925), *tolerance* (Burns 1920), *reaction* or *coaction* (Clements *et al.* 1929), to categorise sorts of relationships among neighbouring plants and between them and their environmental requirements (light, water, etc.). Among zoologists, the entomologists Howard & Fiske (1911) featured a *facultative factor* as a biotic one (e.g., disease) killing more (host) individuals as the population in question increased in abundance (**Table 2**). Within the same field of insect biocontrol, and after citing his two contemporaneous colleagues, Smith (1935, p. 889) named the former facultative factors *density-dependent mortality factors*, thus giving birth to the adjective *density-dependent* in ecology (**Table 2; Figure 8**). Smith (1935) further recognised that “...there is still another category which destroys a percentage that decreases as the density increases... this type of mortality factor is of relatively little importance in the determination of average population densities” (i.e., *inverse* DD, see below) without suggesting any particular nomenclature for such statistical relationship. Harper (1977) noted the synonymy between *density-dependent*, as defined by Smith (1935) for animal populations, and the botanic term *self-thinning* (Shinozaki & Kira 1956) or “...self-adjustment of excess density due to competitive interaction within overcrowded pure stands of higher plants” (Yoda *et al.* 1963). Noticeably, new DD terms created by zoologists and botanists over the history of this concept have concentrated mainly on temporal or spatial demography, respectively, reflecting the distinct life histories of both groups of organisms and different research areas of enquiry (see below).

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In all foundational terminology from Smith to Neave and Haldane (see below), *density dependent* prevails as an expression of a statistical relationship between a demographic rate and population size, while the nominalisation of this adjective into *density dependence* is contemporaneous (~ 1970s). Clearly, the usage of the terms *density-dependent* or *density dependence* as such can be prone to vagueness today because it does not scrutinise types of DD. Smith (1935) referred to DD factors as drivers of population stability, invoking the ideas of *balance* or *control*: “Those species which have persisted have done so because their relations with their environment are such that there is an inherent tendency toward stability of numbers”. Along the same rationale, Nicholson (1933, 1954a) constructed a general theory of population dynamics (and a complex library of DD terms; **Table 2**) where (intra-specific) competition for depletable resources was the main DD factor balancing populations with their environment (further expanded in **Chapter 6** and **Appendix A1**). This theory has since fuelled much research into population dynamics (reviewed by Sinclair 1989; Hanski 1990; Turchin 1995; Hixon *et al.* 2002), and ecology as a whole (Kingsland 1996).

Direct, delayed, and inverse density-dependent

Allee’s work on animal aggregations was well-illustrated in his earliest research into freshwater isopods (Allee 1931b). Based on those ideas and others from research on protozoa (e.g., ‘allelocatalytic effect’ in ‘infusoria’ defined as “acceleration of multiplication by the contiguity of a second organism in a restricted volume of nutrient medium”, Robertson 1924), social insects (e.g., ‘trophallaxis’ as the mutualistic or cooperative bond between parents and offspring, Wheeler 1918), and animal cells and organisms in general (e.g., ‘prototaxis’ as the tendency to form aggregations [positive prototaxis] or to stay solitary [negative prototaxis], Wallin 1923), Allee (1941) stated that: “There is another type of density-dependent factor, which recognised by ... entomologists, is dismissed by certain of them as of no importance in population control. I refer to those eliminating influences which take a decreasing percentage of the individuals present as the population increases”. Therein he made the terms *direct density-dependent mortality factors* [synonymous with Smith’s (1935) *density-dependent*] and *inverse density-dependent mortality factors* (**Table 2**). Such a lexicon depicts change in mortality as positively (i.e., *directly*) correlated with change in population size, whereas an inverse relationship implies a negative relationship (**Table 3; Figure 8**). Through inverse DD, Allee (1941) highlighted the benefits of being a group: “...crowding may have a positive survival value for some or all of the individuals. In so far as they operate, the protection furnished by numbers is shown by the decrease in percentage eliminated by the inverse density-dependent agencies”.

Varley (1947) observed in pest flies that what he called *delayed density dependent factors* should be used when mortality factors (i.e., predator, parasites, pathogens) operate with time lags (**Table 2**): "...the parasites and predators also exercise a reciprocal influence on the numbers of the species on which they feed... the percentage of hosts destroyed by the first parasite generation will not increase, but remain unchanged. The number of hosts killed, and therefore the number of parasites emerging in the next generation, will be proportionately greater". The lag is explained mechanistically by the density check on prey/hosts being retarded until their predators/parasites/pathogens respond functionally (increase in consumption rates) and numerically (increase in numbers) (Sinclair & Pech 1996; Williams & Collins 2008), and typically results in cycles of population size in both prey/hosts and their 'enemies'. Yet maternal effects, the environment provided by parents to their offspring (Beckerman *et al.* 2002), as well as life history (Lande *et al.* 2002) and a range of carry-over effects (Ratikainen *et al.* 2008; Harrison *et al.* 2011), have also been proposed to occasion *apparent* delayed DD. Delayed DD is often assessed through autocorrelation coefficients (Moran 1953; Turchin 1990) as well as autoregressive models including, as a predictor, population size lagged over two or more time steps (Royama 1977, 1981).

In contemporaneous ecological works, some authors respect Allee's (1941) nomenclature contrasting *direct* versus *inverse* DD given the sign of the statistical relationship (e.g., Pech *et al.* 1992; Courchamp *et al.* 2000; Jennings 2000; Hixon *et al.* 2002; Wallin & Raffa 2004; Sandin & Pacala 2005). In contrast, others differentiate *direct* and *delayed* DD in terms of whether the density feedback is immediate or retarded (e.g., Holyoak & Lawton 1992; Bjørnstad *et al.* 1995; Yoccoz *et al.* 2001; Williams *et al.* 2004; Brook & Bradshaw 2006; Saitoh *et al.* 2006). As a result, the term *direct* DD has become pervasively polysemous. Berryman *et al.* (2002) argued that the reason for such polysemy is that when authors use population growth curves (Eberhardt *et al.* 2008), the relationship between population size and population growth rate is (i) inverse (negative) for what Allee (1941) called *direct* DD, and (ii) direct (positive) for what Allee (1941) called *inverse* DD (**Table 2**). The former twist of signs and terms simply originate from the fact that Allee used mortality rates instead of population growth rates as a response (**Figure 8**)!

Compensatory and depensatory

With reference to salmonids, Neave (1953) propounded the expressions *compensatory mortality factors* as opposed to *depensatory mortality factors* [he actually invented the word *depensatory*] to refer to statistical relationships which could be coupled with specific population dynamics: "...mortality which becomes relatively heavier [compensate] as

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populations *increase* in density, thereby tending to stabilise the prevailing population level”, and “...mortality which becomes relatively heavier [depensate] as populations *decrease* in density, thereby tending to exaggerate fluctuations initiated by other causes” (Neave 1953) (**Table 2**). Clearly, *compensatory* and *depensatory* are synonymous with *direct* and *inverse* DD, respectively, as used by Allee (1941) (**Table 3; Figure 8**). The intuitive meaning of compensatory mortality in a demographic context (that is, mortality compensating for increase in population numbers) explains why Nicholson (1954c) already referred to *compensatory reactions* in his classical experiments with blowflies, whereas Varley added another semantic layer to this jargon (see *overcompensation* below).

The terms *compensatory* and *depensatory* DD have been employed predominantly in fisheries papers (e.g., Myers *et al.* 1995; Liermann & Hilborn 1997; Rose *et al.* 2001; Mullon *et al.* 2005; Walters *et al.* 2008), in which new jargon designed in other disciplines has been largely neglected. Thus, Neave’s (1953) only quotation outside fisheries was: “...for [compensatory] mortality which operates in this manner the term ‘density-dependent mortality’ has been used in other fields, particularly in entomological studies (Solomon 1949)”. Curiously, due to his dual expertise on stonefly taxonomy and fisheries, Ricker was certainly an exception, and ideas and papers of contemporaneous entomologists impregnated his writings – thus, his famous paper describing stock-recruitment (Ricker 1954) was inspired by ‘the Nicholsonian point of view’ (Garfield 1982).

As *density-dependent* (qualifying a demographic mechanism or factor) turned to *density dependence* (representing a statistical relationship), *compensatory* and *depensatory* quickly became nominalised as *compensation* and *depensation*, and have not resisted polysemy either. Thus, compensation is polysemous in population dynamics, most often associated with any ecological factor that takes over the role of others. Thus, harvesting can compensate for DD mortality of target species (Sinclair & Pech 1996; Heino & Dieckman 2008), and more generally “...compensation is the demographic response to predation or harvest mortality ... usually due to density dependence” (Boyce *et al.* 1999). In examining tree canopy-gap formation, Clark (1992) defined *density compensation* as “...the degree to which mortality caused by density-independent factors is alleviated by reductions in density-dependent mortality”. Furthermore, Ricker (1958) borrowed body *growth compensation* from fisheries (Gilbert 1914; van Oosten 1928) and body *growth depensation* from Neave (1953): “Negative correlations [i.e., “increments in [body] size in successive years of life, among the fish of a given year-class”] indicate growth compensation, because they show that the smaller fish tend to catch up with the larger. Positive correlations have been called ‘reverse growth

compensation’, but a shorter term might be ‘growth depensation’ — adopting a word that was proposed in a different context by Neave (1954)” [year misquoted from 1953].

Positive and negative density-dependent

Haldane (1953) introduced the terms *negative density-dependent* and *positive density-dependent factors* to describe when overall population growth rates decrease or increase with population size, respectively (**Table 2**): “Smith called these density-dependent factors. It is perhaps better to call them negative density-dependent factors to distinguish them from [positive DD] factors, also dependent on density, which act in the opposite way, and make for instability”. Once more, Haldane synonymised *negative* with *direct* (Allee 1941) and *compensatory* (Neave 1953), and *positive* with *inverse* (Allee 1941) and *depensatory* (Neave 1953). Although Haldane (1953) did quote Varley and Allee, he ignored their older DD terms and remarked that negative DD could be *immediate* (= direct DD, Allee 1941) or *delayed* (= delayed DD, Varley 1947) (**Table 2** and **Table 3**): “...the number of parasites emerging next year depends both on the number of hosts and that of parasites the year before, so control is delayed”.

In the modern literature, *positive* and *negative* DD are often used to indicate the sign of a DD statistical relationship, irrespective of whether DD is compensatory or depensatory (contrary to Haldane’s terms), provoking further polysemy. Thus, compensatory DD (theoretically associated with population stability) equates both (i) with a negative relationship of population size with recruitment, reproduction, survival, immigration and/or population growth rates, and (ii) with a positive relationship of population size with mortality and/or emigration (**Table 3; Figure 8**). The converse statistical signs hold for depensatory DD (theoretically associated with population instability) (**Table 3; Figure 8**). The literature is plagued with examples that contradict Haldane’s (1953) lexicon. As an illustration, McCarthy (1997) wrote: “The Allee effect (negative density dependence) occurs when population growth rate is reduced at low population size (Allee, 1931, 1938)”; and Choi & Kimmerer (2008) wrote: “Mate limitation at low population levels can result in negative or depensatory density dependence, a form of positive feedback by which reproductive success declines as the population shrinks (Allee, 1931)”. Plant ecologists refer to *negative density dependence* (or *positive* for the opposite relationship) where dead individuals (e.g., trees) might have lower chances of being replaced by a conspecific if crowding exacerbates attack rates by specialised enemies, so facilitating the coexistence of common and rare species (Wright 2002).

Positive and negative feedback

In its simplest expression, a feedback occurs when the intensity of a factor affecting a system is modulated by the system itself via a reciprocal response or internal loop (**Figure 5**). The terms *negative feedback* and *positive feedback* originated from systems theory which recognises that natural, social and economic systems comprise groups of interacting entities governed by similar principles, however differently named per discipline (von Bertalanffy 1968). Feedback is one of those principles, its co-occurrence in machines and living organisms being the foundation of cybernetics (Wiener 1948). Wiener (1948) took the term feedback from the engineering sciences, and Milsum (1966) was among the earliest authors to relate it to population dynamics. The foundation of the term is certainly diffuse and can be frequently found before the 1970s in generic papers on biological systems (e.g., Dempster 1960; Manier 1970). The first authoritative usage of feedback terminology in population dynamics can be traced to Pimentel (1961, 1968), Slobodkin (1968) and Andrewartha (1970), and was much later rescued by Berryman (1989, 2002). Pimentel (1961) related mechanisms of *genetic feedback* with population regulation. Slobodkin (1968) overviewed different types of positive feedback in relation to changes in behaviour, evolution, and demography: "...these alterations, in general, operate as feedback devices", with no further reference to foundational nomenclature. This author had earlier commented on Nicholson's cumbersome vocabulary (Slobodkin 1963) (see **Table 2**). Interestingly and rarely cited, after denigrating DD in the 1950s and 1960s, Andrewartha (1970) partly restated the biological meaning of this concept using systems theory lexicon after modifying considerably one section in the second edition of one of his books (see his Fig. 9.10 classifying positive and negative feedbacks): "So much has been written about negative feed-back [*sic*] to density in natural populations... I think that when the ecology of more species are known well density-dependent reactions will be found to be important in relatively few of them. This is not to deny that density-dependent reactions may occur in many ecologies and may prove to be important in some". Recently, Kokko and López-Sepulcre (2007) defined an *ecogenetic feedback* whereby (evolution-based) life-history decisions cause population change and, in turn, (demography-based) density feedback shapes life-history selection.

Negative feedback is synonymous with *direct* (Allee 1941), *compensatory* (Neave 1953) and *negative* (Haldane 1953) DD, whereas *positive feedback* is synonymous with *inverse* (Allee 1941), *depensatory* (Neave 1953) and *positive* (Haldane 1953) DD (**Table 3; Figure 8**). Many conform to feedback nomenclature (e.g., Berryman 1989; Rodenhouse *et al.* 1997; Hunter & Price 1998; Watson *et al.* 1998; Amarasekare 2004; Tavecchia *et al.* 2007; Dornier

et al. 2008; McCarthy-Neumann & Kobe 2008; Holt 2009). However, feedback loops are not exclusive to demography, occurring in many biological (and non-biological) systems, whereas the terms *negative/positive* feedback are indistinctly used for genetic and demographic responses. Besides, they are also not safe from the polysemous qualifiers presented above, e.g., *direct negative feedback* (Lima *et al.* 2001b; Hofstetter *et al.* 2006).

Allee effect

This term refers to *depensatory* (Neave 1953) or *inverse* (Allee 1941) DD measured only at low population numbers (Courchamp *et al.* 1999) (**Table 2** and **Table 3; Figure 8**). The origin of the expression *Allee effect* is mysterious across all DD jargon. For obvious reasons of humility, Allee did not brand the expression himself. It was Odum (1953) who labelled *Allee's principle* only two years before the death of his colleague, and *Allee growth type* later when describing the Allee effect graphically (Odum 1963) (**Table 2**). Odum's linkage of Allee's surname to a DD type seems crucial for the settlement of such a linkage thereafter. The question of who used *Allee effect* for the first time is still unresolved, but I have found it cited from the early 1970s onwards. When referring to it, authors misquote either Allee's earliest publications in the 1930s and 1940s, or the four most cited (review) papers on Allee effects, namely Dennis (1989), Courchamp *et al.* (1999), Stephens & Sutherland (1999) and Stephens *et al.* (1999). The former four reviews, and even a recent book devoted entirely to Allee effects (Courchamp *et al.* 2008), point towards *Allee's principle* (Odum 1953) as the stepping stone to current lexicon, but do not clarify the foundation of the term. I observe its first record as a note in small font at the end of May (1972): "... 'Allee effect' ... whereby the per capita birth rate falls off at small x [population size]. This result makes sense biologically: models incorporating the effect should permit the possibility of extinction" [therein *Allee effect* misquoted as Allee (1938)]. However, May has asserted that his work does not constitute the genesis of the term (R. May, pers. comm.).

Biologically speaking, the steady extirpation of individuals at low population size can lead to extinction, while steady addition of individuals can counteract the benefits of crowding, both effects potentially dismantling social organisation. Allee effects are of obvious relevance to the conservation of populations and management of detrimental human impacts, being attributed to mechanisms such as failure of potential mates to encounter, collapse of social packing, inbreeding depression, demographic stochasticity (e.g., sex ratios), low fertility in threatened species, and overharvesting (Stephens & Sutherland 1999; Berec *et al.* 2007; Courchamp *et al.* 2008; Gascoigne *et al.* 2009; Kramer *et al.* 2009). By virtue of similar mechanisms, Allee effects are also applied in pest and invasion control (Fagan *et al.* 2002;

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Tobin *et al.* 2011). Population growth models including Allee effects must be able to track a typically hump-shaped nonlinearity at the low spectrum of population sizes (Courchamp *et al.* 1999; Gregory *et al.* 2010, see associated terms in next section).

Overcompensation

Varley created several modifiers for *compensation* by treating DD mortality relative to population return to carrying capacity: “The efficacy of a density dependent [sic] factor can be best considered in terms of compensation. Exact compensation is provided when a population [at density] N_0 above the equilibrium population [at density] N_e is brought down in a single step to that level” (Varley 1963). The entire idea fell within key-factor analysis, where the intensity of compensation was measured as the slope (β) of survivors (mathematically identical to the ‘instantaneous growth rate’, Sibly & Hone 2002) to logarithms of densities before mortality operated. So a population underwent *overcompensation* ($\beta > 1$), *exact compensation* ($\beta = 1$), or *undercompensation* ($0 < \beta < 1$) when, following a population increase, a mortality factor brought numbers below, to or above carrying capacity, respectively (Varley & Gradwell 1970; Varley *et al.* 1973) (**Table 2**). This conceptualisation stresses the fact that the magnitude of DD compensation must be quantified in response to proportional changes in population size (e.g., logarithmic scale) (Doncaster 2006; Doncaster 2008), such as in the Gompertz model (Medawar 1940; Nelder 1961) (formulated in **Table 4** and **Chapter 3**). Varley’s work pioneered the identification of thresholds of single-species population-model parameters relative to different population trajectories, overcompensation being from then on associated with population instability and chaotic phenomena (Hassell *et al.* 1976; Hastings 2009) and mechanisms such as scramble competition in response to limited resources (Bellows 1981). A recent food-addition experiment showed that, irrespective of low or high nutrient availability, stochastic provision of beans to beetle populations shifted the strength and shape of DD and triggered remarkably wider population fluctuations compared to controls with regular food provision (Bull & Bonsall 2008). Those authors defined *overcompensation* as “...a nonlinear density dependence leading to populations overshooting equilibrium” [with no reference to Varley’s seminal work and terms].

Overcompensation has also succumbed to polysemy. Botanists and fish ecologists use *compensation* and *overcompensation* to label different degrees of nonlinearity of density feedbacks. Thus, *overcompensating negative density dependence* refers to a steep nonlinear decline in plant recruitment as seed density increases across several sites (Freckleton & Lewis 2006; Bagchi *et al.* 2010), whereas *overcompensation* also relates to pronounced declines in

fish recruitment across stocks from low to high spawner abundances (Bjorkstedt 2000; Myers 2001). In a different context, *overcompensation* means a human-induced feedback where fishing pressure magnifies stock size by (i) promoting sex inversion (Beentjes & Carbines 2005), or (ii) increasing juvenile (*reproduction regulation*) or adult (*maturation regulation*) biomass through stage-specific demographic responses (de Roos *et al.* 2007; Zipkin *et al.* 2008). Moreover, plant demographers commonly describe individuals that overcompensate for herbivory through increasing branching and fruit and seed production (Belsky 1986).

Figure 8. Terminology mainly used in modern ecological literature to label contrasting dependant and compensatory density feedbacks on different demographic rates (modified from Solomon 1976) (see also **Table 2** and **Table 3**). For simplicity, we have used nominalized terms (e.g., *Densation* for *Dependant mortality factor*). Lines represent linear and nonlinear feedbacks. When authors name density feedback types literally by the sign of the statistical relationship (i.e., *positive/negative* or *direct/inverse*), terms will potentially fall in conflict with original nomenclature. For instance, Haldane (1953) labelled compensatory feedback on any demographic rate as *negative density dependence*, but the positive relationship between population size and mortality (or emigration) rates also represents a compensatory feedback.

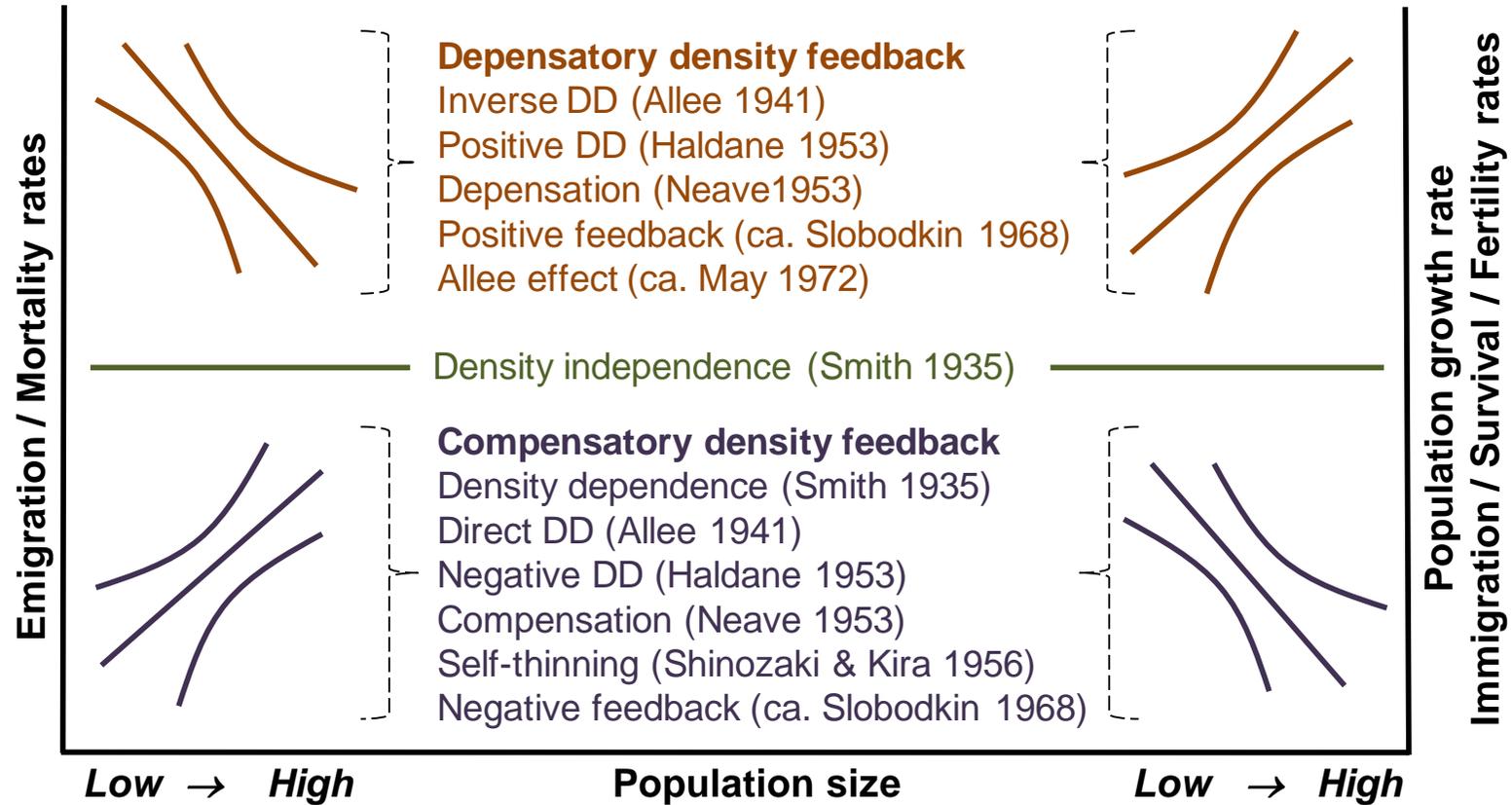


Table 2. Historical summary of qualifiers used to name density-dependent¹ factors and relationships between demographic rates and population size, and their linkage to temporal phenomena of change in population size (stability, cycles, instability). References are arranged chronologically. Creation of jargon peaked in the 1940s-1950s, with new terms seeing the light in each decade from the 1910s to 2000s. N = population size; DD = density dependence/density-dependent; r = overall population growth rate.

Stability	Cycles	Instability	Rate related to N	Foundational reference
facultative			mortality/species multiplication	(Howard & Fiske 1911)
environmental resistance			reproduction	(Chapman 1928) ²
individualised			mortality	(Thompson 1928)
		co-operation	survival (in particular)	(Allee 1931a) ³
controlling			offspring production/survival	(Nicholson 1933)
density-dependent			mortality	(Smith 1935)
direct DD		inverse DD	mortality	(Allee 1941)
dependent R-factor			r	(Voûte 1943)
	delayed DD		host/prey mortality	(Varley 1947)
disoperation			r	(Allee <i>et al.</i> 1949) ³
concurrent			(killing) action	(Solomon 1949)
(immediate) negative DD	delayed negative DD	positive DD	emigration/mortality/natality/ r	(Haldane 1953)
compensatory		depensatory	mortality	(Neave 1953)
		Allee's principle	survival/ r	(Odum 1953)
		underpopulation	r	(Andrewartha & Birch 1954)
		Allee type	oviposition	(Fujita 1954)
self-decimation			mortality	(Lysenko 1954)
density governing		density disturbing	r	(Nicholson 1954a) ⁴
self-thinning			mortality	(Shinozaki & Kira 1956) ⁵
perfectly/imperfectly DD			mortality	(Milne & Solomon 1958; Milne 1962)
directly density-related	alternately density-related	inversely density-related	mortality/reproductive rate/ r	(Solomon 1958)
inversely DD		Allee growth type	r	(Odum 1963)
exact compensation		overcompensation	mortality	(Varley 1963; Varley & Gradwell 1970)
undercompensation				
negative feedback		positive feedback	r	(ca. Slobodkin 1968)
negatively DD		positively DD	r	(Reddingius 1971)
		Allee effect	<i>per capita</i> birth rate	(ca. May 1972)

Table 2. Continuation.

linear first order process	linear second order process			
nonlinear first order process	nonlinear second order process		r	(Royama 1977)
	lag effect			
causal/causally/type A DD				
statistical/statistically/type B DD				(Royama 1977, 1981)
intensity-dependent			parasite load	(Margolis <i>et al.</i> 1982)
effective DD			survival/reproduction	(Murray 1982)
explicit DD			r	(Strong 1986a)
centripetality			r	(Caughley & Sinclair 1994)
	demographic Allee effect		total fitness	
	component Allee effect		component fitness	(Stephens <i>et al.</i> 1999)
direct density control				
classical Nicholsonian DD				(Sale & Tolimieri 2000)
phenomenological DD				
weak causal DD			r	(Cooper 2001)
strong causal DD				
compensatory DD		depensatory DD	population size	(Rose <i>et al.</i> 2001)
first-order feedback	higher-order feedback		r	(Berryman <i>et al.</i> 2002) ⁶
	delayed compensatory density feedback	ensemble Allee effect ⁷	r	(Herrando-Pérez <i>et al.</i> 2012b)[Chapter 2]
compensatory density feedback		depensatory density feedback ⁷	r	(Herrando-Pérez <i>et al.</i> 2012a)[Chapter 5]

¹ The hyphenated expression density-dependent is the correct one, though the use of density dependent is widespread – this is a grammatical issue

² “The environmental resistance will include the physical factors of the environment, temperature, humidity, etc. and also the biotic factors of the environment, parasites, competitors, etc.”

³ Allee used these terms with an explicit DD meaning, yet *disoperation* can be traced to Clements (1935) and *cooperation* has use beyond last century. Allee and many others often used *undercrowding* (= cooperation) and *overcrowding* (= disoperation) which have a diffuse origin in nonhuman-demography literature

⁴ Nicholson (1954a; see his Fig. 1) classified nine new terms under two different perspectives. On one hand, terms identifying the effects of population size on factors driving population dynamics (factors were named ‘requisites’ under this perspective). On the other hand, terms identifying the effect of driving factors on population size (named ‘density factors’ under this perspective). His ‘reactive responsive requisites’ could be governing or disturbing which are germane to *direct* and *inverse* DD (Allee 1941), respectively

⁵ The term *self-thinning* can be tracked to European and American literature on plant cultivation and gardening from the 19th Century; however, mid-20th Century Japanese botanists, led by Tatum Kira, reinforced its application in demography (see Harper 1977)

⁶ Berryman *et al.* (2002) promulgated the vocabulary from systems theory. Negative feedback operating without lags is known as *first-order process* or *first-order feedback*, while *delayed negative feedback* is germane to *higher-order process* (Royama 1977) or *higher-order feedback* (Berryman *et al.* 2002)

⁷ The terms *ensemble density feedback* and *component density feedback* refer to feedbacks measured on r or single demographic rates, respectively (see main text), so both can be depensatory or compensatory; whereas *ensemble Allee effect* is synonymous with *demographic Allee effect* (Stephens *et al.* 1999), and implies a depensatory density feedback on r at low N

Table 3. Foundational terminology for the qualifiers of density dependence (DD) used in the modern literature of ecology, including the earliest terms coined to name each of four DD types, synonymous terms created by other authors (see references in **Table 2**), and population phenomena linked to those DD types in the ecological literature. Included those qualifiers proposed in this study. N = population size; r = overall population growth rate.

Qualifiers of density dependence/feedback			Linked demographic phenomena			
Earliest	Synonyms	Proposed	Crowding effect ¹ on r , immigration, fertility, recruitment, survival	Emerging N dynamics	Population regulation	Population extinction
direct (Allee 1941)	compensatory first-order immediate negative self-thinning	compensatory	Depression	Stability (dampening)	Yes	No
delayed (Varley 1947)	lagged second-order ²	delayed compensatory	Depression	Stability (cycles)	Yes	No
overcompensation (Varley <i>et al.</i> 1973)	overcompensatory	overcompensatory	Depression	Instability (chaos)	No ³	Yes
inverse (Allee 1941)	(Allee effect) ⁴ depensatory positive	Allee effect depensatory	Enhancement	Instability ⁴ (decline)	No	Yes

¹ Effects of opposite sign, from those reported in this column, are expected on emigration and mortality (**Figure 8**)

² Second-order DD implies a lag of two time steps, yet higher-order dynamics are possible (Royama 1977; Berryman *et al.* 2002)

³ Chaotic dynamics have been proposed to participate in the regulation of metapopulations (Hanski 1990; Allen *et al.* 1993)

⁴ Allee effects are a sort of depensation only at low N (Courchamp *et al.* 1999). In theoretical scenarios, Allee effects have been shown to lead to population stability (Scheuring 1999), or to reduce the amplitude of oscillations (Fowler & Ruxton 2002)

1.12 Reasons for terminological inconsistency

The biography of DD terms reveals five reasons why this terminology has become inconsistent, namely: (i) Ecologists who forged the DD concept appointed terms from their own areas of expertise, often ignoring (deliberately or unintentionally) those of their colleagues in the same (e.g., entomology) and different (e.g., botany, ecology, fisheries, zoology) disciplines. (ii) From the earliest to modern DD literature, polysemy reveals carelessness among authors to check the correct semantics of their lexicon with regard to the original nomenclature, a problem that is spread throughout the ecological literature given the enormity of the knowledge base which now exists. (iii) Experts have furnished new terms to ground their views in debates about the biological meaning of DD and demographic role of DD mechanisms, and how to provide statistical evidence for that role, particularly relative to population regulation. (iv) Modern ecologists work in different philosophically based paradigms to study population dynamics, and the semantic range of lexicon overlaps across those paradigms. (v) Research progress leads to new lexicons as the understanding of concepts is refined, as illustrated by Allee effects. I expand these points below.

Reinventing the wheel

Many authors have described the same concepts from their own areas of expertise, coining new terms and tellingly, often ignoring those of their colleagues. The genesis of redundant terms has root partly in the isolated origin of research disciplines. I outline some examples hereafter. The geneticist Haldane (1953) created *positive/negative* DD that the invertebrate ecologist Allee (1941) had previously named *inverse/direct* DD. Neave (1953) branded *dependantory/compensatory* for *inverse/direct* DD (Allee 1941) — *dependantory* or *dependantion* are classic terms of the fishery literature (see below more diversification of fishery terms of an Allee effect), and now also found in ecological and zoological works. *Self-thinning*, the most distinctive DD term in plant population dynamics for compensatory density feedback, originated from the ground-breaking work of Japanese botanists in the 1950s and 1960s (Kira *et al.* 1953; Kira *et al.* 1954; Hozumi *et al.* 1955; Ikusima *et al.* 1955; Hozumi *et al.* 1956; Kira *et al.* 1956; Koyama & Kira 1956; Shinozaki & Kira 1956; Tadaki & Shidei 1959; Ando 1962; Yoda *et al.* 1963). Lastly, parasitologists suggested *intensity dependence* for DD (Bush *et al.* 1997): "...since 'intensity', rather than 'density', is the term applied to the number of individuals in a parasite 'infrapopulation', 'intensity-dependent' would be the appropriate term when parasite 'infrapopulations' are concerned. It is also improper to use 'density-

dependent' in relation to the synonymous terms relative 'density' or 'abundance' ('density' of some authors) because their calculation uses 'prevalence' and 'intensity', parasite population parameters that are controlled or regulated by different mechanisms" (Margolis *et al.* 1982).

Poor citation practice

All the (foundational) synonymous terms of the style 'qualifier + density-dependent' (**Table 2**) were available to ecologists after the 1950s-1960s. The subsequent and notorious growth and specialisation of DD research into different taxa and ecosystems did not respect the meaning given to those terms, and severe polysemy emerged and lingers today, especially for *direct*, *positive* and *negative* DD. Such a pattern notably indicates carelessness among authors to check the correct semantics of their lexicon with regard to the original nomenclature. The pervasive mis-citation of the *Allee effect* with reference to Allee's work in the 1930s and 1940s, or to the most classical reviews of the concept (Dennis 1989; Courchamp *et al.* 1999; Stephens & Sutherland 1999; Stephens *et al.* 1999), stands out as an obvious example. This is an important problem not only because of communication issues, but also because it distorts bibliometric indicators (Todd & Ladle 2008). Thus, "...the causes of mis-citation are more likely to be deep-rooted within the culture of modern ecological research", reflecting that authors facing publication pressure might not spend enough time reading their cited papers, scientists might have access to abstracts and not to full publications at their working sites, and inappropriate undergraduate training (Todd *et al.* 2007), as well as an overall neglect of old literature (Belovsky *et al.* 2004).

Statistical versus biological significance

Many DD terms emerged around how to quantify DD from the genesis of the concept. By the 1950s, Smith's (1935) generic term for a *density-dependent mortality factor* had become too narrow to differentiate *inverse* from *direct* DD (Allee 1941), with or without time lags (Solomon 1958; Varley 1958). The crux of the distinction was mathematical and mechanistic for Varley (1958), who advocated the term *density-dependent* with regard to the single-species logistic model of Pearl (1922), and for *delayed* DD relative to the predator/prey or parasite/host models by Lotka (1925), Volterra (1926), and Nicholson & Bailey (1935). Under a similar reasoning, Milne & Solomon (1958) suggested *perfect* and *imperfect* DD whether the causes of feedback were intra-specific competition or 'enemies', respectively, while the earliest terms had all been related to mechanisms (Howard & Fiske 1911; Thompson 1928) (**Table 2**). However, Solomon (1958) warned that sparse empirical evidence for those mechanism-DD type links should prevent lexical separation. He had already

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attributed “...divergences of opinion... [to]... outcomes of specialisation” of researchers adopting “...partial, one-sided explanations” by focusing on different taxa, on only biotic or only abiotic factors, and “...misunderstanding over the use of certain terms” — which he discouraged by noting that they “...are newly defined or given a more precise meaning than usual... to avoid misleading usages, it may assist the reader to have the following reference list [23 terms!], showing the pages where the terms are defined or explained” (Solomon 1949).

After the 1970s, debates turned philosophical (often with mathematical backing) about the biological meaning of DD with regard to the role of trophic/social interactions in population regulation, as illustrated by Murray (1982): “...the issue that divided population ecologists in the past was not whether birth rate declined and death rate increased at higher densities. On this, everyone was agreed. The debate concerned the *causes* of these rate of changes”, Royama (1992, p. 43): “...density dependence can no longer be sought with statistics. We must determine the nature of the factor as an ecological entity... Once the factor has been identified, the evaluation of its effect on reproductive rate then becomes a subject of statistics”, and Berryman *et al.* (2002): “...it makes sense to use this term [DD] to describe any response that is proportional to population density... The problem arises when it is used in defining the process of population regulation”. Examples of the most recent DD terms in such philosophical guise are *effective* and *ineffective density dependence* (Murray 1982); *explicit density dependence* (Strong 1986a); *phenomenological*, *weak* and *causal density dependence* (Cooper 2001); *classical Nicholsonian density dependence*, *direct density-dependent control of density*, *classical density independence* and *density-related determination* (Sale & Tolimieri 2000); or *statistical* and *causal density dependence* with regard to *weaker* and *stronger regulation* (Royama 1977, 1981) (**Table 2**).

Distinction between biological and statistical DD is pointless, providing that DD is simply regarded as a statistical concept. If authors are ready to coin new terms to differentiate the statistical from biological significance of DD, we should be prepared to do the same with any other statistical relationships with potential biological significance in other contexts, e.g., is there *statistical* and *causal* pollination, or global warming, etc.? That matters to statistical reporting and inferences (Reese 2004) rather than to concepts and their terms.

Paradigms fragment lexicon

Krebs (1995, 2002b) has championed the distinction of two paradigms in the study of population dynamics: (*i*) the ‘density paradigm’ (equilibrium-oriented stability, phenomenological focus, observational approach, backwards in time, long-term data, highly

amenable to modelling and drawing generalities, low management utility, simple/additive causes of death), and (ii) the ‘mechanistic paradigm’ (not oriented to equilibrium stability, mechanistic focus, experimental approach, forward in time, short-term data, not generally amenable to modelling or drawing generalities, high management utility, complex/compensatory causes of death) (Krebs 1995; but see Sinclair & Pech 1996). Krebs’ paradigms are formulated from a pragmatic-philosophical stance: “...the mechanistic paradigm short-circuited the search for density dependence, on the assumption that no predictive science of population dynamics could be founded on describing relationships between vital rates and population density without specifying the ecological mechanisms driving these rates... the density paradigm is remarkably useless in solving management problems or in providing an understanding of why populations change in size” (Krebs 2002b).

Synthetically, to Krebs (2002b) the ‘density paradigm’ relies on the analysis of census data before mechanisms are addressed, while his ‘mechanistic paradigm’ centres directly on mechanisms affecting reproductive, mortality or dispersal rates. Then, he alleges that DD measures add little understanding to population dynamics because population size might merely represent a poor surrogate for the true drivers of population change such as food supply, territorial space and predation pressure (Krebs 2002a, b). By advocating the ‘mechanistic paradigm’ against the ‘density paradigm’, Krebs also got rid of the DD jargon created mostly within the latter paradigm. However, two alternative paradigms, as Krebs proposed, potentially means two sources of lexicon. Indeed the terminological separation that Milne & Solomon (1958), Solomon (1958) and Varley (1947, 1958) made between mechanisms related to delayed DD (predators, parasites or pathogens) and inverse and direct DD (competition and social interactions), was also applied by Caughley & Krebs (1983; updated in Krebs 2009) to coin the terms *extrinsic regulation* and *intrinsic regulation*, respectively. In doing so, different terms for identical and overlapping concepts have been created within different paradigms. So, if ecologists studying population dynamics work in different philosophically based paradigms, and the semantic range of some lexicon merges to a greater or lesser extent across paradigms, how could a consistent terminology be accomplished?

Research progress produces new terms

The addition of new terms to the ecological dictionary can result from both broad and specific, innovative enquiries. Thus, the incorporation of temporal structure in a DD model recognised that processes driving density feedback could vary seasonally from harsh (e.g., winter) to benign (e.g., summer) conditions year after year, resulting in *sequential* (Åström *et*

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al. 1996) or *seasonal* (Kokko & Lindström 1998) DD. Building on sequential processes (Ratikainen et al. 2008; Harrison et al. 2011), Bjorkstedt (2000) proposed *sequential* or *serial* versus *concurrent* DD when density feedbacks on a given stage affect only the next stage or several stages of the life history of fish, respectively.

Likewise, along with the DD terms created by zoologists, plant ecologists have also often employed generic expressions like *density response*, *yield-density relationship*, *neighbour effect* (Antonovics & Levin 1980; Watkinson 1980; Vandermeer 1984) or *fecundity predictors* (Pacala & Silander 1985). Yoda *et al.* (1963) characterised *self-thinning* (Shinozaki & Kira 1956) by representing initial density of plants (abscissas) against density of surviving plants (ordinates) [both log-transformed] across different experimental initial densities and at different time intervals. *Self-thinning rules* (Tadaki & Shidei 1959) result from converting the number of surviving plants to their biomass, and such *total basal area-age* (Reineke 1933), *competition-density effect* (Kira *et al.* 1953), *density-management* (Ando 1962; Drew & Hewelling 1977), or *biomass-density* (Westoby 1984) diagrams, indicate how plant stands vary according to different biomass-density combinations, or (in other words) the simultaneous effect of population size on body growth and survival. Now zoologists also use the concept and the term *self-thinning* (Begon *et al.* 1986; Latto 1994; Fréchette & Lefaire 1995; Damuth 1998), i.e., "...a reduction in density of a cohort of organisms due to intraspecific competition for a limiting resource as mean body size increases" (Rincón & Lobón-Cerviá 2002). Ratikainen *et al.* (2008) pointed out that the study of *sequential density dependence* on a range of taxa has produced different terms for similar population phenomena, e.g., "...the self-thinning principle... which is the relationship between mean weight and mean density, then constitutes an equivalent of a carrying capacity". Further, Harper & McNaughton (1962) described *alien thinning* as "...the reduction in the chance of a seed forming a mature plant caused by an increase in the density of the associated species".

Allee effects are exemplar in illustrating the splitting of terms, to designate both statistical metrics and different forms of this type of depensatory feedback, as theoretical and empirical studies have been developed in the last three decades. On one hand, terminological expansion has originated from the characterisation of one single statistical property: the *Allee threshold*. A population growth curve showing an Allee effect has a typical nonlinear shape with a hump located towards lower population sizes (Courchamp *et al.* 1999). Across the range of population sizes, the peak of the hump separates depensatory from compensatory population

growth, also denoted as the density ranges between *cooperation* and *disoperation* (Odum & Allee 1954), respectively. Ecologists refer to the *Allee threshold*¹ as the population size below which an Allee effect makes the population growth rate negative at low numbers (Berec *et al.* 2007). The *Allee threshold* was termed as a *low-density threshold* by Jacobs (1984), *critical density* by Dennis (1989), and *critical population size* or *critical population threshold* by Courchamp *et al.* (1999). In an attempt to alleviate the effects of observation error (in the context of invasion ecology), Tobin *et al.* (2007) defined and measured the Allee threshold “...as the lowest abundance in year $t-1$ at which a local population is equally likely to replace itself in the next year [t], below which it is more likely to decrease, and above which it is more likely to increase.

The dynamical properties of the Allee threshold were already described by Odum & Allee (1954): “...should the population possess a density below the birth-death balance line on the left, unless conditions change it would move to extinction” and “...isolated populations cannot... conceivably survive without some form of disoperative intraspecific competition in operation. They will either become extinct or increase until disoperative intraspecific competition does begin to operate”. Allee effects that push the population size below the Allee threshold are known as *strong Allee effects* — so (theoretically) a population must get over the Allee threshold to be able to grow again (Wang & Kot 2001), and where inbreeding depression operates the new individuals must inject new genetic material for population recovery to occur (Berec *et al.* 2007; Courchamp *et al.* 2008). *Weak Allee effects* keep population growth rate positive and such populations have no identifiable Allee threshold (Wang & Kot 2001). Clarke (1976) christened *noncritical depensation* in fisheries bioeconomics for *weak Allee effects* and *critical depensation* for *strong Allee effects* well before these concepts had their ecological counterparts by Wang & Kot (2001). Likewise, Clarke (1976) linked the Allee threshold to a *minimum viable population level* below which fish stock extinction is more probable irrespective of harvesting effort.

¹ Thresholds are termed *attractors* or *repellers* in systems theory. A well-known attractor is the equilibrium *carrying capacity* (as opposed to a ceiling carrying capacity which acts as a reflector, Traill *et al.* 2007) above which compensatory density feedback turns population growth rate negative in statistical space (Bjørnstad & Grenfell 2001; Berryman *et al.* 2002). Contrastingly, the Allee threshold is a repeller. Thresholds can theoretically be points or complex structures such as cyclical or chaotic probability distributions (May 1974; 1977). Thus, carrying capacity is not necessarily a point (fixed), but can also be a ‘probabilistic smoke cloud’ of points (May 1973). Finally, compensatory density feedback around a variable carrying capacity has been branded as *centripetality* (Caughley & Sinclair 1994) (**Table 2**), and this idea is central to population theory of deterministic versus stochastic environments (Chesson 1978, 1982).

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On the other hand, terminology of Allee effects has multiplied with recent multi-faceted research advances. Berec *et al.* (2007) present a glossary of 17 different types of Allee effects with as many terms. Those terms that define specific statistical properties of the relationship between population size and demographic rates (*dormant, multiple, nonadditive, subadditive* and *superadditive Allee effects, double dormancy, weak and strong Allee effects*) are appropriate. However, experts should reflect that those other terms labelling mechanisms violate the statistical nature of the foundational DD terminology, namely *genetic Allee effect* (“...genetic level mechanism resulting in a positive relationship between any measurable fitness component and population size or density”), *human-induced Allee effect* (“...any component Allee effect induced by a human activity”), *predation-driven Allee effect* (“...any component Allee effect in survival caused by one or multiple predators whereby the per capita predation-driven mortality rate of prey increases as prey number or density decline”) (Berec *et al.* 2007), or *emergent Allee effect* (de Roos *et al.* 2003: “...a small increase in predator mortality causes a catastrophic collapse of the food chain in which the predator species is lost and the system reaches a stable equilibrium without it”). When the relationship between compensatory or depensatory feedbacks and a mechanism has been ascertained, to create a new term becomes an unnecessary inflation of lexicon. Under the same rationale, I could expand a glossary with terms such as ‘parasite-driven density feedback’, ‘behaviour-driven density feedback’, and so forth. This quickly becomes untenable. Finally, the *anthropogenic Allee effect* (Courchamp *et al.* 2006) would also be conceptually dubious a term, and not only because it refers to a mechanism. This term represents enhanced exploitation of species as they become rarer and more attractive for (normally illegal) trade, and is modelled by a relationship between population size (predictor variable) and market price and exploitation cost, so the response variables are not demographic as are essential in Allee’s concept and terminology. Courchamp *et al.* (2006) do state: “...this human-generated feedback loop is very similar to the Allee effect”, the phenomenological similarity being both relate to population extirpation.

1.13 Simple rules of nomenclature

I acknowledge that “...language seldom changes by prescription” (Hodges 2008), and it might be unrealistic to attempt to change current DD nomenclature habits (however necessary this might be) strengthened by nearly a century of usage. Nevertheless, I hope to encourage ecologists by suggesting that much terminological inconsistency can be overcome by applying three simple rules that are rigorous with respect to the biological meaning of DD.

Rule 1: Density feedback is semantically more precise than density dependence

Density dependence evokes a correlation, *density feedback* recreates the causality inherent in the concept DD; so *density feedback* is a better term (Berryman 1989; Berryman *et al.* 2002). Berryman *et al.* (2002) advocated changing from *density dependence* to *density feedback*, yet forecast correctly that: “Many ecologists... will disagree with our recommendation that the traditional terminology be abandoned”. The choice between the two expressions is semantic, and does not cause terminological ambiguity.

Rule 2: Compensatory and depensatory density feedbacks are independent of the sign of statistical relationships

The DD vocabulary has attempted to discriminate two broad types of density feedback, whether the effect of increasing population size on a demographic rate contributes to either enhancing or arresting a population’s overall rate of growth (**Table 3; Figure 8**). The qualifiers *compensatory* and *depensatory* (Neave 1953) density feedback [or *compensation* and *depensation*] make such distinction neatly (e.g., Rose *et al.* 2001), circumventing terminological ambiguities to name the sign of DD statistical relationships.

It is equally important to acknowledge that: (i) *Allee effects* are a form of depensatory feedback occurring only at low population numbers, so not all depensation matches an Allee effect. (ii) When assessing the ‘order’ of compensatory density feedback, *immediate* and *delayed* (Haldane 1953) identify feedbacks between consecutive or longer time steps, respectively; systems theory provides the qualifiers to name unequivocally the number of time steps involved: e.g., *first-order* and *second-order* equal immediate and delayed (with two time steps) compensatory density feedback. (iii) When measures of strength of density feedback are linked to measures of temporal variance of population size, *undercompensatory* and *overcompensatory* (Varley *et al.* 1973) density feedback separate population stability from instability, respectively. However, the thresholds of density-feedback strength, distinguishing contrasting dynamics, will be model-dependent, as May (1974, 1976) exemplified for simple equations. I caution that the meaning of (*over/under*)*compensatory* feedback has been split within three different theoretical frameworks of demography: (i) temporal population dynamics (population-size predictor N = density over a sequence of times), (ii) plant-species coexistence (N = seed/seedling/adult density at different sites), and fishery stock-recruitment models (N = spawner density at different stocks), which has in turn pumped new DD terms such as *symmetric* (Volkov *et al.* 2005) and *asymmetric* (Comita *et al.* 2010) *density dependence* into the lexical balloon. This partly indicates terminological friction between

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temporal and spatial population demography, which needs cross-discipline revision beyond the scope of my review (see below and **Chapter 6** for concepts/terms challenging population regulation in a spatial context).

In summary, five DD qualifiers (*compensatory*, *delayed compensatory*, *overcompensatory* and *depensatory/Allee effects*) seem necessary to describe four population phenomena that might be theoretically linked to the action of density feedbacks, namely dampening, cycles, chaos, and decline (**Table 3**). In **Appendix A3**, I exemplify their use with four study cases from the ecological literature.

Rule 3: Ensemble density feedback encapsulates the interplay of components of density feedback

Stephens *et al.* (1999) coined the terms *component Allee effects* when measured on single demographic rates (components of total fitness), and *demographic Allee effects* when measured on the overall rate of population growth (total fitness). I suggest that this terminological distinction is routinely employed by ecologists to report both depensatory and compensatory density feedbacks. However, I favour the qualifier *ensemble* over *demographic*, because *ensemble density feedback* engrains the notion that the overall density effect on a population's growth rate is the synthesis of all component feedbacks on single demographic rates (**Chapter 5**) — whereas *demographic density feedback* might be confused with *component density feedback* operating on *demographic* rates. Note that *ensemble* and *component* density feedbacks do not refer to the sign of DD relationships, so both can therefore be compensatory or depensatory, while *ensemble Allee effects* will be synonymous with Stephens *et al.*'s (1999) *demographic Allee effects* (**Table 2**).

The conceptual (hence terminological) distinction of component and ensemble feedbacks has essential implications in the way ecologists relate DD measurements to population dynamics and resulting management and conservation actions. Essentially, unless component feedbacks are measured on all relevant demographic rates of a population (a nearly impossible task even for the best-studied populations), finding statistical evidence for single component feedbacks is no guarantee that an ensemble feedback exists or can be measured, or that phenomena such as population regulation emerge from component feedback (**Chapter 5**) — a common inference in the ecological literature (e.g., Pöysä & Pesonen 2003; Gough & Kerley 2006; Pistorius *et al.* 2008). According to Sinclair and Pech (1996), *regulation* entails that the effect of all component compensatory feedbacks must exceed that of all component depensatory feedbacks ('net density dependence effect'). So in theory, a suite of component

compensatory and depensatory feedbacks (see Bjorkstedt 2000 for concurrent DD; and Berec et al. 2007 for multiple Allee effects) can act simultaneously on reproduction, survival and dispersal rates. Kolb *et al.* (2010) found depensatory density feedback on single demographic rates (e.g., potential seed production) of a rare perennial herb that had no effect on its population growth rate, and alerted that: "...we need to be cautious when assessing the consequences of habitat fragmentation for population viability based on [density] effects on only one or a few vital rates". Likewise, I (**Chapter 5**) have identified decoupling of component and ensemble density feedbacks in > 100 populations of birds and mammals, and concluded that "...the management of anthropogenic impacts on populations using component feedbacks alone is ill-advised, just as managing on the basis of ensemble feedbacks without a mechanistic understanding of the contributions made by its components and environmental variability can lead to suboptimal decisions".

1.14 Density feedback and regulation are not the same

DD measurements of any kind (i.e., statistical evidence, strength or shape of both component and ensemble density feedback) do not imply population regulation. DD contributes to principles in crucial areas like ecosystem services, population viability or harvest quotas, but linking those tenets conceptually to population regulation only through a DD metric/model is potentially flawed (e.g., Henle *et al.* 2004; Sibly *et al.* 2005; Brook & Bradshaw 2006; Bohan *et al.* 2011). In essence, compensatory density feedback is one of the statistical requirements of, but not a test for, regulation; hence the plain statements that density feedback "...is necessary but not sufficient for population regulation" (Turchin 1995; Hixon *et al.* 2002), and "...the necessary and *sufficient* condition for regulation in a population model is the presence of negative feedback *and* parameter values that allow the population to persist". I agree with Krebs (1995) that "...most ecologists now seem to assume that the proper approach to population regulation is through density dependence, and the two terms regulation and density dependence [my emphasis] are virtual synonyms in much of the current literature".

I attribute this historical confusion to three reasons. First, the quest for population regulation over most of the second half of the 20th Century was subordinate to the development of continuously evolving DD tests (Holyoak & Lawton 1992) (e.g., Hassell 1986; May 1989; Wolda *et al.* 1994; Fox & Ridsdillsmith 1995; Freckleton *et al.* 2006) (**Table 4**); therein, seeking evidence for DD was often implicitly meant also to be evidence for regulation: "Many populations appear to fluctuate about an equilibrium value ... such a population is said to be density dependent or regulated" (Bulmer 1975) (see below). Second,

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the recent turn from DD testing to modelling (Bjørnstad & Grenfell 2001) (**Table 5**) makes DD parameters implicit in mathematical equations (although not necessarily biologically meaningful, Clark *et al.* 2010), which might theoretically account for population regulation — so again, with one stroke, statistical evidence for a given model is assumed to bring about joint evidence for both DD and population regulation (e.g., Ziebarth *et al.* 2010; Reznick *et al.* 2012). Third, both the conceptual and mathematical definitions of the concept *population regulation* remain to be unified, which is exemplified by Murdoch's (1994) droll observation that "...regulation seems best defined by defining non-regulation" (see more quotations in **Appendix A2; Table 21**).

For some authors, the existence of an *equilibrium* (or *carrying capacity*) and a *return tendency* (i.e., through the operation of a factor driven by compensatory density feedback) are the key elements for population regulation, thus the definition "...return tendency of a population to equilibrium density" (Murdoch 1970), or "...presence of a long-term stationary probability of population densities... if we define equilibrium broadly as a stationary probability distribution, then being regulated and having an equilibrium are one and the same thing" (Turchin 1995) — detractors have questioned the difficulty of interpreting what this equilibrium means in nature (Wolda 1989; Berryman 1991a). Nevertheless, the former definitions certainly harmonise with DD tests and models that incorporate some measure of equilibrium, be they stochastic [as in Dennis and Taper's (1994) parametric-bootstrap likelihood-ratio test, Crowley's (1992) density-attractor test, or sophisticated models such as ARMA (Ives *et al.* 2010)], or fixed [e.g., equilibrium = average $\log_e(N_t)$ in Bulmer's (1975) test, or the magnitude of evidence for logistic models as assessed using information-theoretic approaches (Brook & Bradshaw 2006)] (**Table 4**).

Other authors invoke several phenomenological properties such that "...by definition, a population is regulated when it displays three closely related phenomena: (1) persistence, (2) boundedness, and (3) return tendency" (Hixon *et al.* 2002), which have also encountered opposition in that "...interpretations which equate regulation with persistence of populations (Reddingius & den Boer 1989; Hanski 1990; Krebs 1995) merely lead to confusion" (Sinclair & Pech 1996), and a gamut of rival concepts as a result of incorporating spatial structure into population models, such as *spreading the risk* (den Boer 1968) and *stabilisation* (den Boer 1986b), *vagueness* (Strong 1986a), *metapopulation regulation* (Hanski 1990), *site-dependent regulation* (Rodenhouse *et al.* 1997), *determination* (Sale & Tolimieri 2000) and *limitation* (White 2001) (I define these concepts in **Chapter 6**). Such concepts all represent the friction of terminology between temporal and spatial demography, while those debates have

resurrected the popular exchanges between Nicholson and Andrewartha (Andrewartha 1958; Nicholson 1958a; Andrewartha 1959; Nicholson 1959) (**Chapter 6; Appendix A1**), but are currently quiescent. Meanwhile, it remains unclear what needs to be measured, how, and even whether it is of any use, to characterise when a population is regulated. The common use of the expression *density-dependent regulation* firms up the marriage of both concepts, and disregards that (see Hassell *et al.* 1976) "...the detection of density dependence will not, in itself, prove that regulation is occurring, since the density-dependent response must be of the right form and size if it is to be capable of damping fluctuations in population size" (Dempster 1983).

Table 4. Sample of popular tests for density dependence (DD) in censuses of population abundance. All models equate population size at time $t+1$ (alone or combined with other terms) [response] against population size at the previous time point t [predictor] ($t =$ days, months, seasons, years, generations).

Reference	Statistic	Statistic source	Models	Outcome thresholds
(Moran 1953)	ρ [serial correlation, lag k]	p -value table	$\rho[N_{t+k}, N_t]$ for all t	$H_0: \rho = 0 \rightarrow$ DI $H_1: \rho \neq 0 \rightarrow$ (delayed if $k > 1$) DD
(Tanner 1966)	ρ [correlation]	p -value table	$\rho\left[\frac{N_{t+1} - N_t}{N_t}, N_t\right]$ for all t	$H_0: \rho = 0 \rightarrow$ DI $H_1: \rho \neq 0 \rightarrow$ DD
(Varley 1963)	t -student [regression]	p -value table	(0) Random walk: $r = \varepsilon_t$ (1) Linear regression ¹ : $r = \beta X_t + \varepsilon_t$	$H_0: \beta = 0 \rightarrow$ DI $H_1: \beta \neq 0 \rightarrow$ DD
(Bulmer 1975)	R [\sim serial correlation, lag 1] R^* [\sim serial correlation, lag k]	Simulation	(0) Random walk: $X_{t+1} - \mu = (X_t - \mu) + \varepsilon_t$ (1) Density dependence: $X_{t+1} - \mu = \beta(X_t - \mu) + \varepsilon_t$	$H_0: \beta = 1 \rightarrow$ DI $H_1: \beta < 1 \rightarrow$ (delayed if $k > 1$) DD
(Pollard <i>et al.</i> 1987)	T or rdx (0,1) [LR] T or rdx (0,2) [LR] T or rdx (1,2) [LR]	Randomisation	(0) Random walk: $X_{t+1} = X_t + \varepsilon_t$ (1) Random walk with drift: $X_{t+1} = d + X_t + \varepsilon_t$ (2) Density-dependence: $X_{t+1} = d + \beta X_t + \varepsilon_t$	$H_0: d = 0, \beta = 1 \rightarrow$ DI $H_1: d \neq 0, \beta = 1 \rightarrow$ DI $H_2: d \neq 0, \beta \neq 1 \rightarrow$ DD (Pair-wise contrasts)
(Dennis & Taper 1994) ²	T_{01} [LR] T_{02} [LR] T_{12} [LR]	Parametric bootstrapping	(0) Random walk: $X_{t+1} = X_t + \varepsilon_t$ (1) Random walk with drift: $X_{t+1} = d + X_t + \varepsilon_t$ (2,2a,b) Stochastic logistic: $X_{t+1} = d + X_t + \beta e^{X_t} + \varepsilon_t$	$H_0: d = 0, \beta = 0 \rightarrow$ DI $H_1: d \neq 0, \beta = 0 \rightarrow$ DI $H_2: d \neq 0, \beta \neq 0 \rightarrow$ DD $H_{2a}: d \neq 0, \beta < 0 \rightarrow$ CDD $H_{2b}: d \neq 0, \beta > 0 \rightarrow$ DDD (Pair-wise contrasts)
(Brook & Bradshaw 2006)	wt DD [Multi-model inference]	Akaike's information criterion adjusted for finite sample size (AIC_c)	(0) Random walk: $r = \varepsilon_t$ (1) Exponential: $r = r_m + \varepsilon_t$ (2) Ricker-logistic: $r = r_m \left[1 - \left(\frac{N_t}{K}\right)\right] + \varepsilon_t$ (3) Theta-logistic: $r = r_m \left[1 - \left(\frac{N_t}{K}\right)^\theta\right] + \varepsilon_t$ (4) Gompertz ¹ : $r = \beta X_t + \varepsilon_t$	$M_0: r_m = 0 \rightarrow$ DI $M_1: r_m \neq 0, \theta = -\infty \rightarrow$ DI $M_2: r_m \neq 0, \theta = 1 \rightarrow$ DD $M_3: r_m \neq 0, \theta \neq 1 \rightarrow$ DD $M_4: \beta \neq 0 \rightarrow$ DD (Multi-model contrast: wt DD = $wAIC_{c-M2} + wAIC_{c-M3} + wAIC_{c-M4}$)

¹ Gompertz model (Medawar 1940; Nelder 1961)

² Dennis & Taper (1994) used a stochastic logistic model (shown), and a stochastic Gompertz model

Variables: t = time; N = population size; $X = \log_e(N)$; $r = \log(N_{t+1}/N_t)$ = overall population growth rate; d = drift parameter
Constants: μ = mean(X) [\sim equilibrium]; a, b = constants; K = carrying capacity, r_m = maximum growth rate without DD
Methods: LR = likelihood ratio; $wAIC_c$ = model weight; **wt DD** = $\Sigma wAIC_c$ for DD models; **$\Sigma wAIC_c$ for DD+DI models = 1**
Evidence: \rightarrow DI = density independence; \rightarrow (C/D)DD = (compensatory/depensatory) density feedback

Table 5. Sample of models capturing density feedback.

Study	Model	Parameters
Competition in a experimental setting with two <i>Drosophila</i> species (Gilpin & Ayala 1973)	θ-logistic $r = r_m \left[1 - \left(\frac{N_t}{K} \right)^\theta \right] + \varepsilon_t$	θ = DD shape
Cross-taxa population dynamics of harvested fish at low population levels (Myers <i>et al.</i> 1995)	Age-structured Beverton-Holt $R = \frac{r_m N_s^\delta}{\left(1 + \frac{N_s^\delta}{K} \right)}$	δ = shape of recruitment depensation N_s = abundance of stock S (spawners) R = recruitment of new fish
Total ‘density dependence’ in a species’ life history at equilibrium (Lande <i>et al.</i> 2002)	Elasticity $DD = - \left(T \frac{\partial \ln \lambda}{\partial \ln N} \right)_K$	λ = finite population growth rate; $(\partial \log_e \lambda / \partial \log_e N)_K = \lambda$ elasticity to N change at K T = mean age of mothers of new born when age-structure is stable (generation time)
Response to climate of interacting species of owls and small mammals (Lima <i>et al.</i> 2002)	Autoregressive with environmental forcing $X_t = \beta_0 + (\beta_1 + 1)X_{t-1} + \beta_2 X_{t-2} + \omega_1 R_{t-1} + \omega_2 I_{t-1} + \varepsilon_t$	β_0 = intercept; β_1 & β_2 = (immediate & two-year-delayed) DD strength; R = annual rainfall; ω_1 = weather forcing; I = Southern Oscillation Index; ω_2 = climate forcing
Population dynamics and harvesting of the edible palm (<i>Euterpe edulis</i>) along the Atlantic coast of Brazil (Freckleton <i>et al.</i> 2003)	Size-structured $N_{t+1}^7 = P_t^1 N_t^1 + h_t^7 F_t^7 N_t^7$	N^1 = seedling abundance (size class 1 = 0-3 leaves); N^7 = reproductive adult density (size class 7 >120 mm); P^1 or P^7 = annual probability of surviving and remaining in seedling (1) or reproductive (7) classes; F^7 = number of offspring produced per palm and year; h^7 = reproductive-class fraction surviving harvesting
Demographic responses of crown-of-thorns starfish (<i>Acanthaster planci</i>) to fishing and predation (Dulvy <i>et al.</i> 2004)	Linear model with Allee effect $\frac{N_{t+1} - N_t}{N_t} = \beta N_t + \delta N_t^2$	β = DD strength δ = DD shape
Synchronicity of outbreaks of gipsy moth (<i>Lymantria dispar</i>) in northeastern USA (Liebhold <i>et al.</i> 2006)	Second-order autoregressive $r = (\beta_1 - 1)X_t + \beta_2 X_{t-1} + \varepsilon_t$	β_1 & β_2 = (immediate & two-year-delayed) DD strength
Dynamics of African elephant (<i>Loxodonta loxodonta</i>) in Hwange National Park, Zimbabwe (Chamaillé-Jammes <i>et al.</i> 2008)	Ricker-logistic with variable K $r = r_m \left[1 - \left(\frac{N_t}{\alpha R_t} \right) \right] + \varepsilon_t$	α = elephant numbers that can be sustained / rain in mm R = annual rainfall
Cross-taxa Allee effect evidence in population censuses (Gregory <i>et al.</i> 2010)	Allee Ricker-logistic $r = r_m \left[1 - \left(\frac{N_t}{K} \right) \right] \left[1 - \left(\frac{A}{N_t} \right) \right] + \varepsilon_t$	A = population size at Allee threshold, where $K > A$
Cross-taxa evidence for population regulation in population censuses (Ziebarth <i>et al.</i> 2010)	Autoregressive moving average $(X_t - \mu) = \sum_i^k \beta_i (X_t - \mu) + \sum_j^q \alpha_j \varepsilon_{t-j}$ $X_t^* = X_t + m \phi_t$	α = moving average; μ = mean of X_t ; k = DD order (lag); q = order of moving average; X_t^* = observed N with measurement error; ϕ = random variable $N(0,1)$; m = standard deviation (measurement error)

DD = density feedback or density dependence; t = time; N = population size; $X = \log_e(N)$; K = carrying capacity; $r = \log(N_{t+1}/N_t)$ = overall population growth rate; r_m = maximum growth rate with no DD; ε_t = random variable, with given a priori distribution, reflecting uncorrelated stochastic variability

1.15 Conclusions

Ecology is a realm of scientific enquiry still to make a reputation for lexical standards (Whittaker 1957; Adams *et al.* 1997; Hodges 2008), where context-specific comprehension of terminology (i.e., within single publications) seems to be taken as the silent rule, regardless of consistency across the literature. Experts with a strong numerical background will surely argue that theoretical models define ecological concepts accurately in the universal and unambiguous language of mathematics, thus dispensing with the need for standardising terminology. However, sound statistical expertise belongs to a minority of ecologists and biologists (Johnson *et al.* 2001), such that mathematical language will not improve communication in our field until education providers improve the quality of statistical training at the earliest undergraduate and postgraduate stages (see **Foreword**). Further, scientific papers are written in (mostly) English, not entirely with equations. Meanwhile, it is hardly conceivable that mathematics have bettered the understanding of DD among ecologists; rather, I argue the contrary. I concur with Krebs (1995) that this concept owes popularity among ecologists to its amenability to mathematical treatment. As a result, DD models have become increasingly complex (Clark *et al.* 2010), and “...a serious drawback is that almost all such models are truly understood only by those who do the actual construction of a given model, and readers of reports on the results have to take a lot on faith” (Eberhardt *et al.* 2008).

The pace of progress of ecological knowledge does not follow the pace of review, updating and even creation of new terminology, which leads directly to terms acquiring polysemy and synonymy. Among the > 60 DD terms, foundational terminology by Smith, Allee, Varley, Neave and Haldane is still in use, but its meaning is often not respected, mis-cited relative to original literature, or incorrectly equated with *population regulation*. Historically, controversial concepts such as DD face unavoidable semantic inflation, as authors debate theoretical and empirical aspects fundamental to those concepts. Each scientist can defend a different definition of ecological concepts, but this will inevitably trigger polemics that overemphasise individual points of view at the expense of general understanding. Importantly, students and early-career researchers will be challenged by those concepts if the very experts, from whom they take instruction, disagree in their terminology and definitions.

A gradual unification of the nomenclature of ecology, currently fragmented by disciplines and strongly opinionated schools of thought (as exemplified by the history of DD; Krebs 2002b), could ameliorate the classification scheme of ecological knowledge. Journals could

improve terminological standards by featuring permanent sections uniquely focusing on review of terminology, and by enforcing guidelines whereby authors could not invent new definitions but instead must authorise the foundational ones. In addition, the entire field of ecology would benefit enormously if a *Journal of Ecological Nomenclature* was created. Terminology represents one of those matters about which many voices complain but see no solution. The establishment of regulatory rules for ecological terminology (once attempted by the Ecological Society of America; Hanson *et al.* 1931; Eggleton *et al.* 1952; Appendix A3) is condemned *a priori* to be an unpopular idea for many scientists. Yet it is already taken as a self-evident necessity in many diverse fields like astronomy, chemistry, genetics, medicine, or taxonomy. If words were taxa, one can imagine the herculean enterprise of reviewing an entire taxonomic family consisting of tens of different genera and species (or words) bearing etymology subject to no rules — the ecological literature is exemplary in the frequency of such semantic chameleons (e.g., *carrying capacity*, *niche*, *population regulation*, *species*). Certainly, terminology is the key for communication and merits more respected recognition in ecology.

Finally, ecologists are increasingly interacting with society through policy makers, management and conservation planners and the media (Murphy & Noon 1991; Adams *et al.* 1997; Weber & Word 2001). There, scientific discourse becomes a tool of communication with non-scientists, and clear terminology is instrumental to important matters like the attraction of research funding and precise conveyance of scientific information for societal benefit. Social abilities are now needed and, among them, a dosage of linguistics and philosophy is perhaps missing in the curricula of skills of modern ecologists. A reflection has been put forward elsewhere that “...the ecological approach to language requires a considerable amount of unlearning or re-evaluation of existing linguistic knowledge” (Mühlhäusler 2003) — as Elton (1950) satirised: “We have to be prepared for an insistence on philosophical definition of terms and concepts which makes the average empirical British ecologist feel rather as if he were having all his familiar old clothing removed by stages for cleaning and pressing”. Yet terminology is important, but not a panacea: “The next generation of ecologists must be prepared to interact with such disciplines as history, religion, philosophy, geography, economics, and political science. The requisite training must involve not only words, but core skills in these disciplines” (Ludwig *et al.* 2001).

CHAPTER 3

— LIFE HISTORY

1.16 Title

Strength of density feedback in census data increases from slow to fast life histories

1.17 Abstract

Life-history theory predicts an increasing rate of population growth among species arranged along a continuum from slow to fast life histories. I examine the effects of this continuum on density-feedback strength estimated using long-term census data from > 700 vertebrates, invertebrates and plants. Four life-history traits (age at first reproduction, body size, fertility, longevity) were related statistically to Gompertz strength of density feedback using generalised linear mixed-effects models and multi-model inference. Life history traits alone explained 10 to 30 % of the variation in strength across species (after controlling for time series length, phylogenetic non-independence and allometry). Effect sizes were largest for body size in mammals and longevity in birds, and density feedback was consistently stronger for smaller-bodied and shorter-lived species. Overcompensatory density feedback (strength < -1) occurred in 20 % of species, predominantly at the fast end of the life-history continuum, implying relatively high population variability. These results support the idea that life history leaves an evolutionary signal in long-term population trends as inferred from census data. Where there is a lack of detailed demographic data, broad life-history information can inform management and conservation decisions about rebound capacity from low numbers, and propensity to fluctuate, of arrays of species in areas planned for development, harvesting, protection and population recovery.

1.18 **Key words:** Age at first reproduction; Body size; Density dependence; Evolution; Fertility; Longevity; Population dynamics

STATEMENT OF AUTHORSHIP

Accepted in *Ecology and Evolution*, by Herrando-Pérez, Delean, Brook & Bradshaw

Lead author Herrando-Pérez conceived the work, reviewed the literature, did the statistical analyses and wrote the first draft of the paper. Delean contributed to statistical programming and design. Herrando-Pérez (total score of 0.70), Delean (0.15), Bradshaw (0.10) and Brook (0.05) contributed substantially to revisions.

All co-authors certify that the statement of contribution is accurate, and give permission for the inclusion of the paper in the thesis.

SIGNATURES:

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Life history theory tries to explain how evolution designs organisms to achieve reproductive success (Stearns 2000)

1.19 Introduction

Density dependence (Smith 1935; Allee 1941) represents a causal relationship between population size [predictor] and a demographic rate [response], that is, a ‘density feedback’. Such relationship can be ‘compensatory’ or ‘depensatory’ if population growth, survival and/or fertility rates decrease or increase with population boom, respectively (**Chapters 2 and 5; Table 3; Figure 8**). Statistical support for those feedbacks (theoretically) indicates that demographic rates are shaped by social and trophic interactions such as competition, cooperation, disease, parasitism or predation, because the intensity of these ecological mechanisms varies with population size (**Chapter 2; Figure 5**). In single-species population models that quantify density feedback (Brook & Bradshaw 2006; Eberhardt *et al.* 2008), it has been suggested that cross-taxa patterns of population dynamics can be predicted from information on life-history traits by arranging species along a continuum from ‘slow’ to ‘fast’ life histories (Saether *et al.* 2002). This continuum had been thoroughly investigated in the 1980s in homeotherms (e.g., Saether 1987; Gaillard *et al.* 1989; Read and Harvey 1989) — the prediction being that fast taxa should be capable of growing to larger population sizes at much higher rates than slow taxa via the former’s shorter gestation, shorter intervals between reproductive bouts, earlier maturity, smaller adult size, shorter life, shorter lactation, smaller and more prolific offspring, and more litters per year, regardless of whether one controls for body size (Stearns 1983; Saether *et al.* 1996). In support of such predictions, changes in population growth rate (sensitivities) arise mainly from variability in reproductive rates in fast species and in survival rates for slow species of birds (Saether & Bakke 2000), mammals (Heppell *et al.* 2000; Oli & Dobson 2003, 2005), fish (Cortés 2002), insects (Blackburn 1991) and plants (Franco & Silvertown 2004). It is therefore reasonable to postulate that the position of a species along this continuum could also reflect the propensity of population growth rates to vary in response to social/trophic interactions among individuals, as inferred from metrics of density feedback.

Evidence for density feedback increases with longevity based on census data from bird species (Holyoak & Baillie 1996), and species with slow life histories (longer generation times, larger body size, smaller litters) experience more demographic stability when compensatory density feedbacks operate than fast species with recruitment-driven dynamics

(Saether *et al.* 2002). The only two studies that have investigated this matter over broad taxonomic groups have focused on the shape (i.e., nonlinearity) of density feedback and provided conflicting results. First, Fowler (1981) formalised the links between convex (compensatory feedback strongest at high numbers) and concave (compensatory feedback strongest at low numbers) density feedback with the life histories of (large-bodied) mammals and (small-bodied) insects, respectively. He later showed that the inflection point of animal population growth curves declined with accelerating growth per generation (hence from slow to fast species), irrespective of body size (Fowler 1988). Conversely, Sibly *et al.* (2005) claimed an unprecedented ubiquity of concave density feedback across mammals, birds, bony fish and insects by applying a modified, curve-fitting form of the theta-logistic equation (Gilpin & Ayala 1973), with a change from concave to convex density feedback from large to small body-sized mammals. This paper was repeatedly challenged immediately after publication (Doncaster 2006; Getz & Lloyd-Smith 2006; Ross 2006), and its conclusions soundly refuted due to fundamental flaws in the model-fitting approach employed (Doncaster 2008; Polansky *et al.* 2009; Ross 2009; Clark *et al.* 2010).

However controversial, the conclusions from these kinds of studies are of immediate relevance to conservation and management, because strength and shape of density feedback can dictate the (theoretical) capacity of a population to recover from declines following natural perturbations and/or harvest, thus exerting a strong influence on predictions of population extinction and viability (Henle *et al.* 2004; Sabo *et al.* 2004), and harvesting quotas (Boyce *et al.* 1999; Rose *et al.* 2001). So, while Fowler (1981) suggested that large mammals should be harvested at population sizes close to carrying capacity (where their productivity is expected to peak given convex density feedback), Sibly *et al.* (2005) stated that population growth rates could be overestimated if convex density feedback is assumed from life-history data (e.g., body size), with potentially serious implications for harvesting and management.

Here I quantify strength of density feedback across several hundred taxa (vertebrates, invertebrates, plants), and determine effect sizes of and how much variance can be explained by four life-history traits (age at first reproduction, body size, fertility, longevity) which capture the slow-fast continuum. I hypothesise that the strength of compensatory density feedbacks increases along this continuum, i.e., from low to high fertility, extended to short longevity, late to early age at first reproduction, and large to small body size.

1.20 **Methods**

Data

I used the dataset of Brook & Bradshaw (2006) and Brook *et al.* (2006). In summary, these data consist of one census of population abundance and one estimate of four life-history traits for each of 1,198 species (603 insects, 225 birds, 152 mammals, 115 fish, 36 aquatic invertebrates, 30 plants, 27 amphibians and 10 reptiles; **Table 6**), and feature > 10 population counts per census (median = 20, with 95th percentile range of [10 to 65]). I present a revised rationale of data selection in **Appendix A4 (Table 23 and Table 24)**. I deemed an annual time step appropriate to estimate population turnover because most species' census data were collected from temperate regions, hence they generally experience pronounced annual seasonality in reproductive events and survival.

The species-specific life-history traits from independent sources (e.g., www.demogr.mpg.de/longevityrecords, www.bto.org, or genomics.senescence.info) for each of the 1,198 species were: (i) average age at first reproduction (months), (ii) maximum body size (length in mm), (iii) fertility (number of young per year) and (iv) longevity (maximum age attained in the wild in months) (Brook *et al.* 2006). These traits suffice to capture the principal features of the slow-fast continuum in mammals and birds (Gaillard *et al.* 1989), and fall within the group of traits originally used to define this continuum (Stearns 1983). I explored correlations between traits representing gradients of (log-transformed) life history across taxa through principal component analysis (Jolliffe 2004).

Strength of density feedback

Following Brook & Bradshaw (2006), I ranked evidence for Ricker-logistic and Gompertz population growth [density feedback present] against models of random walk and exponential growth [density feedback absent] (**Table 4**) by means of Akaike's information criterion corrected for finite sample size, AIC_c (Sugiura 1978). AIC_c and the Bayesian information criterion, BIC (Schwarz 1978), had approximately equivalent penalty terms for the median time-series length in my samples and thus produced qualitatively similar results.

For those time series supported for Gompertz growth, and having similar support for both Gompertz and Ricker-logistic growth ($\Delta AIC_c < 4$), I collated the estimates of strength of compensatory density feedback from the Gompertz equation (Medawar 1940; Nelder 1961), i.e., the slope of the relationship of $r [= \log_e(N_{t+1}/N_t)]$ versus population size on a log scale:

$$\log_e \left(\frac{N_{t+1}}{N_t} \right) = \alpha + \beta \log_e (N_t) + \varepsilon_t$$

where N_t = population size at time t , α = intercept, β = strength of density feedback, and ε_t = Gaussian random variable with a mean of zero and a variance σ^2 reflecting stochastic variability in r . This model (i) is measured on a proportional scale and so characterises the multiplicative nature of demographic rates (Bjørnstad et al. 1995), (ii) clearly informs the magnitude of the compensatory response of demographic rates to changes in population size relative to nonlinear models (Doncaster 2006), and (iii) slopes above and below -1 represent the threshold between expected stable and chaotic dynamics, respectively, and so provide a simple metric with which to assess population variability (Varley *et al.* 1973; Doncaster 2008) — slopes < -1 imply that the proportional number of individuals over any time step of a census decreases by $> 100\%$ for a one-order-magnitude increase in population size. Furthermore, the Gompertz model has performed robustly in describing the general dynamics of populations over a wide range of body sizes (e.g., Saitoh *et al.* 1999; Wang *et al.* 2002; White *et al.* 2007; Seavy *et al.* 2009; Wang *et al.* 2009; Pasinelli *et al.* 2011), is present in multi-model inference scenarios where competing models are contrasted (Saitoh *et al.* 1997; Zeng *et al.* 1998; Fryxell *et al.* 2005; Chamaillé-Jammes *et al.* 2008; McMahon *et al.* 2009), is the top-ranked model in meta-analyses of hundreds of species in which various alternatives have also been evaluated (e.g., Brook & Bradshaw 2006), and has been a model used in theoretical development about density feedback (e.g., Dennis *et al.* 2006). I avoided fitting the fully parameterised theta-logistic model (see Introduction), or other highly parameterised analogues (e.g., hyperbolic growth). Yet, I also did all analyses using the Ricker-logistic strength of density feedback as response. In my study, I make no claim about the regulation of populations, because moderate compensatory density feedback is only one requirement for population regulation (Hixon *et al.* 2002) (**Chapters 2 and 5**).

Model set

With Gompertz strength of compensatory density feedback as the common response, my model set included 10 models with the following predictors (**Table 7**): (i) four models with each single life-history trait alone, (ii) four models with fertility and one of the other traits, (iii) the intercept-only (null) model with no fitted predictor terms, and (iv) one model controlling for sample size only. The ratio of fertility to age at first reproduction has been proposed as a metric of the slow-fast continuum in mammals (Oli & Dobson 2003) and was also included in the model set. Fertility is an obvious proxy for reproductive rates, while body

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size, longevity and age at first reproduction are directly related to survival (Gaillard *et al.* 1989; Saether *et al.* 1996), so my models incorporated life-history selection for those demographic rates. Since the length of the time series affects the detection probability of density feedback (Brook & Bradshaw 2006), I included it in all models encompassing life-history traits and then calculated the variance explained by life-history parameters alone. *A priori*, I explored pair-wise correlations between life-history traits and did not include strongly co-linear traits in my model contrasts [except when controlling for body size (see below)]; and I dispensed with any interaction terms due to the difficulty of their interpretation in this context, thus avoiding over-parameterising models. Finally, I did not use the principal components of my PCA analyses (see above) as predictors in my models because I was not interested in (potentially) maximising model goodness of fit, but mainly in teasing apart the relative fixed effects of single life history traits.

Model fitting

I fitted all models using generalised linear mixed-effects models (GLMM, Breslow & Clayton 1993). Model assumptions were met using a Gaussian variance function after a square-root transformation of density-feedback strengths, such transformation being supported by a likelihood-based test of Box and Cox (1964). Covariance between life-history traits should be incorporated in cross-taxa comparisons of demographic and evolutionary responses (Felsenstein 1985), and can be accounted for by allowing different intercepts for species grouped by higher taxonomic levels (Blackburn & Duncan 2001). I did so by including the Linnaean taxonomic level of *Class* as a random effect in my GLMMs (**Table 7**). I discarded nested random factors by *Family* and *Order* due to insufficient replication over half of the families and orders; I also replicated my analyses for birds and mammals separately using generalised linear models (GLM).

I quantified relative support for models in a set by means of the Bayesian information criterion (BIC, Schwarz 1978) because BIC favours more parsimonious models than AIC when sample sizes are large (~ 50 to 300 estimates of strength in any of my model contrasts) and I wanted to distinguish main from tapering effects (Burnham & Anderson 2002; Link & Barker 2006). Nevertheless, both BIC and AIC yielded nearly identical model support and the same biological conclusions emerged. Exploratory analyses confirmed that, within each of 12 ('redundant studies' hereafter) of the 204 peer-reviewed data sources, individual species' time series had equal time-series length, and life-history traits had equal or similar values. Such redundant information (originating from long-term monitoring programs at some field stations) was bound to overwhelm model fitting since it affected 613 species (~ 60 % of the

dataset, of which 519 were insects, mainly aphids and moths). To avoid this, I separated ‘redundant species’ from the remaining (non-redundant) ‘core species’. Of the 772 time series supported for Gompertz growth (and after removing two time series showing depensatory density feedback), 326 belonged to ‘core species’ and 446 were from ‘redundant species’ (**Table 6**). After accounting for data redundancy, I could fit my models robustly to all taxa, mammals and birds. To do so, I calculated model ranking and relative fixed effects on 100 data subsets, each consisting of one bootstrapped sample of all core species *and* one randomly sampled species from each of the redundant studies — i.e., 100 contrasts of the same model set, each time on a different bootstrapped sample. I measured relative model support across the set by the medians and 95th percentile confidence intervals of BIC metrics (Δ BIC, model probabilities, deviances) over the 100 bootstrapped samples. Further, I used model averaging (Burnham & Anderson 2002) to estimate the coefficients of the fixed effects for each life-history trait on strength of density feedback. Thus, I summed model probabilities for each model containing a given life-history trait weighted by its effect size as a measure of across-model effect size. To confirm that effect sizes were comparable among life-history traits of different range, I assessed them with and without a *post hoc* standardisation [trait \times standard deviation (response) / standard deviation (trait)].

Complementary analyses

To avoid the confounding effects of measuring error, authors *either* set stringent criteria for data selection (Knappe & de Valpine 2011), *or* use state-space models (Dennis *et al.* 2006; Knappe 2008; Ives *et al.* 2010), which themselves are not, however, exempt of caveats (Knappe 2008) and add further model complexity to cross-taxa comparisons. Therefore, I decided to replicate all analyses for (i) the entire dataset, (ii) a subset of ‘high-quality’ time series featuring stationarity, no temporal trending, few missing values, no outliers and length of counts of > 14 time steps [these criteria are fully explained in **Appendix A4, Table 25**], and (iii) simulated time series from the observed Gompertz parameters with incorporation of 5 %, 10 % and 15 % of measurement error [I explain the simulation in **Appendix A5**].

I did not have access to estimates of each species’ ‘generation time’ as used elsewhere to relate single-species population models to life history (e.g., Saether *et al.* 2004; Saether *et al.* 2005). Since body size correlates with generation time and intrinsic growth rates (Peters 1983), and needs to be accounted for when studying the slow-fast life-history continuum (Stearns 1983; Gaillard *et al.* 1989; Jeschke & Kokko 2009), I controlled for allometric relationships among species by redoing all analyses with a model set including body size in all models, then compared relative effect sizes of each life-history trait in model sets with and

without the control for body size (**Table 7**). As a further control for generation time, I repeated all analyses using the number of generations monitored in each census ($G = \text{time-series length/age at first reproduction}$); this model set had seven candidate models after removing those including age at first reproduction (**Table 7**). I summarise samples sizes in **Table 6**, and figures and tables from all analyses undertaken in **Appendix A5 (Table 26)**.

Table 6. Number of species analysed after (i) removing missing life-history traits, (ii) selecting only time series supported by Gompertz growth, and (iii) removing time series supported for depensatory density feedback. Time series supported for Gompertz growth were split by core and redundant species, and all analyses were replicated for all species' time series, and only ('high quality') stationary time series with length ≥ 14 years and no extreme outliers. Coloured numbers in table match with coloured text below relative to the three types of analyses undertaken.

Taxa	All series		High-quality series	
Total	1198¹		812¹	
<i>no missing data</i>	1177²		795²	
Aquatic invertebrates	36		21	
Birds	225		145	
Fish	109		65	
Herpetiles	37		17	
Insects	588		476	
Mammals	152		62	
Plants	30		9	
	Gompertz support			
	Core species	Redundant species	Core species	Redundant species
Total	328	446	191	392
<i>no depensation</i>	326³	446³	190³	392³
Aquatic invertebrates	13	5	6	5
Birds	123⁴	26⁴	80⁴	24⁴
Fish	37	16	22	13
Herpetiles	20	0	13	0
Insects	38	390	20	350
Mammals	90⁴	0⁴	45⁴	0⁴
Plants	5	9	4	0

¹ **Single-species population models** (Ricker-logistic and Gompertz, exponential and random walk) fitted to time series of population abundance.

² **Principal component analysis** based on correlations among the four life-history traits (Age at first reproduction, Body size, Fertility, Longevity).

³ **GLMM** relating strength of compensatory density feedback (response) to life-history traits (predictors) across all taxa [Taxonomic Class = random factor].

⁴ **GLM** relating strength of compensatory density feedback (response) to life-history traits (predictors) in birds and mammals

Table 7. Model sets used, including predictors (see note below) of variation in strength of compensatory density feedback (*EN*) across taxa (fitted by GLMM using as random factor CL = taxonomic class), and bird and mammal species (fitted by GLM, no phylogenetic random effect). Control variables were included in all models (except the null), namely *q* = length of time series, *G* = number of generations monitored (*q*/*Age*), and *Body* = Body size.

Control variables	<i>q</i> or <i>G</i>	Body size
<i>q</i>	$EN \sim 1 + (1 CL)$	$EN \sim 1 + (1 CL)$
	$EN \sim q + (1 CL)$	$EN \sim q + (1 CL)$
	$EN \sim q + Body + (1 CL)$	$EN \sim q + Body + (1 CL)$
	$EN \sim q + Age + (1 CL)$	$EN \sim q + Body + Age + (1 CL)$
	$EN \sim q + Fert + (1 CL)$	$EN \sim q + Body + Fert + (1 CL)$
	$EN \sim q + Long + (1 CL)$	$EN \sim q + Body + Long + (1 CL)$
	$EN \sim q + Body + Fert + (1 CL)$	$EN \sim q + Body + Age + Fert + (1 CL)$
	$EN \sim q + Age + Fert + (1 CL)$	$EN \sim q + Body + Long + Fert + (1 CL)$
	$EN \sim q + Long + Fert + (1 CL)$	$EN \sim q + Body + Fert/Age + (1 CL)$
	$EN \sim q + Fert/Age + (1 CL)$	
<i>G</i>	$EN \sim 1 + (1 CL)$	$EN \sim 1 + (1 CL)$
	$EN \sim G + (1 CL)$	$EN \sim G + (1 CL)$
	$EN \sim G + Body + (1 CL)$	$EN \sim G + Body + (1 CL)$
	$EN \sim G + Fert + (1 CL)$	$EN \sim G + Body + Fert + (1 CL)$
	$EN \sim G + Long + (1 CL)$	$EN \sim G + Body + Long + (1 CL)$
	$EN \sim G + Body + Fert + (1 CL)$	$EN \sim G + Body + Long + Fert + (1 CL)$
	$EN \sim G + Long + Fert + (1 CL)$	

Life-history predictors: *Age* = Age at first reproduction (months); *Body* = Body size (millimeters); *Fert* = Fertility (number of young per year); *Long* = Longevity (maximum age attained in the wild, months)

1.21 Results

Magnitude of density feedback across taxa

Median model probabilities [with 95th percentile ranges] for all species were 0.38 [0.07 to 0.97] for Gompertz, 0.23 [0.02 to 0.75] for Ricker-logistic, 0.16 [< 0.01 to 0.67] for random walk, and 0.05 [< 0.01 to 0.30] for exponential population growth (**Appendix A5; Figure 16**). I found support for either of the two density-dependent models in 865 censuses, with total median evidence of 0.78 [0.14 to 1.00] (pooled model probability for Gompertz and Ricker-logistic models). Overall, the median probability of a population to show evidence for compensatory density feedback was 3.5 times that of not showing so. A total of 772 time

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series (64 %, all data) [and 583 or 73 % of the high-quality time series] were supported for Gompertz growth. I employed those subsets of 772 and 583 censuses in further analyses.

Median strength of density feedback was -0.7 [-1.4 to -0.2], so increases in population size by a factor of ~ 3 (i.e., one order of magnitude on a natural logarithm scale) caused a median 70 % reduction in population growth rates. In order of strength by major taxonomic groups, plants were highest at -0.9 [-1.3 to -0.6], followed by herpetiles at -0.9 [-1.4 to -0.5], aquatic invertebrates at -0.8 [-1.5 to -0.2], insects at -0.8 [-1.4 to -0.3], fish at -0.7 [-1.3 to -0.2], birds at -0.6 [-1.3 to -0.2] and mammals at -0.4 [-1.4 to -0.1]. I found similar magnitude and across-taxa ordering of strength of density feedback for the high-quality time series.

Overcompensatory density feedback (strength < -1) occurred in ~ 20 % of the censuses (all and high-quality time series), being relatively common among some of the small-bodied species of amphibians (7 species, 40 % of amphibians), insects (96, 22 %), fish (11, 21 %), mammals (16, 18 %) and birds (15, 10 %). For instance, the five strongest density feedbacks were for the small tortoiseshell nymphalid *Aglais urticae* (-1.9 ± 0.4 SE), the common shrew *Sorex araneus* (-1.8 ± 0.2 SE), the leaf miner agromyzid *Chromatomyia suikazurae* (-1.7 ± 0.5 SE), the red crossbill finch *Loxia curvirostra* (-1.6 ± 0.3 SE), and the oak aphid *Tuberculatus annulatus* (-1.6 ± 0.3 SE).

Predicting strength of density feedback from life history

The variation in strength of density feedback explained by life-history traits alone was 8 to 25 % across all species, 28 to 34 % for mammals and 10 to 17 % for birds over models controlling for census length (**Table 8**) and number of generations monitored (**Appendix A5; Table 27**). Top-ranked models included longevity for all species and for just birds, and body size in mammals (**Table 8** and **Table 27**). Length of time series alone explained up to 21 % (all species), 17 % (mammals) and 10 % (birds) of the variation in strength (**Table 8**), while the explanatory capacity was much lower for the number of generations monitored, i.e., 0.1 % (all species), 9 % (mammals) and 2 % (birds) (**Table 27**). Moreover, models including life-history traits had between 20 and > 1,000 times higher statistical support than models including only either of the two control variables (evidence ratios given in **Table 8** and **Table 27**). Importantly, the *same* model rankings and *similar* explained deviances occurred in simulated time series after incorporation of 5 % measurement error in all taxa and birds, and up to 10 % in mammals (**Appendix A5; Table 30**).

BIC model-averaged fixed effects were largest for longevity (all species and birds) and body size (mammals) (**Figure 9** and [**Appendix A5**] **Figure 17**, a,c,e). All effect sizes were

negative (**Figure 9** and **Figure 17**, a,c,e). Thus, the strength of density feedback increased from long- to short-lived life history across all species and birds, and from large- to small-bodied mammals. Age at first reproduction and fertility effects scored relatively small model-averaged effect sizes (**Figure 9** and **Figure 17**, a,c,e). The trends above prevailed when I controlled for body size (**Figure 9** and **Figure 17**, b,d,f), for the high-quality dataset (**Appendix A5**; **Table 28** and **Table 29**; **Figure 18** and **Figure 19**), and using the Ricker-logistic strength of density feedback as response in all model contrasts.

Life-history gradients

The first two principal-component axes (**Figure 10**) explained 92 % of the correlation structure among life-history traits across all species. The PC1 gradient separated insects from all other taxa, indicating (from right to left) increasing age at first reproduction, body size and longevity, with considerable variation in life history within major vertebrate groups and aquatic invertebrates. The PC1 gradient is representative of the slow-fast continuum, and accounts for 65.4 % of life-history correlations. The PC2 gradient separated homeothermic vertebrates (birds and mammals) from poikilothermic vertebrates (fish, reptiles and amphibians), plants, and most insects and aquatic invertebrates (**Figure 10**). This second gradient mainly represented (from bottom to top) increasing fertility, especially in aquatic species with broadcast-spawning bony fish (e.g., Atlantic blue marlin *Makaira nigricans*, southern bluefin tuna *Thunus maccoyii*) and megamolluscs (e.g., green abalone *Haliotis fulgens*, pismo clam *Tivela stultorum*). Fish species showed the largest relative life-history variation (i.e., spread in PCA space) within major taxa. This PC2 gradient is representative of reproductive output, explaining 26.6 % of life-history correlations. Thus, given a species' position along the slow-fast continuum (PC1), relatively disparate interspecific reproduction output (PC2) occurred in all taxa except birds and mammals. Considering species within the best represented taxa, fertility correlated negatively with age at first reproduction, body size, and longevity in mammals and birds, and positively in fish and insects. The former represented overall increase in fertility from small- to large-bodied poikilotherms, and from large- to small-bodied homeotherms. I observed a similar gradient of life history for the high-quality data subset. Given the results of the PCA, my data provide a biological meaningful ranking of species along the slow-fast continuum of life histories.

Table 8. Bayesian information criterion (BIC) support for the top-ranked models¹ relating life history to strength of compensatory density feedback (*EN*) through GLMM for all taxa (aquatic invertebrates, amphibians, birds, fish, insects, mammals, plants, reptiles), and GLM for the subsets of mammal and bird species. *w*BIC, %DE and %DE_{LH} are medians (in bold) from 100 bootstrapped samples [95th percentile range]². Models included time series length (*q*) and body size (*Body*) as controls. I show sample sizes in **Table 6**, model sets in **Table 7**, and effect sizes in **Figure 9**.

Dataset	Control variable	Top-ranked model per model set	<i>w</i> BIC	%DE	%DE _{LH}	ER	Top rank
All taxa	<i>q</i>	<i>EN</i> ~ <i>q</i> + <i>Long</i>	0.57 [0.00 to 1.00]	30.7 [22.2 to 42.2]	9.5 [5.2 to 15.4]	> 1000	54 (19)
All taxa	<i>q</i> , <i>Body</i>	<i>EN</i> ~ <i>q</i> + <i>Body</i> + <i>Long</i>	0.64 [0.01 to 0.99]	29.0 [21.1 to 40.4]	8.2 [3.4 to 13.8]	> 1000	63 (16)
Mammals	<i>q</i>	<i>EN</i> ~ <i>q</i> + <i>Body</i>	0.79 [0.07 to 0.90]	45.2 [31.6 to 61.8]	28.9 [12.2 to 50.5]	> 1000	85 (11)
Mammals	<i>q</i> , <i>Body</i>	<i>EN</i> ~ <i>q</i> + <i>Body</i>	0.59 [0.09 to 0.71]	45.2 [31.6 to 61.8]	28.3 [12.2 to 50.5]	> 1000	80 (18)
Birds	<i>q</i>	<i>EN</i> ~ <i>q</i> + <i>Long</i>	0.60 [0.04 to 0.91]	19.4 [8.8 to 34.4]	10.0 [2.4 to 20.4]	200	75 (20)
Birds	<i>q</i> , <i>Body</i>	<i>EN</i> ~ <i>q</i> + <i>Body</i> + <i>Long</i>	0.29 [0.02 to 0.88]	21.1 [9.2 to 35.5]	11.0 [3.2 to 21.3]	20	43 (42)

¹**Model sets:** 1 single response [Strength of compensatory density feedback (*EN*)], and 1 or 2 life-history predictors [*Age* = Age at first reproduction (months), *Body* = Body size (mm), *Fert* = Fertility (number of young per year) and *Long* = Longevity (maximum age attained in the wild, months)].

²**BIC metrics:** *w*BIC = BIC Model probabilities given each data and model set, %DE = % Deviance in *EN* explained by each model within each model set, %DE_{LH} = % Deviance in *EN* explained by each model minus % Deviance in *EN* explained by the model including only *q* (i.e., Deviance in *EN* explained by life history conditional on *q*), ER = Evidence ratio of the top-ranked model *w*BIC compared to *q*-only model *w*BIC for each model set (i.e., times support for top-ranked model equating life-history traits was larger than for the only-*q* model), and **Top rank** = times a model was top-ranked over the 100 bootstrapped samples (times each model was not the top ranked model yet received considerable support [Δ BIC < 4]).

Figure 9. Standardised BIC-weighted effect sizes for four life-history traits (*Body size* [*Body*], *Longevity*, *Age at first reproduction*, *Fertility*) as predictors of variation in strength of density feedback (response) for all major taxa (a,b: aquatic invertebrates, amphibians, birds, fish, insects, mammals, plants, reptiles), and the subsets of mammal (c,d) and bird (e,f) species. Left panels (a,c,e) come from a model set controlling for census length (q), and right panels (b,d,f) from a model set controlling for q and *Body*. Bold lines represent $wBIC$ medians as obtained from 100 bootstrapped samples. Fits were obtained using GLMM which accounted for phylogenetic non-independence at the Linnean taxonomical level of *Class*, and GLM for mammals and birds. I show sample sizes in **Table 6**, model sets in **Table 7**, and BIC metrics in **Table 8**.

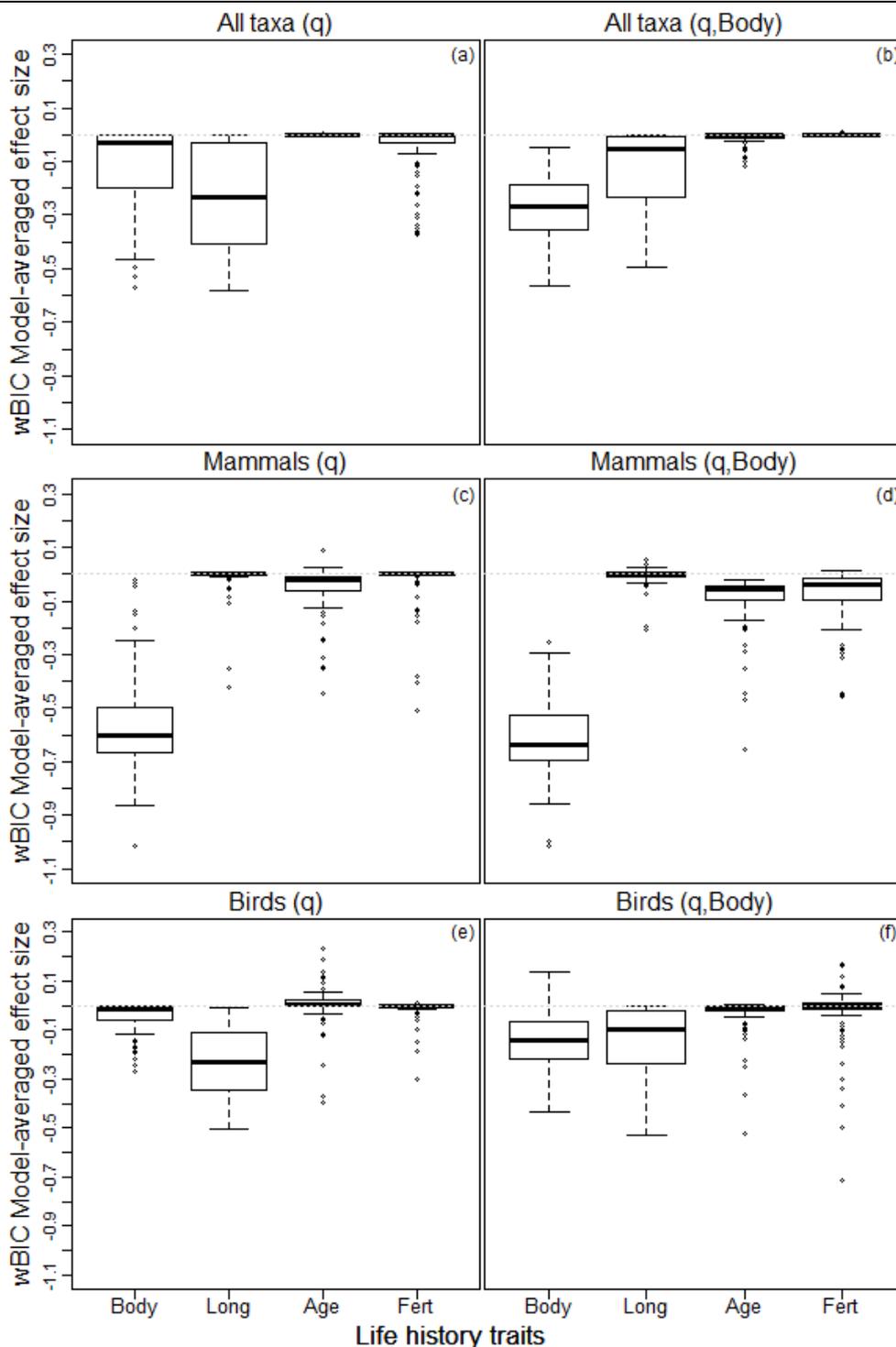
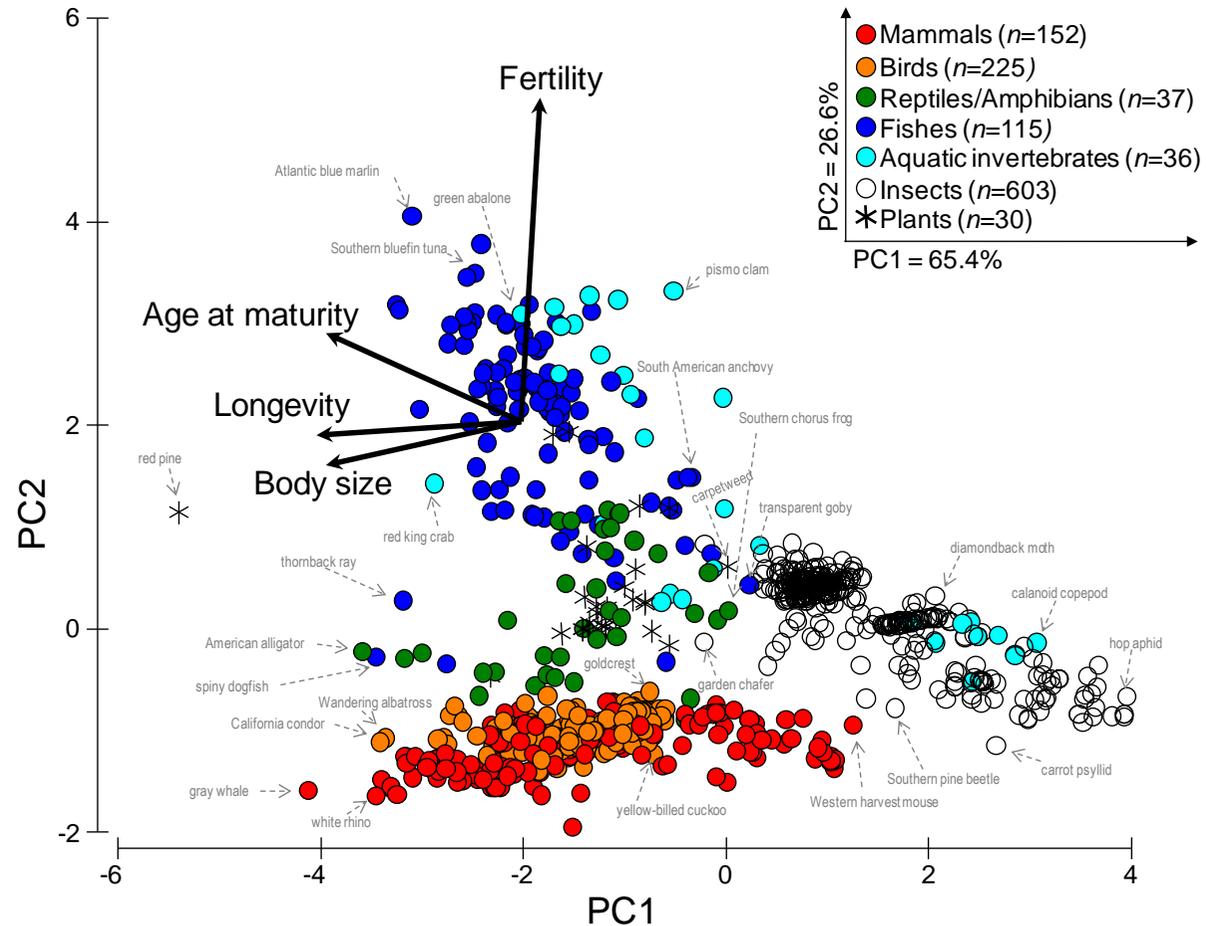


Figure 10. Correlation-based PCA of species based on log-transformed values of four life-history traits: age at first reproduction (months), body size (mm), fertility (number of young per year) and longevity (maximum age attained in the wild in months). Arrows represent principal coefficients assigned to each life-history trait in the direction of increasing magnitude. Percentage correlation structure explained by each axis and number of species within broad taxa are given in legend. Examples of some species' common names are overlain in light grey and their position indicated with dashed arrows along life-history gradients.



1.22 Discussion

My results support the hypothesis that the position of a species along the slow-fast continuum of life histories imprints an evolutionary signal in population trajectories apparently shaped by density feedback across several hundred species of invertebrates, vertebrates and plants. Previous studies, using different statistical approaches and plagued by violated assumptions (see below), provided simple correlations between life history and metrics of density feedback (Saether *et al.* 2002; Saether *et al.* 2005; Sibly *et al.* 2005), inflection points (Fowler 1981, 1988; Sibly *et al.* 2005), return to carrying capacity (Sibly *et al.* 2007) or sensitivities (Heppell *et al.* 2000; Saether & Bakke 2000; Oli & Dobson 2003; Franco & Silvertown 2004). I thus give the first robust quantitative assessment of the correlation between density feedback and life history, simultaneously including controls for taxonomy, allometry, prediction for several traits ecologically and evolutionarily related to fertility and survival, and a quantification of relative effect sizes.

Matching metabolic expectations, allometry (i.e., body size) accounts for most of the explained variation in strength of density feedback across all taxa, especially in mammals (Duncan *et al.* 2007; Sibly & Brown 2007). Indeed, fast life histories characterise species with relatively low *per capita* biomass production (Ernest *et al.* 2003), high intrinsic rates of increase and high population densities and larger energy investments in reproduction relative to body maintenance (Fenchel 1974; Blueweiss *et al.* 1978; Brown *et al.* 2004); as a result, stronger compensatory density feedbacks are expected. After accounting for allometry, I found that the effect sizes of other life-history traits on the strength of compensatory density feedbacks remain low in mammals, but longevity remains a good predictor for birds. Mammals show the widest range of body sizes among living vertebrates; however, body size in most birds is constrained by flight, and longevity instead seems to be selected for along the slow-fast continuum for this group (Gaillard *et al.* 1989). Further, Gompertz strengths < -1 are indicative of overcompensatory density feedback, which can result in populations overshooting carrying capacity and undergoing chaotic fluctuations (Varley *et al.* 1973). I predicted such overcompensatory feedbacks in ~ 20 % of all taxa and mammals, and ~ 10 % of birds, mainly at the fast end of the life-history continuum. This implies more population variability in the long term for fast species, as has indeed been shown for birds (Saether & Engen 2002; Saether *et al.* 2002; Saether *et al.* 2004) and mammals (Sinclair 1996; Erb *et al.* 2001; Fagan *et al.* 2001).

I used four life-history traits (age at first reproduction, body size, fertility, longevity) to represent the slow-fast continuum. However, life-history signalling in census data might be even stronger than detected here if other traits (particularly size of individual offspring and frequency of reproductive bouts) were available to represent other gradients of life history, such as those of altricial/precocial homeotherms (Stearns 1983), periodic/ equilibrium/ opportunistic fish (Winemiller & Rose 1992), and bet-hedgers (Saether *et al.* 1996). For insects and other invertebrates, the slow-fast continuum has been investigated only in some hymenopterans and odonates (Blackburn 1991; Johansson 2000), and future studies should carefully consider tradeoffs between life-history traits operating from larval to adult stages.

The link between density feedback and the slow-fast continuum has been previously assessed in a few studies, albeit using contrasting metrics (i.e., density feedback shape and strength, population growth rate inflection points, process error, return rates), and from different population growth models such as theta-logistic variants (Saether & Engen 2002; Saether *et al.* 2002; Saether *et al.* 2004), age-structured autoregression (Lande *et al.* 2002; Saether *et al.* 2005; Lande *et al.* 2006), and polynomials (Fowler 1981, 1988; Sibly *et al.* 2007). Given these various choices, it is unclear to what extent results across those studies are comparable. Due to severe fitting issues with the theta-logistic model (formulated in **Chapter 2; Table 4** and **Table 5**) such as the inherent play-offs between the shape parameter θ and maximum rate of population increase r_m (Clark *et al.* 2010), correlations between θ and life history must be revisited. The assignment of clear biological meaning to model parameters would certainly facilitate understanding of the generality of results across taxa and studies. Of particular relevance to assessing correlations between long-term demographic data and life history, is the understanding of how measurement error affects estimates of density feedback (Freckleton *et al.* 2006; Knappe & de Valpine 2012). I found that model rankings remained unchanged after the introduction of between 5 % (all taxa and birds) and 10 % (mammals) additive measurement error in simulated time series. Further work is required to specify, not only whether measurement error can affect feedback detection and parameter estimation by phenomenological models (Freckleton *et al.* 2006), but which error thresholds begin to erode the characteristics and biological interpretation of population growth curves.

1.23 Conclusions

The mechanistic implication of my findings is that life history is correlated with a degree of measurable demographic variation by making species prone to experience larger or smaller negative crowding effects through trophic and social processes, regardless of stochastic

forces. How and what processes relate to life history remains controversial, even for (the best-studied) mammals (Caughley & Krebs 1983; Krebs 2009). Increasing strength of density feedback can enhance population recovery, yet also magnify population variability in the smallest species, hence potentially making these species more vulnerable to extinction — an outcome of high predictive value for fishery collapses (Anderson *et al.* 2008). Recent emphasis on extinction dynamics caused by stochastic factors (Melbourne & Hastings 2008) should also take into account (deterministic) social/trophic interactions driving strong density feedback with extreme population variability (Brook *et al.* 2008). Methodologically, this underlines the need for broader application of models capturing eruptive dynamics in the analysis of long-term censuses, but for both slow (Forsyth & Caley 2006) and fast species.

Managers and conservationists can resort to generalised life-history estimates to predict population recoveries following harvesting and environmental shocks, and to rank species by the propensity to undergo particular patterns of change. In particular, my results are applicable where management and conservation priorities need to be made on the basis of rankings of species' conservation status (Knapp *et al.* 2003), and in the absence of detailed demographic or, in general, quantitative data (Tulloch *et al.* 2011), such as in the monitoring of areas planned for development, exploitation, protection, or focal investment on population recovery (Possingham *et al.* 2002). The strength of density feedback indicates rebound capacity from low numbers, which can be approximated by the position of a species along the slow-fast continuum, and such approximation could complement other qualitative measures of conservation status attempting to optimise the allocation of always-limited resources (Possingham *et al.* 2002; Tulloch *et al.* 2011).

CHAPTER 4

— CLIMATE

1.24 Title

Spatial climate patterns do not explain variation in strength of density feedback in birds and mammals

1.25 Abstract

The combined effects of climate and density-modified (e.g., competition, predation, disease) demographic processes determine the dynamics of all populations. Although we have some understanding of the (intrinsic) evolutionary processes influencing density feedback patterns, the degree to which (extrinsic) climate gradients shape these processes remains unclear. Recent work on large ungulates has postulated that feedback strength will increase from more variable, colder and/or drier (relatively scarce/variable resources) to less variable, warmer and/or wetter (relatively abundant/stable resources) environments. Here I test this prediction by investigating the relationships between long-term average temperature and precipitation, and the strength of density feedback in a global dataset of high-quality abundance time series from 158 populations of birds and mammals (125 species, 116 localities in 29 countries). I used information-theoretic metrics to rank generalised linear mixed-effects models to control for sample size (time series length), body mass (allometry) and phylogenetic non-independence (random effect = taxonomic level). Models including spatial variation in climate predictors had > 10 times less support than simple variants that only included time-series length and body size to explain variation in density-feedback strength. Indeed, model-averaged coefficients and confidence intervals for the climate fixed effects were all near zero. I hypothesise that censuses of multiple populations within a given species, and a priori knowledge of the spatial scales at which density feedback interacts with climate, will be necessary to determine cross-taxa variation in density feedback in a biogeographical context. Such data are rare for most species, resulting in an inability of macroecological research to uncover so far any robust generalisations about how demographic feedbacks interact with climate.

1.26 **Key words:** Density dependence, Population dynamics, Precipitation, Temperature, Time series

STATEMENT OF AUTHORSHIP

Submitted to *Oikos*, by Herrando-Pérez, Delean, Brook & Bradshaw

Lead author Herrando-Pérez conceived the work, reviewed the literature, did the statistical analyses and wrote the first draft of the paper. Delean contributed to statistical programming and design. Herrando-Pérez (total score of 0.75), Bradshaw (0.10), Delean (0.10) and Brook (0.05) contributed substantially to revisions.

All co-authors certify that the statement of contribution is accurate, and give permission for the inclusion of the paper in the thesis.

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Date: 10 June 2012

The quality of the food or the temperature prevailing, however, may have an important effect upon the level at which a population is adjusted by governing factors (Nicholson 1954a)

1.27 Introduction

The last decade has seen a proliferation of field and experimental studies investigating the interplay of density-independent (environmental forcing via weather, climate, or food supply) and density-dependent (i.e., trophic and social interactions between individuals) drivers in long-term time series of population abundance (Bjørnstad & Grenfell 2001; Stenseth *et al.* 2002). Cross-taxa patterns have only been compared for a few phylogenetically and/or trophically related species, with increasing attention being devoted to examining variation in the strength of density feedbacks using a variety of modelling methods (e.g., Krüger *et al.* 2002; Lima *et al.* 2002; Saether *et al.* 2005; Stige *et al.* 2010; Knape & de Valpine 2011; Mutshinda *et al.* 2011; WallisDeVries *et al.* 2011).

Thus, Post (2005) analysed data on 27 populations of caribou/reindeer (*Rangifer tarandus*) in Greenland using an autoregressive model and found a ‘tension’ (negative correlation) between the strength of density-dependent (higher at higher latitudes) and -independent (higher at lower latitudes) factors, concluding that “...populations limited strongly by density-independent factors may be prevented from reaching carrying capacity and/or sufficiently high densities to be limited by population-intrinsic processes”. In the only two cross-taxa studies correlating density-feedback strength explicitly with broad climate predictors, Wang *et al.* (2006) showed that for large herbivores (bison *Bison bison* and elk *Cervus elaphus*) in northern America, temporal heterogeneity in weather accentuated the model-averaged density-feedback strength while spatial heterogeneity in food resources weakened it. Diminishing feedback strength was also related to increasing (altitudinal) resource heterogeneity and (theoretical) predation pressure in 11 ungulate species from northern America and Europe (Wang *et al.* 2009).

To advance this under-studied area of population dynamics, here I look for broad climatic signals in density-feedback variation in a large sample of 125 birds and mammals with contrasting life histories and long-term high-quality time-series data, distributed worldwide. Following the predictions by Post (2005) and Wang *et al.* (2006), I test the hypothesis that the strength of density feedback should increase in response to the availability of depletable resources from more variable, colder and/or drier (relatively scarce/variable resources) to less variable, warmer and/or wetter (relatively abundant/stable resources) environments. To do

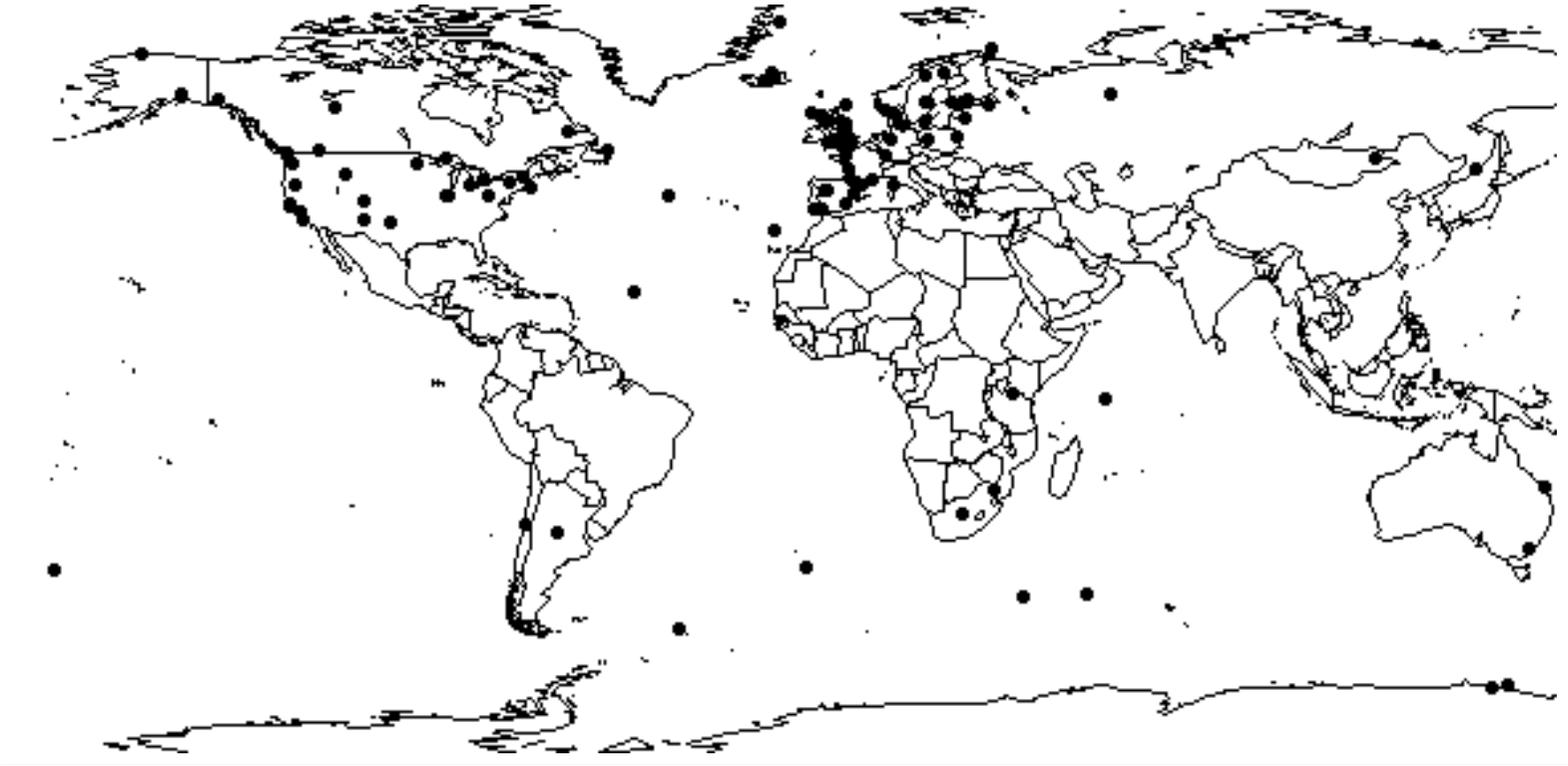
this, I collated average values of the magnitude and variability of precipitation and temperature in the last five decades at a coarse spatial resolution (21 km²), then correlated them with density-feedback strength estimated from geo-referenced long-term censuses of population size.

1.28 Methods

Data

I collected 487 year-round population censuses of birds and mammals from Clark *et al.* (2010) and **Chapter 5**. Following **Chapter 3** and **Appendix A4 (Table 25)**, from the initial dataset, I imposed stringent criteria to select a subset of high-quality time series of abundance (N). Essentially, I first assessed stationarity through the ‘return rate’, i.e., “the time it takes [for a population] to return to equilibrium following disturbance” (Berryman 1999) in $\log_e(N)$ - t space, and excluded time series with a coefficient of variation of the return rate (> 4.6) above the 75th percentile. Then, I left out time series for which linear trending of log-transformed population sizes had more statistical support (based on AIC_c, defined below) than an intercept-only model and slopes $> |0.1|$ ($< 25^{\text{th}}$ and $> 75^{\text{th}}$ percentiles). I further removed time series where missing-value frequency was $\geq 20\%$ of the time-series length. I detected time series with extreme outliers by studentising the residuals (Cook 1982) from the linear-trending model used above, and removed those with residuals above the 75th percentile (> 3.3). I only kept time series of well-defined populations, mostly resident in their native ranges or, for some birds, in their breeding localities, and for which I had access to environmental data (see below). After applying the selection criteria, my final collection contained 158 populations (104 birds, 54 mammals) belonging to 125 species, and representing 116 different localities in 29 countries spanning deserts, temperate and boreal forests, polar regions, mainland sea shores and oceanic islands — 88% of the populations were from the Northern Hemisphere (mainly Europe and northern America; **Figure 11**). The median length of time series was 26 years, with 95th percentile ranges of 10 to 79.

Figure 11. Location of the 158 populations (125 species) of birds and mammals examined.



I geo-referenced the ‘position’ of each population as the latitude/longitude reported in the papers/sources from which I retrieved the census data (**Figure 11**). For each population’s geographic position, I collated one broad estimate of four environmental predictors from the *Bioclim* suite (www.worldclim.org): (i) annual temperature (mean, in °C), (ii) temperature seasonality (standard deviation, in °C), (iii) annual precipitation (mean, in mm), and (iv) precipitation seasonality (coefficient of variation). These estimates are averages between 1950 and 2000 as derived from monthly data collected by weather stations at a 1-km² resolution (Hijmans *et al.* 2005). I used interpolated data with 2.5° resolution (21 km²) (Hijmans *et al.* 2005) because that was the prevailing resolution of my population data. The magnitudes of each environmental predictor at 2.5° resolution and 5° (42 km²) or 10° (84 km²) resolutions were highly correlated ($\rho > 0.99$), so my results held at those three spatial scales. For a few oceanic islands (e.g., Gough, Cosin, Marion) and some localities from remote areas (e.g., Antarctica), I could not obtain adequate climatic data so did not use the abundance time series for those localities.

Strength of density feedback

I estimated strength of density feedback as the slope of the relationship of the intrinsic growth rate (r) versus population size on a log scale, i.e., the Gompertz model (Medawar 1940; Nelder 1961) — I justify the use of this model in **Chapter 3**. Feedback strength in this model expresses change in r per unit order of magnitude change in population size. The slope of such relationship can be compensatory or depensatory [growth rates decrease or increase as population size increases, respectively] (**Chapters 2 and 5**). In this study, I focus only on compensatory density feedbacks (**Chapter 2; Figure 8**), which are common signals of intra-specific competition for food resources (Sinclair & Pech 1996).

Model set

I included nine models in my *a priori* set (**Table 9**). With strength of compensatory density feedback (none of the selected time series were depensating) as the common response, the null model equated time-series length and body size (control variables, see below), and the remaining eight models included a single environmental predictor (four models), and each temperature predictor with one of the two precipitation predictors (four models). I discarded combinations of highly co-linear predictors. More complex models could not be fitted due to precision-bias trade-offs related to sample size (Burnham & Anderson 2002). My analyses quantify the effects of temperature and precipitation on density-feedback strength over and above any effects due to time-series length, allometry and phylogenetic relatedness among

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species. Time-series length correlates positively with increasing statistical support for density-feedback in multiple-species studies (e.g., Brook & Bradshaw 2006), so I accounted for this correlation by including this predictor in all models. Since the strength of density feedback also varies with generation time and intrinsic growth rates, and the latter descriptors correlate with body size (Peters 1983), I also controlled for them by using body length as a measure of body size in all models (as in **Chapter 3; Table 7**). I collected maximum body length recorded in the wild for each species (mm, from tip of nose/beak to end tail) from experts and online sources (e.g., www.bto.org, www.demogr.mpg.de/longevityrecords, genomics.senescence.info/species). Body length had an approximately Gaussian distribution on a log-scale — indicating no bias towards either end of the body-size spectra. Finally, covariance between life-history traits should be incorporated in comparisons of demographic responses across taxa (Felsenstein 1985), and can be controlled for by allowing different intercepts for species grouped by higher taxonomic levels (Blackburn & Duncan 2001). I did so by including the Linnaean taxonomic level of *Order* as a random factor in each model of my set (controls by *Class* in the model set gave identical model support and similar fixed effects); lower taxonomic ranks were not possible to model due to many *Families* and *Genera* represented by only one species), while taxonomic classification followed the IUCN template (www.iucnredlist.org).

Table 9. Model set used, including climate predictors (see note below) of variation in strength of compensatory density feedback (*EN*) across taxa (fitted by GLMM using as random factor OR = taxonomic class), and bird and mammal species (fitted by GLM, no phylogenetic random effect). Control variables were included in all models, namely *q* = length of time series, and *Body* = Body size. Climate predictors encompassed: *mT* = annual temperature (mean, in °C), *mP* = annual precipitation (mean, in mm), *sT* = seasonality of temperature (standard deviation, in °C), and *sP* = seasonality of precipitation (coefficient of variation).

$$EN \sim q + Body + (1 | OR)$$

$$EN \sim q + Body + mT (1 | OR)$$

$$EN \sim q + Body + mP (1 | OR)$$

$$EN \sim q + Body + sT (1 | OR)$$

$$EN \sim q + Body + sP (1 | OR)$$

$$EN \sim q + Body + mT + mP (1 | OR)$$

$$EN \sim q + Body + mT + sP (1 | OR)$$

$$EN \sim q + Body + sT + mP (1 | OR)$$

$$EN \sim q + Body + sT + sP (1 | OR)$$

Model fitting

I fitted my data using generalised linear mixed-effects models (Breslow & Clayton 1993). Prior to model fitting, I converted the strengths of density feedback to their absolute values, and log-transformed time-series length, body size and climate predictors to approximate a linear relationship with the response. Residuals only met model assumptions by means of a Gaussian variance function, and the response being on a proportional scale through a square-root-transformation, which was supported by a likelihood-based test of Box and Cox (1964). I replicated the analyses for all taxa, and only the subsets of mammals and birds. Low sample sizes for specific geographical areas or taxonomical orders precluded further subsetting.

I ranked model support by means of Akaike's information criteria corrected for finite sample size, AIC_c (Sugiura 1978). I calculated model ranking and relative fixed effects on 100 bootstrapped samples of the response and predictors measured in all populations. A total of 25 localities contributed two to 12 populations (20 % of the dataset), so to avoid correlations of the response within those localities, each of the 100 bootstrapped samples consisted of a bootstrapped sample from localities with one single population and one population selected randomly from each of the localities with several populations. I measured relative model support across the model set by the medians and 95th percentile ranges of AIC_c metrics (ΔAIC_c , model probabilities, deviances) over all bootstrapped samples. Further, I used model averaging (Burnham & Anderson 2002) to estimate the coefficients of the fixed effects of each predictor on the strength of compensatory density feedback. Thus, I summed model probabilities for each model containing a given predictor weighted by its effect size as a measure of model-averaged effect size. To confirm that effect sizes were comparable among predictors of different range, I assessed them with and without a *post hoc* standardisation [trait \times standard deviation (response) / standard deviation (predictor)].

1.29 Results

The null model (including only the control variables of time-series and body length) was top-ranked in all model contrasts, and explained 36.1 % of the deviance in density-feedback strength across populations (all taxa) and 36.8 % and 43.5 % for mammals and birds, respectively (**Table 10**). This null model was top-ranked in 71 to 86 % of the bootstrapped samples, and had 11 to 17 times more median information-theoretic support than any second-ranked model including environmental predictors (**Table 10**), based on the evidence ratio of the respective AIC_c weights.

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The next-best-ranked model included the fixed effect of mean annual temperature (mT), wherein mT explained 3.2 % of the deviance in strength for all taxa and 12.9 % for mammals. For birds, the best non-control predictor was mean annual precipitation (mP), explaining 4.2 % of the deviance. In support of the model rankings above, median model-averaged effect sizes (standardised over all predictors) were all close to zero for the four environmental predictors (**Table 11**). The standardised effect sizes for body length varied from -0.04 (all taxa and birds) to -0.03 (mammals), so density-feedback strength increased from large to small body sizes across species (**Table 11**).

Table 10. Akaike information criterion (AIC_c) support for the first- and second-ranked models correlating (*via* GLMM) climate predictors to strength of compensatory density feedback (EN) for all taxa, and only mammals or birds. Models include length of the time series (q) and body size ($Body$) as controls, with the taxonomic level of $Class$ as random factor, and the predictors: mT = annual temperature (mean, in $^{\circ}C$), mP = annual precipitation (mean, in mm), sT = seasonality of temperature (standard deviation, $^{\circ}C$), and sP = seasonality of precipitation (coefficient of variation) (**Table 9**). Model-ranking descriptors ($wAIC_c$, %DE and ER)¹ are medians from 100 bootstrapped samples [95th percentile ranges]; n indicates the number of populations available before bootstrapping.

Dataset	n	Top-ranked models	$wAIC_c$	%DE	ER	Top rank
All taxa	158	$EN \sim q + Body$	0.76 [0.01 to 0.93]	36.1 [10.6 to 53.2]	17	71 (17)
		$EN \sim q + Body + mT$	0.03 [0.00 to 0.88]	39.3 [14.8 to 56.8]		16 (25)
Mammals	54	$EN \sim q + Body$	0.77 [0.09 to 0.92]	36.8 [17.1 to 64.0]	13	88 (7)
		$EN \sim q + Body + mT$	0.06 [0.00 to 0.63]	49.7 [28.5 to 73.5]		8 (31)
Birds	104	$EN \sim q + Body$	0.83 [0.02 to 0.91]	43.5 [19.7 to 63.9]	11	86 (13)
		$EN \sim q + Body + mP$	0.08 [0.04 to 0.740]	47.7 [26.3 to 65.5]		12 (63)

¹ $wAIC_c$ = model probabilities given each data and model sets; %DE = % deviance in density-feedback strength (EN) explained by each model within the set; ER = Evidence ratio of first- over second-ranked model $wAIC_c$; and **Top rank** = times each model was top-ranked over the 100 bootstrapped samples (times each model was second-ranked).

Table 11. Standardised model-averaged effect sizes of time-series length (q , years), body size (Body, mm), mean annual temperature (mT, °C), mean annual precipitation (mP, mm), seasonality of temperature (sT = standard deviation, °C) and seasonality of precipitation (sP = coefficient of variation) as predictors of variation in strength of compensatory density feedback (response), for all taxa, and only mammals or birds (158 populations, 125 species). Statistical models were fitted as generalised linear-mixed effects, with a total of 9 models in each contrasted set (**Table 9**). Effect sizes are medians (in bold) for 100 bootstrapped samples [95th percentile ranges].

Predictors	All taxa	Mammals	Birds
q	-0.04 [-0.09 to 0.00]	-0.06E-2 [-0.07 to 0.07]	-0.07 [-0.12 to -0.03]
Body	-0.03 [-0.04 to -0.01]	-0.03 [-0.05 to -0.01]	-0.04 [-0.09 to -0.01]
mT	-0.02E-3 [-0.06E-2 to -0.02E-5]	-0.04E-3 [-0.06E-2 to -0.09E-5]	-0.01E-5 [-0.06E-3 to 0.09E-4]
mP	0.06E-2 [-0.09E-2 to 0.05]	-0.01E-2 [-0.02 to 0.02]	0.04E-1 [-0.05E-1 to 0.01E-1]
sT	0.01E-11 [0.01E-13 to 0.02E-9]	0.02E-9 [0.04E-11 to 0.08E-8]	0.03E-8 [0.06E-10 to 0.02E-5]
sP	-0.02E-2 [-0.08E-1 to 0.07E-2]	-0.01E-1 [-0.03 to 0.02E-2]	0.03E-2 [-0.02E-1 to 0.06E-1]

1.30 Discussion

I found virtually no support for the hypothesis that spatial variation in broad-scale and long-term precipitation and temperature predictors (mean, standard deviation, coefficient of variation) correlates with spatial variation in compensatory density-feedback strength, based on censuses of 158 populations (125 species) of birds and mammals. The results contrast with the strong, but small-sample-size, correlations reported for ungulates (several populations of several species) in the only other two cross-taxa studies testing the same hypothesis with a similar modelling structure (Wang *et al.* 2006; Wang *et al.* 2009). Such apparent discrepancy might reflect an interplay between density-dependent and density-independent factors at the population level that does not leave a species-specific signal.

In another relevant cross-taxa study, Knappe & de Valpine (2011) modelled (via autoregression) fluctuations in population size (rather than my metric of density-feedback strength) in response to immediate and delayed density feedback, weather (temperature, precipitation) and climate (North Atlantic Oscillation, Southern Oscillation) for 492 populations of mammals, birds and insects (327 species; J. Knappe, pers. com.). This work showed that model-averaged prediction error (of population size from one year to the next) was poorly correlated with latitude, although no phylogenetic control was applied. The lack of

pattern of climate signals in population dynamics across species contrasts with unequivocal signals found in some well-studied, single populations in both terrestrial and aquatic ecosystems (Stenseth *et al.* 2002). For instance, in Soay sheep (*Ovis aries*) at Hirta (St Kilda Archipelago, Scotland), broad climatic indices are robust predictors (better than local weather) of population change because pulses of mortality (mainly by starvation resulting from crowding) consistently occur from January to May every year (Hallett *et al.* 2004). The relative effects of climate and density feedback have also been teased apart in groups of sympatric species, e.g., large ungulates (Post 2005; Månsson *et al.* 2007), ducks (Saether *et al.* 2008), diurnal or nocturnal butterflies (Mutshinda *et al.* 2011; WallisDeVries *et al.* 2011), and flatfish (Spencer 2008). Moreover, latitude has often been used as a proxy for climate, with numerous studies reporting the predominance of immediate versus delayed density feedback (and contrasting dynamics from damping through cycles or chaos) along large latitudinal bands, especially in small rodents, pest insects and game homeotherms (reviewed in Ims *et al.* 2008). All the latter studies reveal considerable variation in the interplay between climate and density feedbacks at the population level. Therefore, the choice of populations used to represent a species might lead to different results and varying patterns.

A further caveat in examining cross-taxa patterns of density feedback, population dynamics, and climate, is to use a common spatial climate-data resolution for all species, as in my study. This disregards the fact that climate processes driving population change might operate at different spatial scales for different populations and species. For instance, territorial birds can compete for food resources mainly at the scale of territories (Brouwer *et al.* 2006); the quality of a few plant individuals can override the strength of density feedback at a population level in herbivorous insects (Helms & Hunter 2005); or, more intricately, the strength of density feedback in reef fish can increase at small scales, or decrease at large scales, with increasing habitat complexity (Johnson 2006). For future studies over broad taxonomical groups, I suggest the compilation of data from replicate populations for each species [then use *species* as random factor in the model set], and from species whose demography is known *a priori* to respond to common scales of environmental variation, such as in territorial, long-distance migratory or small oceanic-island species — this enterprise might require collaborative effort among many researchers sharing their data on individual populations, or access to data from national environmental agencies monitoring populations and species for decades (e.g., Foley 1994). Body size explained most variation in density-feedback strength across taxa in my models, reflecting the position of species along a continuum from slow (milder feedbacks) to fast (stronger feedbacks) life histories (Saether *et*

al. 2002) (**Chapter 3**); therefore, controls for body size variation are also indispensable in comparisons of multiple species.

In the last two decades, new developments in mathematical demography have shifted the focus from *testing for* (the presence of) to *explaining variation in* density feedback (Bjørnstad & Grenfell 2001). In the above discussion, I have cited a sample of a large body of recently published studies aiming to elucidate the relative demographic role of exogenous and endogenous mechanisms. Meta-analytical techniques hold a promising future application here (e.g., Osenberg *et al.* 2002), but care must be taken to ensure that parameter estimates are comparable across species and studies. For instance, the estimation of additive effects of autoregressive parameters of climate/weather and lagged population size is often used to explain or predict spatial change in a range of different responses, such as process error (e.g., Knappe & de Valpine 2011), population size (e.g., Bjørnstad *et al.* 1995) or population growth rate (e.g., Lima *et al.* 2006). In contrast, in my study and similar analyses (e.g., Wang *et al.* 2006), the explicit link between model-based estimates of density-feedback strength to raw environmental variables from independent sources captures how the intensity of trophic/social interactions (as inferred from density feedback) within populations and across species can vary with long-term average external forcing. Thus, the selection of different responses and predictors, and of different model sets and modelling approaches, potentially addresses similar questions from different angles, but comes at the expense of ease of comparability.

1.31 Further directions

Mechanistic understanding lags behind mathematical development and model fitting in ecology and such a mismatch has handicapped the identification of ‘general principles’ in population dynamics (Belovsky *et al.* 2004). Among those developments, time-series analyses have become an important tool in macroecological research (Bjørnstad & Grenfell 2001; Inchausti & Halley 2001; Stenseth *et al.* 2002), and shed light on fundamental themes such as the relationship between demography and life history (Fowler 1981), evolution (Hairston *et al.* 2005) or extinction (Fagan *et al.* 2001), often using datasets spanning aquatic and terrestrial realms, and invertebrates, vertebrates and plants. Yet, the disparity of the spatial scales at which environmental forcing might affect the population dynamics of species with extremely different body sizes, mobility and habitat dependencies suggests that the study of the interplay of density-dependent and -independent factors through time-series analysis might only be biologically meaningful (and result in some general cross-taxa patterns) among closely related species. Furthermore, long-term studies based on census data and summary

statistics of reproductive fitness (like r) are largely opaque in identifying the actual mechanisms causing demographic feedbacks (Krebs 2002b); for that, experimentation is likely to be more appropriate (Bassar *et al.* 2010). Indeed, the conceptual rationale of my study stems from Nicholson's iconic experiments on blowflies (*Lucilia cuprina*), where he hypothesised that intraspecific competition drove oscillations in numbers of larvae and adults exposed to different amounts of food resources (Nicholson 1954a) (**Chapter 6; Appendix A1**). Surprisingly, this kind of experimentation has received little attention thereafter, and the results from already published experiments still await meta-analytical enquiry (e.g., Fox & Morin 2001; Bull & Bonsall 2008; Hart & Gotelli 2011). Along with a more unified theoretical framework, the connection between long-term/large-scale and short-term/small-scale studies, presently confined to focal taxa and specialities (e.g., Osenberg *et al.* 2002; Steele & Forrester 2005; Pfister 2006; de Valpine & Rosenheim 2008), seems crucial to improve our mechanistic understanding of population dynamics.

CHAPTER 5

— DEMOGRAPHIC RATES

1.32 Title

Decoupling of component and ensemble density feedbacks in birds and mammals

1.33 Abstract

A ‘component’ density feedback represents the effect of change in population size on single demographic rates, whereas an ‘ensemble’ density feedback captures that effect on the overall growth rate of a population. Given that a population’s growth rate is a synthesis of the interplay of all demographic rates operating in a population, I test the hypothesis that the strength of ensemble density feedback must augment with increasing strength of component density feedback, using long-term censuses of population size, fertility and survival rates of 109 bird and mammal populations (97 species). I found that compensatory and depensatory component feedbacks were common (each detected in ~ 50 % of the demographic rates). However, component feedback strength only explained < 10 % of the variation in ensemble feedback strength. To explain why, I illustrate the different sources of decoupling between component and ensemble feedbacks. I argue that the management of anthropogenic impacts on populations using component feedbacks alone is ill-advised, just as managing on the basis of ensemble feedbacks without a mechanistic understanding of the contributions made by its components and environmental variability can lead to suboptimal decisions.

1.34 **Key words:** Compensation; Conservation; Density dependence; Depensation; Fertility; Mortality; Population regulation; Recruitment; Survival

STATEMENT OF AUTHORSHIP

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All co-authors certify that the statement of contribution is accurate, and give permission for the inclusion of the paper in the thesis.

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“...only those mechanisms that affect some measurable component of individual fitness should be included within the definition of Allee effects” (Stephens & Sutherland 1999)

1.35 Introduction

Quantifying variation in population size is an important element for predicting population dynamics. In models where a demographic rate responds to change in population size, such ‘density-dependent’ relationships are ecologically understood as demographic signals of trophic and social interactions, because the intensity of those interactions varies with population size (**Chapter 2**). As the populations of long-lived species refill their environments following disturbance, the mechanisms associated with compensatory density feedback can sequentially reduce survival of juveniles, delay age of primiparity, depress fertility and reduce adult survival, and this cascade of events can shape population trajectories (Eberhardt 2002). In fact, compensatory density feedback describes the theoretical capacity of populations to adjust growth and rebound from low, or decline from high, numbers (Fowler 1981; Eberhardt *et al.* 2008) as *per capita* availability of resources and exposure to processes such as competition, migration, predation and/or parasitism shift. As a determinant of a population’s growth rate, density feedback is thus a key metric in the management of human influences on populations (Henle *et al.* 2004), often modelled in combination with weather and climatic conditions (e.g., Coulson *et al.* 2001; Post *et al.* 2009).

Population growth models, which encompass the family of models of self-limiting growth (e.g., logistic equations), have become a popular tool in describing and predicting trajectories of population growth in time series of abundance (Eberhardt *et al.* 2008). Whenever ecological research focuses on assessing long-term population trends, those models are pragmatically cost-effective because a census of abundance alone can capture the net effects of population size on the ‘instantaneous growth rate’ r (*i.e.*, proportional change in population size between two time steps such as years, generations) — the mechanistic underpinning being that r encapsulates the compound interplay (ensemble) of all component fertility and survival rates (Münster-Swendsen & Berryman 2005). There is considerable empirical and theoretical support for such an assumption in homeotherms; thus, r has been decomposed into the contributions of age-structured fertility and survival rates (Coulson *et al.* 2005). Further, the largest sensitivities to population growth rate can shift from survival to fertility across species from slow to fast life histories (Oli & Dobson 2003), and both fertility and survival can track population trends in some mammals (Owen-Smith *et al.* 2005) and

birds (Paradis *et al.* 2002). It can therefore be expected that the deterministic (i.e., via density feedback from trophic and social interactions) and stochastic (e.g., from system shocks such as storms, fires, floods) variation in demographic rates should leave a signal in time series of abundance. For instance, density feedback on adult survival (particularly females) exerts strong effects on growth rates of long-lived vertebrates, and those effects are measurable through population growth curves (Eberhardt 2002; Owen-Smith 2006). Understanding such signals has important implications; Kolb *et al.* (2010) illustrated that population growth rates can be insensitive to density feedback on some demographic rates (e.g., seed production). Consequently, limited resources and conservation measures can be wasted, and population trends can be inferred mistakenly, particularly because populations might be "... able to buffer the detrimental effects of small population size on vital rates that have a relatively small influence on population growth rate" (Kolb *et al.* 2010). Here I test the hypothesis that the strength of density feedback on r correlates positively with the strength of density feedback on single demographic rates in a dataset consisting of long-term, annual estimates of population size and demographic rates for 97 species of birds and mammals. I conclude that even though stage-structured demographic rates are essential to elucidate important demographic mechanisms, long-term monitoring of population size as the basis of population growth models remains an irreplaceable component in ecological, management and conservation research.

1.36 Methods

Data

I selected bird and mammal studies in the *Science Citation Index* focussing on year-round time series of both abundance and demographic rates from single populations. Subsequently, I gathered datasets from authors by e-mail, and from the selected publications when the data were provided. The final collection of datasets contained 294 time series of demographic rates (182 for fertility, 112 for survival) from 109 populations (74 birds, 35 mammals) and 97 species (65 birds, 32 mammals) — I give data sources in **Appendix A6 (Table 31)** and photos of some species in **Figure 15**. Fertility rates predominated in birds (80 %), and survival rates did so in mammals (61 %). Each population was represented by one time series of population size, and one to 11 demographic rates (median = 2 rates/population with a 95th percentile range = [1 to 6]). Fertility (e.g., clutch size, number of daughters per female) and mortality (proportion of dead bodies to total density) rates were single annual estimates, and survival (e.g., survival probability) and recruitment (e.g., % surviving between two age

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classes) rates were relative estimates from one year to the next — I provide a concise description of all demographic rates in **Appendix A6**. As opposed to ‘fecundity’ (physiological maximum reproductive potential), all fertility rates were measures of current reproductive output (sensu Bradshaw & McMahon 2008). Time-series length varied between 8 and 56 years (median = 18 years [9 to 45]). I obtained species’ body sizes (length from tip of nose/beak to tip of tail) through experts and online sources (e.g., www.bto.org); body lengths ranged from 100-200 mm (e.g., pied flycatcher *Ficedula hypoleuca* or short-tailed shrew *Blarina brevicauda*) to > 1 m (e.g., mute swan *Cygnus olor* or moose *Alces alces*), and had an approximately Gaussian distribution on a log-scale — indicating no bias towards either end of the spectrum of body sizes.

Given the historical confusion in the lexicon of density dependence (Berryman *et al.* 2002) (**Chapter 2**), a terminological note is mandatory here. In this study, I refer to ‘density dependence’ and ‘density feedback’ interchangeably. I partially follow the unambiguous terms by Stephens *et al.* (1999), whereby density operating on single demographic rates (individual fitness) represents ‘component’ feedback, and density operating on r (total fitness) represents ‘ensemble’ [Stephens *et al.* (1999) refer to this term as ‘demographic’] feedback (**Chapter 2**). As to component feedbacks, they can be ‘compensatory’ when fertility and survival rates decrease with increasing population size (direct density dependence, Allee 1941), and ‘depensatory’ when those rates decrease with declining numbers (inverse density dependence, Allee 1941) (**Chapter 2; Figure 8**). I assessed depensatory feedbacks across the measured range of population sizes, so make no claim for the evidence of Allee effects (i.e., depensation only at low numbers). Because different density feedbacks can operate in the same population both between consecutive, and delayed beyond two, time steps (Brook & Bradshaw 2006), and ‘immediate’ and ‘delayed’ density dependence are associated with different ecological mechanisms (Turchin 1990), I focused my analyses only on density feedbacks measurable between consecutive years.

Strength of density feedback

I estimated ensemble feedback strength as the slope of the relationship of $r [= \log_e(N_{t+1}/N_t)]$ versus population size on a log scale, namely the Gompertz model (Medawar 1940; Nelder 1961) [see justification in **Chapter 3**]. I estimated component feedback strength as the slope of the relationship of each demographic rate and population size on a log scale (e.g., Paradis *et al.* 2002). Prior to model fitting, I expressed all demographic rates in standard deviation units by z-score standardisation; for proportions p (most survival and recruitment rates), the standard deviation was calculated as $\sqrt{\text{mean}(p) * [1 - \text{mean}(p)] / q}$, where q is the number of

observations in each time series. In quantifying component feedbacks, I used a Gaussian probability density function for all demographic rates, after checking normality of residuals in Q-Q and residual plots. For each population, I contrasted statistical evidence for both ensemble and component density feedbacks against an intercept-only model by means of Akaike's information criterion adjusted for finite sample size, AIC_c (Sugiura 1978).

Model set and fitting

I counted the number of demographic rates showing compensatory and depensatory component feedbacks for populations with and without AIC_c support for compensatory ensemble feedback (i.e., Gompertz growth). For those populations bearing evidence for Gompertz growth, the strength of compensatory ensemble feedback (response) was correlated with the strength of component feedback (only compensatory, only depensatory, and both pooled) through linear modelling in a model set including: (i) an intercept-only model; (ii) a model including the length of the time series (q), since q can correlate with the weight of evidence for ensemble feedback (Brook & Bradshaw 2006); (iii) a model including both q and body size (following **Chapter 3; Table 7**), to account for the decreasing 'intrinsic growth rate' and increasing generation times from small- to large-bodied species (Peters 1983); and (iv) a full model including q , body size and strength of component feedback (**Table 12**). I applied the same model contrast to subsets of time series of abundance and demographic rates showing different evidence ratios (ER) for ensemble and component feedbacks (see Results). ER for ensemble feedback (ER_{EN}) was $wAIC_{c-Gompertz\ growth}/wAIC_{c-Intercept-only\ model}$, and ER for component feedback (ER_{CF}) was $wAIC_{c-Linear\ model}/wAIC_{c-Intercept-only\ model}$ (Burnham & Anderson 2002).

Table 12. Model set used to assess the correlation between ensemble (EN) and component (CF) density feedback, where q = length of time series and $Body$ = Body size.

$$EN \sim 1$$

$$EN \sim q$$

$$EN \sim q + Body$$

$$EN \sim q + Body + CF$$

Prior to model fitting, I converted the strengths of component and ensemble feedbacks to their absolute values — generally, raw values of feedback strength are negative or positive when compensatory or depensatory, respectively (**Chapter 2; Figure 8**). I re-scaled all

explanatory variables by their logarithms to approximate a linear relationship with the response. Furthermore, to meet assumptions for the saturated model, I used a Gaussian variance function and expressed the response on a proportional scale through a square-root transformation, as supported by a likelihood-based test of Box and Cox (1964) for all data subsets.

1.37 Results

Ensemble density feedback

Of the total of 109 time series of population size used in my study, I found information-theoretic support (i.e., evidence ratio $ER_{EN} > 1$) for compensatory ensemble density feedback (i.e., Gompertz growth) in 71 % of the populations, 51 of 74 birds (69 %) and 26 of 35 mammals (74 %). Five populations of large-bodied species showed depensatory ensemble density feedback — these were steadily recovering from low abundances (bearded vulture *Gypaetus barbatus* and African elephant *Loxodonta loxodonta*), or steadily declining (tsessebe *Damaliscus lunatus*, and sable antelope *Hippotragus niger* and roan antelope *Hippotragus equinus*); I removed those time series from the statistical descriptors hereafter. The median ER_{EN} was 3.3 (95th percentile range = [0.2 to > 1,000]), so overall the density-feedback model was just over three times more likely than the density independent model, given the data. ER_{EN} was relatively skewed (**Figure 12**); this prompted me to investigate ensemble feedbacks (and component feedbacks, see below) over different ER_{EN} magnitudes.

The median strength of compensatory ensemble feedback across the subset of populations with $ER_{EN} > 1$ was -0.4 [-1.3 to -0.1]; thus, an average increase in population size by one order of magnitude resulted in a ~ 0.5-fold decrease ($e^{0.4} - 1$) in population growth rate. For $ER_{EN} > 2, 4, 8, 16$ and 32, median strength of ensemble feedbacks ranged from -0.6 to -0.5. I measured the strongest ensemble feedbacks for the Seychelles warbler *Acrocephalus sechellensis* (-1.5) and the tawny owl *Strix aluco* (-1.3) in birds, and the short-tailed shrew *Blarina brevicauda* (-1.5) and the pygmy possum *Thylamys elegans* (-1.2) in mammals. ER_{EN} and median strengths of ensemble feedback were of the same magnitude in birds and mammals (**Figure 13**).

Figure 12. Proportion of time series of abundance ($n = 109$ populations) and demographic rates ($n = 294$) showing different strengths of AIC_c evidence for ensemble and component feedbacks for 97 species of mammals and birds.

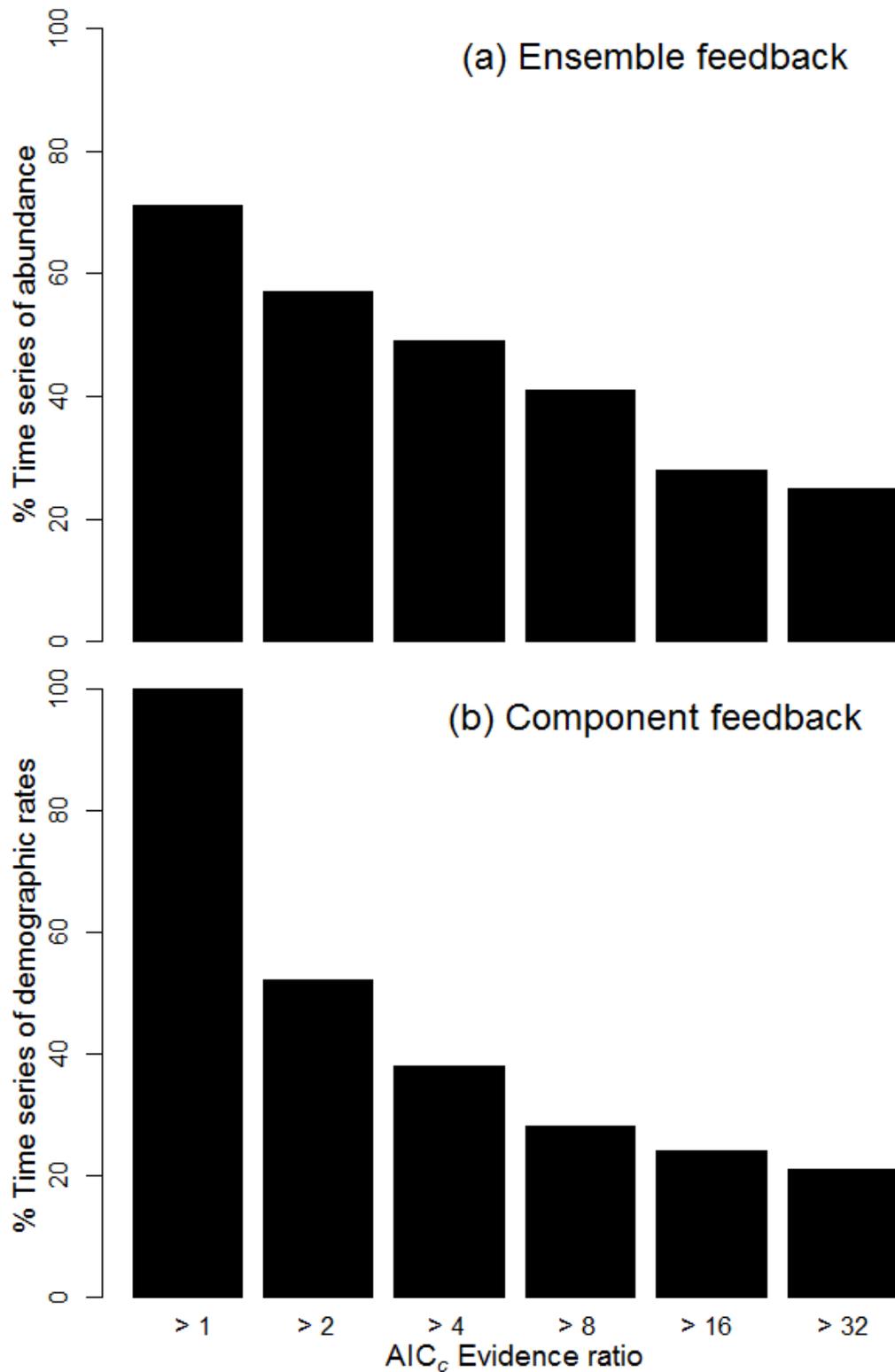
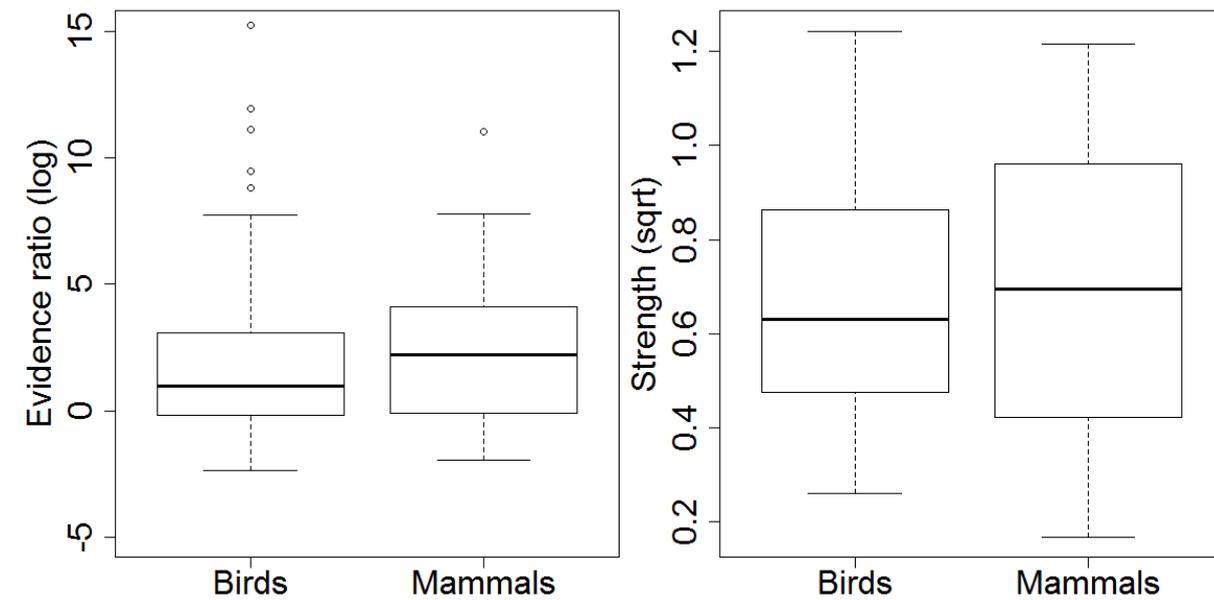


Figure 13. Evidence ratios (ER_{EN}) and strength of ensemble feedback in homeotherms. ER_{EN} represent model probability for Gompertz growth over model probability for an intercept-only model in 72 populations of birds (65 species) and 35 populations of mammals (32 species). Strength is the slope of the relationship between the instantaneous growth rate r and log-transformed population size for populations showing AIC_c -support for compensatory ensemble feedback ($ER_{EN} > 1$), i.e., 50 populations of birds (47 species) and 22 populations and species of mammals. As in my models (**Table 12**), strengths have been square-root transformed.



Component density feedback

I found statistical evidence for component density feedback (i.e., evidence ratio $ER_{CF} > 1$) in all 294 time series of demographic rates. Furthermore, ER_{CF} was more skewed than ER_{EN} (**Figure 12**), with the median $ER_{CF} = 2.1$ [1.0 to $> 1,000$]. About 50 % of the component feedbacks were compensatory, and the other half were depensatory (but not necessarily showing Allee effects, see Methods). I found that (i) both compensatory and depensatory component feedbacks occurred whether or not there was statistical support for ensemble density feedback (**Table 13**), (ii) compensatory feedbacks on survival and fertility dominated when ensemble feedback was present (**Table 13**), and (iii) the predominance of compensatory feedback occurred mainly in survival for those populations showing the highest ER_{EN} (> 4 ; **Appendix A7**; **Table 32** and **Table 33**). That pattern was consistent for other ER_{EN} thresholds higher than 4.

The median strength of compensatory feedback was -1.3 [-5.6 to -0.1] for survival and -0.7 [-5.2 to 0.0] for fertility. In other words, increases in population size by one order of magnitude resulted in ~ 2.6 -fold decrease in survival ($e^{1.3} - 1$) and ~ 1.0 -fold decrease in

fertility ($e^{0.7} - 1$), measured in standard deviation units (see Methods). For depensatory feedback, strength ranged between 0.6 [0.1 to 3.2] (survival) and 0.7 [0.1 to 2.8] (fertility). The strongest component feedbacks by main taxa occurred in the southern elephant seal *Mirounga leonina* (-11.1, births per adult) and common guillemot *Uria aalge* (-3.9, chicks per breeding pair) [compensatory], and giraffe *Giraffa camelopardalis* (12.8, juveniles per female) and eastern kingbird *Tyrannus tyrannus* (3.0, proportion of breeding returnees) [depensatory]. Median strengths were relatively larger in compensatory than in depensatory component feedbacks only for survival rates (**Table 13**), across different ER_{EN} and ER_{CF} magnitudes (**Appendix A7**; Table 32 and **Table 33**). Median ER_{CF} and strength of component feedback were of the same magnitude in mammals and birds (results not shown).

Table 13 . Frequency (%) of occurrence of compensatory and depensatory component density feedbacks on survival rates in bird and mammal populations supported or not for ensemble density feedback (i.e., Gompertz growth). Frequencies are given for survival and fertility showing evidence (evidence ratio = $ER_{CF} > 1$, $n = 106$ survival 176 fertility rates) or strong evidence ($ER_{CF} > 4$, $n = 56$ survival and 70 fertility rates) for component feedback, split by whether or not populations show ensemble density feedback (ER_{EN}). Median strengths of component density feedback with 95th percentile ranges also reported.

Rate	Component feedback	Ensemble-feedback support (ER_{EN})	Component-feedback frequency (%)		Component-feedback strength	
			$ER_{CF} > 1$	$ER_{CF} > 4$	$ER_{CF} > 1$	$ER_{CF} > 4$
Survival	Compensatory	> 1 (Yes)	55	61	-1.2 [-5.7 to -0.1]	-1.8 [-7.7 to -0.5]
		< 1 (No)	6	8	-2.4 [-3.2 to -0.2]	-3.2 [-3.2 to -1.9]
	Depensatory	> 1 (Yes)	25	18	0.6 [0.1 to 3.0]	0.9 [0.5 to 3.2]
		< 1 (No)	14	15	0.6 [0.2 to 4.6]	2.2 [1.1 to 5.2]
Fertility	Compensatory	> 1 (Yes)	36	44	-0.7 [-5.4 to -0.0]	-1.8 [-6.9 to -0.4]
		< 1 (No)	15	11	-0.8 [-3.6 to -0.0]	-1.8 [-3.8 to -0.5]
	Depensatory	> 1 (Yes)	27	29	0.8 [0.1 to 2.8]	1.1 [0.6 to 8.1]
		< 1 (No)	22	16	0.6 [0.1 to 2.5]	2.0 [0.5 to 4.4]

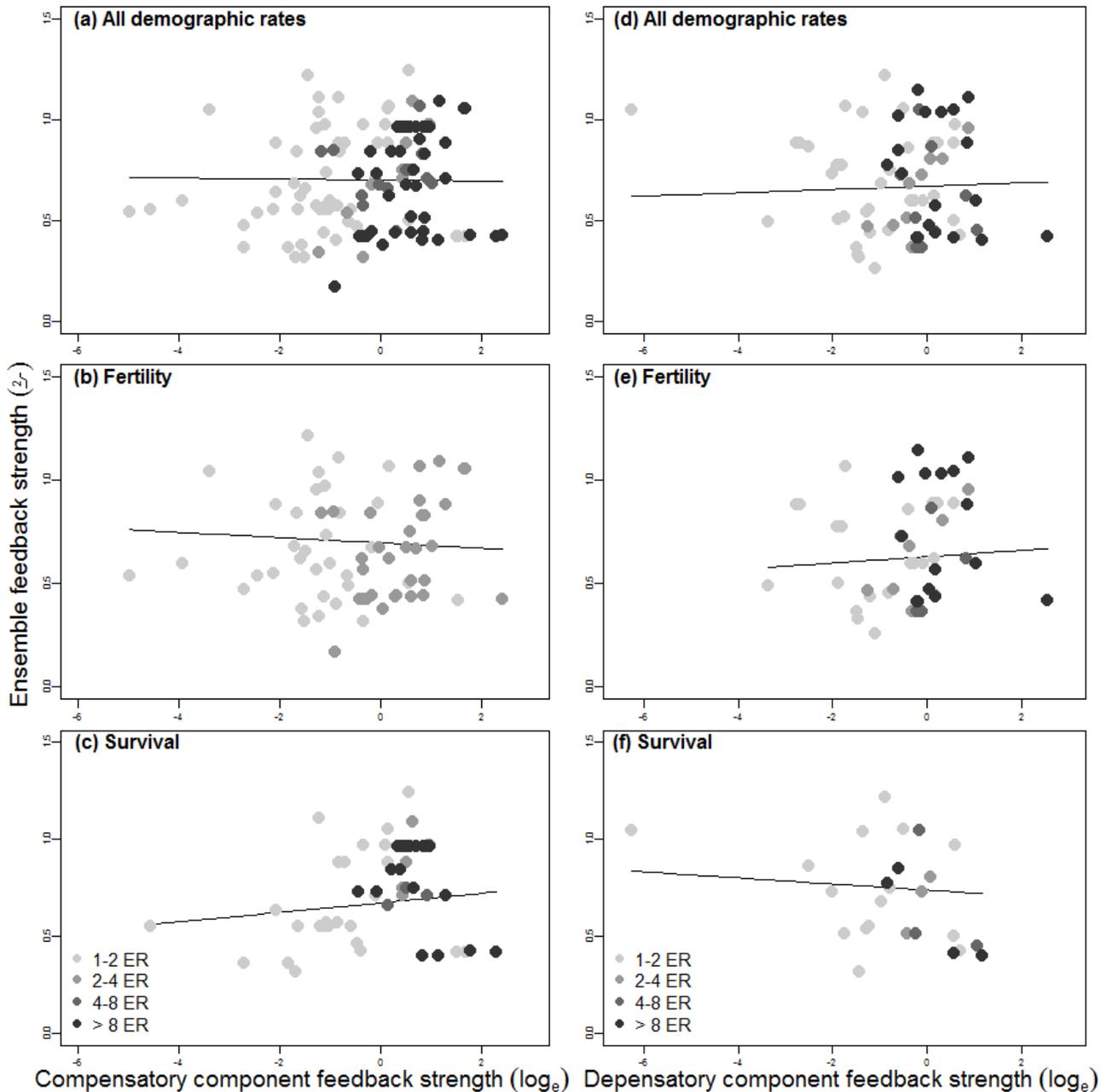
Relationship between ensemble and component feedbacks

I found weak correlation between the strength of ensemble and component feedbacks, after controlling for the length of the time series, and body size (**Table 14; Figure 14**). The AIC_c top-ranked component-feedback models explained between 5 and 33 % of variation (deviance) in ensemble feedback strength across populations. Component feedback strength occurred in a top-ranked model when all survival rates were analysed separately (3.8 % variation in ensemble feedback strength explained), and for survival (9.9 % variation explained), and fertility (4.1 % variation explained) rates experiencing compensatory component feedback (). The length of time series (0.5 to 6.1 %) and body size (2.7 to 28.1 %) accounted for most of the variation explained in ensemble feedback strength in the top-ranked models. When using subsets of demographic rates from populations scoring $ER_{EN} > 4$ and $ER_{CF} > 1$ (**Appendix A7; Table 34**), the best correlation between component and ensemble feedbacks occurred for compensatory survival rates (9.9 % of the variation explained). The effects of component on ensemble feedback strength were not statistically detectable for time series with $ER_{EN} > 4$ and $ER_{CF} > 4$ (**Appendix A7; Table 35**), and when mammals and birds were analysed separately across all ER magnitudes, although sample sizes in all of the former data subsets were small (results not shown).

Table 14. Compensatory ensemble feedback strength (EN) fitted as a function of sample size in the time series (q , years), body size ($Body$ = body length, mm), and component feedback strength (CF) in birds and mammals [n = number of demographic rates included in each model contrast]. $wAIC_c$ are model probabilities (shown only top-ranked models in a set*), and DE is % deviance explained (total and broken down by predictors). Model fits were done using all demographic rates, split by fertility or survival rates; and all types of component feedback, split whether they were compensatory or dependant. Included all demographic rates from populations supported for ensemble feedback ($ER_{EN} > 1$; **Table 13**). See model set in **Table 12**.

Rates	n	Component feedback type	Top-ranked models	$wAIC_c$	DE_{total}	DE_q	DE_{Body}	DE_{CF}
All	195	All	$EN \sim q + Body$	0.70	7.5	3.3	4.2	-
Fertility	112	All	$EN \sim q + Body$	0.60	8.4	4.3	4.1	-
Survival	83	All	$EN \sim q + Body + CF$	0.66	16.4	1.3	11.3	3.8
All	122	Compensatory	$EN \sim q + Body$	0.42	4.6	1.9	2.7	-
Fertility	65	Compensatory	$EN \sim q + Body + CF$	0.44	13.8	4.1	9.7	4.1
Survival	57	Compensatory	$EN \sim q + Body + CF$	0.69	16.1	0.5	5.7	9.9
All	73	Depensatory	$EN \sim q + Body$	0.58	13.8	6.1	7.7	-
Fertility	47	Depensatory	$EN \sim q$	0.34	5.4	5.4	-	-
Survival	26	Depensatory	$EN \sim q + Body$	0.69	33.2	5.1	28.1	-

Figure 14. Relationship between component (CF) and compensatory ensemble (EN) density-feedback strength in populations of birds and mammals. For each population, ensemble feedback strength is the slope of Gompertz growth based on time series of abundance, and component feedback strength is the linear slope between each measured demographic rate and abundance. Left (a, b, c) and right (d, e, f) panels equate compensatory and depensatory component feedbacks, respectively. Overlaid shading distinguishes the magnitude of AIC_c -evidence ratios for component feedback (i.e., ER_{CF}). Linear trends are for the model $EN \sim q + Body + CF$ with q (log-transformed time series length, years) and $Body$ (log-transformed body size, mm) held constant at their mean. Included all demographic rates from populations showing evidence for compensatory ensemble feedback ($ER_{EN} > 1$; **Table 13**). See model set in **Table 12** and model support in **Table 14**.



1.38 Discussion

I have identified a serious decoupling in the strength, direction and occurrence of density feedbacks operating on single demographic rates and population growth rates of birds and mammals (**Table 15** and **Table 16**). With regard to strength, the intensity with which density feedback alters individual demographic rates does not necessarily translate into a similar intensity of feedback on a population's rate of growth (indeed, this seems rare). As to feedback direction, many populations can arrest their growth rate even though some fertility and survival rates are being enhanced (depensating) at high numbers. As for feedback occurrence, depensating and compensating demographic rates occurred in a number of populations showing no compensatory response to population increase. Since a population grows when births and immigration outnumber deaths and emigration, the decoupling of ensemble and component feedbacks must originate from a failure in (i) measuring density feedback on the survival and fertility rates most affected by demographic processes, (ii) accounting for dispersal (i.e., populations are not closed), or (iii) incorporating external forces, such as climate, that can shape demographic rates and relax or remove the demographic effects of the social and trophic interactions eliciting density feedback. In the following, I illustrate those scenarios with selected case studies classified into the three main types of component-ensemble decoupling (**Table 16**). I was mainly interested in cases where decoupling existed, yet there were examples of strongly coupled component and ensemble feedbacks (in terms of strength, direction and occurrence), such as in the great partridge *Perdix perdix* in the Plateau Aigre (Bro *et al.* 2002) (**Figure 15g**), or the African elephant *Loxodonta africana* in Addo National Park, South Africa (Gough & Kerley 2006) (**Table 15**).

Sources of decoupling

The first category of observed decoupling occurred in feedback direction when a compensatory ensemble feedback existed simultaneously with a depensatory component (**Table 15**). An example was the short-tailed shrew *Blarina brevicauda* in the deciduous forest of the Appalachian Plateau, USA. The population had experienced compensatory ensemble feedback for more than two decades. Along those lines, first-order ensemble feedback from competitive interactions has been suggested to govern the dynamics of this population (Merritt *et al.* 2001). Likewise, I found that recruitment (probability of an individual at time $t+1$ being a new recruit from time t) was compensatory, yet survival rates were depensatory. I detected the same pattern in two other small mammals: the leaf-eared mouse *Phyllotis darwini* (Lima *et al.* 2001b) and the

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mouse opossum *Thylamys elegans* (Lima *et al.* 2001a) from thorn scrub in Chile. In small rodents such as the leaf-eared mouse, compensatory population growth rates can buffer depensatory survival when losses of adult individuals are mainly caused by stable populations of generalist predators which do not respond numerically to prey abundance (Lima *et al.* 2001b), so the larger the mouse population, the higher the chances of escaping predation (M. Lima, pers. com.).

Conversely, shrinking ice cover lowered adult survival of emperor penguins *Aptenodytes forsteri* in Terre Adélie, Antarctica (**Figure 15b**), over the last half century, resulting in a steady population decline (Jenouvrier *et al.* 2009). For a population largely affected by climate conditions, I indeed found only moderate compensatory ensemble feedback, and moderate-to-weak compensatory component feedback on survival of adults and yearlings. However, the component feedback was relatively strong and depensatory on all fertility rates, including number of chicks per breeding pair, fledglings per clutch, and proportion of adult breeders and 5-year breeders over adult and 5-year adult population size. This species forms colonies far from open sea, so large ice cover forces individuals to make long foraging trips, compromising food supply to chicks and hatching success (Zimmer *et al.* 2008, and references therein). Therefore, even if the population declines as the ice sheet reduces in extent, surviving adults might improve reproduction if the energetic costs of foraging diminish. Most importantly, those shifts in fertility could be attributed to climate modifying the penguin's habitat, thus not constituting genuine density feedbacks (i.e., triggered by social and/or trophic interactions in the population) (**Chapter 2; Figure 5**).

An extreme case for decoupling in feedback direction is the island fox *Urocyon littoralis* off California, USA. By amalgamating population estimates for six islands, Angulo *et al.* (2007) report depensatory component feedback on adult and pup survival (linked to predation by golden eagles *Aquila chrysaetos*), and on proportion of breeding females. Yet, for the population on San Clemente Island I found strong compensatory ensemble feedback, with strong to moderate compensatory feedbacks on number of kits per female and adult survival, suggesting that survival and fertility rates are not enhanced (Angulo *et al.* 2007) but depressed as fox numbers increase.

The second category of observed decoupling occurred in feedback strength when a relatively weak compensatory ensemble feedback coincided with a relatively strong compensatory component feedback (i.e., the lower-right corner of **Figure 14** panels), or vice versa (i.e., upper-left corners of **Figure 14** panels) (**Table 15**). For instance, the population of elephant seals *Mirounga leonina* on Marion Island, southern Indian Ocean, has fallen by ~ 30 % in the last three

decades, as part of an overall decline of this pinniped in the Southern Hemisphere (McMahon *et al.* 2005). I found a moderate compensatory ensemble feedback, yet relatively strong compensatory feedbacks on the ratio of births to total population size, proportion of pup deaths, and probability of female survival. My estimates for component feedback agree with published studies (Pistorius *et al.* 2008, and references therein). By finding the component feedback on survival, Pistorius *et al.* (2008) claim regulation for this population. However, the weak strength of ensemble feedback suggests that compensatory component feedbacks on unmeasured demographic rates might be counteracting compensatory survival rates, and/or that the change in key demographic rates is actually free of density feedback. Thus, shifts in food availability from environmental fluctuation might drive the dynamics of this and other populations of southern elephant seals (McMahon *et al.* 2005).

A different pattern unfolded for a population of the tawny owl *Strix aluco* in a mosaic of spruce-dominated forest and agricultural land in Lahti, Finland. This population follows vole prey cycles tightly, such that recruitment of first-time breeders builds up the predator's numerical response to prey peaks, but the survival of experienced breeders during low-prey periods has the largest contribution to population growth (Karell *et al.* 2009). Over two decades of available data, I found one of the strongest compensatory ensemble feedbacks in my dataset for this raptor, and contrastingly negligible component feedback on adult survival or number of fledglings per breeding pair. Many first-year recruits in the study area are immigrants (P. Karell, pers. com.); hence, the strong ensemble feedback most likely reflects the emigration of adults out of the study area when the population exceeds carrying capacity.

The third category of observed decoupling consisted of absence of compensatory ensemble feedback even though some demographic rates were compensating (**Table 15**). Two final study cases illustrate this scenario. Eastern kingbird *Tyrannus tyrannus* shows high breeding-site fidelity in northern America following migration from southern America (Murphy 2001b). In a population nesting in upland hawthorns (*Crataegus* spp.) at Charlotte Valley in Delaware County, USA, I found no support for compensatory ensemble feedback ($ER_{EN} < 1$), and relatively large support for component feedback ($ER_{CF} > 6$) with strong compensatory and compensatory components on the number of fledglings per breeding pair, and the proportion of adults returning and breeding, respectively. Thus, fertility decreased in years when the breeding population was relatively large, whereas the number of breeding returnees in a given year tended to be larger when breeding numbers from the previous year were relatively high. Although population growth

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rate is much more sensitive to change in adult survival than fertility (Murphy 2001b), and correlates well with the steady decline in this population in the 1990s (Murphy 2001a), additional simulation work revealed that density feedbacks on survival or fertility are not driving population trends (Murphy 2001a), in consonance with my results. The population of this flycatcher functions as a sink, with adult survival heavily governed by habitat quality (Murphy 2001b, a).

Another illustrative example is the impala *Aepyceros melampus*, which is the most abundant ungulate of small-to-medium body size and the main prey of the largest savannah predators in Kruger National Park, South Africa. Using data spanning more than a decade, I found no support for ensemble feedback ($ER_{EN} < 1$), and relatively strong component feedbacks which were compensatory on adult survival ($ER_{CF} > 4$), and depensatory on yearling survival ($ER_{CF} > 1,000$), and number of juveniles per female ($ER_{CF} > 200$). The direction of component feedbacks coincides with comparable published estimates (Owen-Smith *et al.* 2005). Owen-Smith and Mills (2006) assert that factors driving the dynamics of this stable population remain poorly explained, showing that density (lagged or not) explains the least amount of variation in this population relative to ten other ungulate species at Kruger.

The extent of the decoupling between component and ensemble feedbacks observed across populations (**Figure 14**) can also be partially accounted for by tradeoffs among component feedbacks in populations where multiple vital rates have been measured. For instance, both great tits (*Parus major*) from the Pilis Mountains, Hungary, and bison (*Bison bison*) from Wood Buffalo National Park, Canada, showed strong evidence for compensatory ensemble feedback. In the great tits, the strongest compensatory component feedback involved clutch size, thus the observed milder or null compensatory effects of adult density on brood size and fledgling rates could originate from competition between great tits and blue tits (*P. caeruleus*) only at the time around egg laying (see Sasvári *et al.* 1987). In contrast, the bison population's strength of compensatory component feedback decreased through number of calves, one- and two-year-old individuals per female, a pattern which could be related to specific age-class responses to predation, disease and dispersal (see Bradley & Wilmshurst 2005). Where data exist only for single fertility or survival rates, those tradeoffs therefore indicate strongly that population-based conclusions regarding density dependence can vary substantially according to what demographic rates researchers choose or are able to measure. I had access to only few demographic rates across sequential ages within the same population, so I could not assess this aspect further.

The disparity of types of demographic rates, and the variety of age/stage classes on which they were measured, might be a source of noise in my models. It would be interesting to explore whether the correlation between component and ensemble feedbacks improves by using a consistent set of demographic rates for all populations (e.g., Paradis *et al.* 2002), even for one or several well-represented age classes. If the data are available for a large number of populations involving several co-occurring demographic rates, tradeoffs among component feedbacks could be examined across species. Furthermore, r encapsulates the totality of demographic processes acting on survival and reproduction (Münster-Swendsen & Berryman 2005), yet excludes dispersal effects. However, measured changes in r can partly result from emigration and immigration, and magnify the decoupling between feedback on r and feedback on survival or fertility rates. Future research could circumvent this by controlling for known dispersal across populations, or selecting populations that are closed or monitored on spatial scales large enough to render dispersal effects negligible. My analyses could be further expanded by looking at lags of density feedback on r and single demographic rates, and by exploring nonlinear feedbacks which the Gompertz model might capture poorly. Finally, population growth rate is bound to be shaped by the combined effect of many mechanisms. These can encompass density feedback (e.g., competition, parasitism, predation), environmental stressors (i.e., climate), food availability (e.g., vegetation, prey), and rapid evolution such as change in beak size. To account for these, and should available data permit their robust parameterisation, models can be made arbitrarily complex to capture the dynamical nuisances of any given (meta)population. However, the exploration of macroecological patterns across populations and species relies on models comparable over entire life-history gradients, especially considering the extreme variation in the amount and type of demographic data available in even the best-studied taxa. I advocate that if broad-scale, year-round environmental data can be collated, my analyses could be improved by modelling demographic data along with environmental proxies as predictors in autoregressive models, or to represent variable carrying capacity in logistic models.

1.39 Conclusions

When the purpose is to ascertain the importance of density feedback on a population's growth rate, I see several important caveats in monitoring and/or making ecological inferences only from demographic rates. (i) Spurious compensatory feedbacks on overall demographic rates might occur simply because of the effects population size can have on age structure (Festa-Bianchet *et*

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al. 2003), and how density-dependent and -independent effects are partitioned across age-structured demographic rates. Likewise, tradeoffs among the various demographic rates can be expected to result in feedback operating in some age classes and not others (e.g., Møller 1989).

(ii) Different component feedbacks might have synergistic effects on population growth rates; this seems to be the case for pest, exploited or endangered populations subject to Allee effects, for which extinction thresholds might be highly uncertain if estimated only from single vital rates (Berec *et al.* 2007).

(iii) Some individuals might not experience the effects of regional population density, so component feedbacks pooled over several demographically isolated populations (e.g., Angulo *et al.* 2007) can confuse the direction and strength of the feedbacks experienced by single populations.

(iv) Whereas r will capture losses and gains due to emigration (as if they were survival or reproduction), studies assessing population trends from only survival and/or fertility rates will fail to detect dispersal effects, and again miss crucial tradeoffs among different component feedbacks.

(v) Statistical relationships between population size and demographic rates can indicate environmental forcing free of density feedback over most of the measured range of population density (e.g., Gough & Kerley 2006; Jenouvrier *et al.* 2009), and operate in unison with genuine density feedbacks, as revealed for some populations (e.g., Rodenhouse *et al.* 2003).

(vi) In most situations, it will be logistically impossible to measure all survival, fertility and dispersal rates in a population. Furthermore, the methods to quantify them can vary considerably depending on the type of data collected, and the selection of biologically meaningful demographic rates will always require an extensive, often unavailable knowledge of the study population. Indeed, I collected data on > 20 different types of demographic rates in up to 10 different age/stage classes, separating or not sexes, out of 109 independent studies. The choice of what to measure is unclear and subject to debate.

(vii) Most importantly, population regulation emerges solely as a ‘net effect’, namely when the effect of all compensatory component feedbacks overrides that of all dependant component feedbacks (Sinclair & Pech 1996). In the absence of estimates of all demographic rates, regulation is defined by population parameters capturing long-term persistence, the tendency to return to equilibrium, and bounded fluctuations above extinction (Hixon *et al.* 2002) (**Chapters 2 and 6**). Therefore, conservation and management investment can be misled if occurrence or lack of regulation is inferred only from demographic rates — a common inference in my literature survey (e.g., Pöysä & Pesonen 2003; Gough & Kerley 2006; Pistorius *et al.* 2008). A striking consequence of such inference is that the occurrence of population regulation in wild populations might have been substantially overstated in the ecological literature.

Table 15. Coupled relationships between component and ensemble density feedbacks on populations of birds and mammals. In graphs, N = population size, r = instantaneous growth rate, and blue lines represent ensemble density feedbacks. C = demographic rates (fertility, survival), and red lines represent component density feedbacks. Compensatory feedbacks imply decreasing population growth rates, survival or fertility rates as population size increases (negative slope). Depensatory feedbacks imply increasing population growth, survival and fertility rates as population size increases (positive slope) (Chapter 2; Figure 8). And a null slope indicates absence of density feedback.

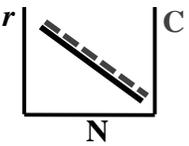
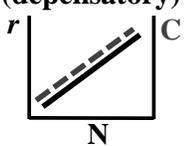
Feedbacks	Species	Site	Rate	Years	Reference
Coupled (compensatory) 	Black-throated blue warbler <i>Dendroica caerulescens</i>	New Hampshire USA	Fledglings/Territory Adult survival	1986-1999	(Rodenhuse et al. 2003)
	Great partridge <i>Perdix perdix</i>	Plateau Aigre France	Chicks/Female in summer	1989-2000	(Bro et al. 2002)
	Pigmy possum <i>Burramys parvus</i>	Snowy Mountain Australia	Daughters/Female Female survival	1986-1997	(McCarthy & Broome 2000)
	Soay sheep <i>Ovis aries</i>	Kilda Archipelago Scotland	Adult & juvenile recruitment Adult & juvenile survival	1985-2007	(Coulson et al. 2005)
Coupled (depensatory) 	African elephant <i>Loxodonta africana</i>	Addo National Park South Africa	Breeding/Reproductive females Non-pregnant/Pregnant females	1976-2002	(Gough & Kerley 2006)
	Sable antelope <i>Hippotragus niger</i>	Kruger National Park South Africa	Juveniles/Female Yearling recruitment	1977-1996	(Owen-Smith et al. 2005)

Table 16. Decoupled relationships between component and ensemble density feedbacks on populations of birds and mammals. In graphs, N = population size, r = instantaneous growth rate, and dark-grey, continuous lines represent ensemble density feedbacks. C = demographic rates (fertility, survival), and light-grey, dashed lines represent component density feedbacks. Negative and positive slopes indicate compensatory and depensatory feedbacks, respectively, and a null slope shows absence of density feedback.

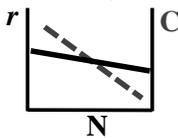
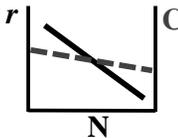
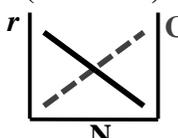
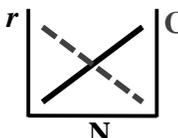
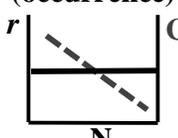
	Decoupled (strength)	Barnacle goose <i>Branta leucopsis</i>	Laus Holmar Islands Sweden	Hatchlings/Successful nest	1985-1993	(Larsson & Forslund 1994)
		Osprey <i>Pandion haliaetus</i>	Corsica France	Fledglings/Breeding pair Fledglings/Hatchlings	1974-2004	(Bretagnolle <i>et al.</i> 2008)
		Southern elephant seal <i>Mirounga leonina</i>	Marion Island Indian Ocean	Births/Adult Proportion of dead pups	1986-1999	(Pistorius <i>et al.</i> 2008)
		Island fox <i>Urocyon littoralis</i>	San Clemente Island California, USA	Adult survival	1988-1997	(Angulo <i>et al.</i> 2007)
		Tawny owl <i>Strix aluco</i>	Lahti, Fennoscandia Finland	Fledglings/Breeding pair	1981-1995	(Karell <i>et al.</i> 2009)
	Decoupled (direction)	Black-browed albatross <i>Diomedea melanophris</i>	Bird island Southern Ocean	Fledglings/Clutch size	1976-1992	(Prince <i>et al.</i> 1994)
		Emperor penguin <i>Aptenodytes forsterii</i>	Terre Adélie Antarctica	Chicks/Breeding pair Fledglings/Breeding pair	1962-2005	(Jenouvrier <i>et al.</i> 2009)
		Leaf-eared mouse <i>Phyllotis darwini</i>	Las Chinchillas Reserve Chile	Female survival	1997-2007	(Lima <i>et al.</i> 2001b)
		Short-tailed shrew <i>Blarina brevicauda</i>	Appalachian Plateau USA	Individual survival	1979-1999	(Merritt <i>et al.</i> 2001)
		Bearded vulture <i>Gypaetus barbatus</i>	Pyrenees Spain	Fledglings/Breeding pair	1978-2002	(Carrete <i>et al.</i> 2006)
		Roan antelope <i>Hippotragus equinus</i>	Kruger National Park South Africa	Juveniles/Female	1977-1996	(Owen-Smith <i>et al.</i> 2005)
	Decoupled (occurrence)	Barn swallow <i>Hirundo rustica</i>	Kraghede Denmark	1 st and 2 nd brood size Adult survival	1971-2009	(Møller 1989)
		Black-tailed deer <i>Odocoileus columbianus</i>	King Creek Washington, USA	Fawn recruitment	1979-1997	(Gilbert & Raedeke 2004)
		Eastern kingbird <i>Tyrannus tyrannus</i>	Charlotte Valley Delaware, USA	Fledglings/Breeding pair	1983-2005	(Murphy 2001b)
		Impala <i>Aepyceros melampus</i>	Kruger National Park South Africa	Adult survival	1982-1995	(Owen-Smith <i>et al.</i> 2005)

Figure 15. Sample of individuals from the study populations/species for which I estimated component and ensemble density feedbacks, including (a) harlequin duck [River Laxá, Iceland; Photo: Daniel Bergmann], (b) emperor penguin [Terre Adélie, Antarctica; Photo: Stephanie Jenouvrier/WHOI], (c) reindeer [Arctic tundra, Nordenskiöld, Svalbard, Norway; Photo Olav Strand/NINA], (d) degus [semi-arid thorn scrub, Bosque Fray Jorge National Park, Chile; photo : Camila Holzapfel], (e) black-throated blue warbler [mature hardwood forest, Washington DC, USA; Photo: Gerhard Hoffman], (f) tawny owl [mixed boreal forest, Lohja, Uusimaa, Finland; Photo: Lasse Laine], (g) Weddell seal [Erebus Bay, Ross Sea, Antarctica; Photo: Jay Rotella], (h) African elephant [subtropical thicket, Addo Elephant National Park, South Africa; Photo: Katie Gough], and (i) great flamingo [Fangassier Lagoon, Camargue, France; Photo: Nicolas Van Ingen].

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CHAPTER 6

— CONCLUDING REMARKS

*There is a lack of appreciation of past literature;
this, in part, leads to ecology's fickleness toward central issues
(Belovsky et al. 2004)*

In my corollary discussion, I elaborate on three principal components of my PhD research. First, I will underline key properties and caveats of phenomenological models (as experienced during my postgraduate training) in the study of long-term demography and macroecological patterns, and propose areas of future development. Second, I will argue that the straightforward, biological meaning of density feedback (i.e., density dependence) has been overshadowed by a body of concepts created to challenge population regulation, all of which evidence the need for a better integration of the spatial and temporal components of population dynamics. Third, I will reflect on how we (ecologists) mistreat terminology, and put forward strategies to improve lexical standards in our discipline. Lastly, I will conclude with my overall perception of the *status quo* of population-dynamics research in our endeavours to find ecological generalities.

1.40 Advocacy for phenomenological models

Macroecological perspective

The framework of my three data chapters has been (i) the fit of single-species population models to derive parameters of strength of density feedback from long-term census data, and (ii) the contextualisation of these parameters in a multi-species multivariate format. Within the former framework, I have assessed macroecological patterns of population dynamics with regard to life-history evolution (**Chapter 3; Appendices A4 and A5**), global gradients of climate (**Chapter 4**), and rates of population reproduction and survival (**Chapter 5; Appendices A6 and A7**).

During peer-review, of individual chapters (submitted for publication in peer-reviewed journals as the thesis progressed), the peculiarity through several acceptances and rejections of my manuscripts has been that different referees praised the robustness of my analyses or, in

diametric opposition, posed insurmountable objections to different aspects of application of phenomenological models. Across the board, referees also contradicted one another by favouring the Ricker-logistic or the Gompertz, the theta-logistic or the hyperbolic models, among others. Thus, it became obvious that the use of models in the study of density feedback, and how to deal with the uncertainties of time-series analyses, is subject to several (preferential) schools of thought. This is commonly observed in studies that discuss, for instance, whether model-derived demographic parameters are biologically meaningful (e.g., Sibly *et al.* 2005; Doncaster 2006; Polansky *et al.* 2009; Clark *et al.* 2010), or how the inclusion or not of complexity (e.g., age-structure) captures long-term population dynamics (Zabel & Levin 2002; Festa-Bianchet *et al.* 2003; Berryman & Lima 2006).

It must be recognised that phenomenological models are *descriptive*, not *mechanistic*, so they *describe* the average properties of a population under investigation, such as the (average long-term) carrying capacity or the strength of density feedback. They can inform experimentation and modelling of mechanisms in the later stages of a investigation (Turchin 1999), if the appropriate data are available (survival and fertility rates, life history traits, dispersal estimates, on the relevant scale and period of time, for the key age/stages). However, the reality is that this information is typically incomplete, even for the best-studied populations. As such, in the study of macro-ecological patterns and long-term population trends, wildlife demographers are compelled to resort to phenomenological models, and arguably finding a *best* general model is chimerical. The selection of such model should be done on *a priori* grounds that include ecological knowledge and considerations of analytical tractability. In my PhD research, I have resorted to single-species linear models on a raw (Ricker) or proportional (Gompertz) magnitude of change in population size (explanatory variable), because the strength of density feedback has then a clear, biologically interpretable meaning, demonstrated in a long body of literature fitting those models to real data. Throughout, I have acknowledged the potentially confounding effects of sampling error (see below), model simplification of real-world dynamics, data redundancy, allometry, collinearity, phylogenetic relatedness, and over-parameterisation, and have dealt with each of those aspects more meticulously than most papers in well-read journals assessing multi-species patterns of density-feedback metrics, whether that be statistical evidence, strength or shape (e.g., Fowler 1981; Stiling 1987; Turchin 1990; Woiwod & Hanski 1992; Fagan *et al.* 2001; Saether *et al.* 2002; Sibly *et al.* 2005; Brook & Bradshaw 2006; Clark *et al.* 2010).

On a different note, while any population ecologist might agree that measurement error can be an important source of bias in time-series analysis of population abundance (Shenk *et*

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al. 1998; Freckleton *et al.* 2006; Knape 2008), and needs to be assessed where plausible (see methods in de Valpine 2002; Dennis *et al.* 2006; Lele 2006; Ives *et al.* 2010), there is a consistent assumption made — with little direct evidence — that it is consistently, categorically and definitively a major problem, thus negating all conclusions derived from phenomenological models. This is not logical, and is typically an untested assumption. The analysis of census data is not flawed *per se* (Inchausti & Halley 2001), providing authors define stringent criteria of data selection (Brook & Bradshaw 2006; Knape & de Valpine 2011). In the absence of real data quantifying measurement error (e.g., by collecting census of population abundance through multiple observers and/or different counting methods), the only means to test its potential effects on observed patterns are (i) to examine subsets of time series known to be of higher quality (i.e., higher precision), and/or (ii) to simulate time series and examine the effect of ramping additive measurement error on model parameters and their consequences for application in other analyses (**Appendix A5**). Along those lines, we know that measurement/observation errors do affect estimation of density feedbacks, but further investigation is required to ascertain *how much* error erodes cross-taxa signals.

Potential developments

Phenomenological models are not, of course, silver bullets. I summarise potential developments, directly or indirectly addressed in my thesis, restricted to cross-taxa studies of long-term density feedback, and within the areas of work of the Global Ecology Lab at The University of Adelaide (**Chapters 2, 3, 4 and 5**).

In **Chapter 5**, I define an ‘ensemble’ density feedback as the compound interplay of (component) density feedbacks on fertility and survival rates. I show a weak coupling between the strength of ensemble and component feedbacks in a sample of > 100 bird and mammal populations. The reasons I provide for such decoupling all gravitate around which demographic rates are measured, or how they have been measured. However, a claim can be made that the strength parameter of density feedback estimated by phenomenological models might simply be insensitive to component feedbacks driving long-term population change, hence lacking biologically mechanistic meaning altogether. I believe this caveat can be assessed theoretically through population projections, e.g., those done during population viability analysis (Brook *et al.* 2000; Brook *et al.* 2002). Thus, population trends can be predicted by simulating component density feedbacks on stage-structured demographic rates that are plausible for a set of species ranging from slow to fast life histories, then the strength of ensemble density feedback can be obtained by fitting phenomenological models to the simulated (projected) abundance time series, then correlated with the input component

feedbacks. The addition of different magnitudes of measurement error can be also explored. The analysis can be extended to evaluate the paradigm of *long-lived homeotherms* whereby density feedbacks are predicted to follow a gradual sequence of effects, namely increased mortality of immature individuals, increased age at primiparity, reduced fertility of mature females, and finally, increased mortality of adults (Eberhardt 2002). Such exercises, if supporting the hypothesised mechanistic underpinnings, could reinforce the utility of phenomenological models against views that have depicted them as a bankrupt paradigm (Krebs 1991), or a search for a holy grail (Krebs 1995).

More succinctly, I outline six further research advances which I deem critically important in cross-taxa comparisons. First, the role of sequential density dependence (through seasons or the life history) has been recently reviewed (Ratikainen *et al.* 2008), highlighting both (i) diverging terminology and analytical methodologies by study taxon, and (ii) management implications [given that density feedbacks might naturally suppress individuals at particular times of the life cycle]; this might be another source of decoupling between ensemble and component density feedbacks worth investigating (**Chapter 5**). Second, much theory supports the notion that population change scales with generation time (Fowler 1988; Gaillard *et al.* 2005), yet most empirical and meta-analytical work is assessed on an annual time scale (e.g., my PhD research); as a result, comparisons across taxa between the two time scales remain largely unexplored in phenomenological models. Third, few studies of density feedback have contemplated different spatial scales, yet this work is crucial to gain understanding about how fine-scale experiments connect mechanistically with broad-scale patterns of biotic interactions (e.g., Steele & Forrester 2005), swaps of compensatory and depensatory density feedback through different scales (e.g., Gascoigne *et al.* 2005), and the relative role of local dispersal and density feedbacks in shaping spatio-temporal population dynamics (Johnson 2000). Fourth, the few samples and (likely) high measurement error of observations at the low end of the spectrum of population abundances largely precludes detection of Allee effects in census data (Gregory *et al.* 2010); alternatively, the incorporation of qualitative measures of population size (e.g., probability of replacement between consecutive times, Tobin *et al.* 2007) qualifies as a potential tool to examine Allee effects in multi-species datasets. Fifth, more generally, recent studies have measured the fraction of population change driven by rapid evolutionary change, for the best-studied populations globally, such as Darwin finches *Geospiza fortis* or Trinidadian guppies *Poecilia reticulata* (reviewed by Pelletier *et al.* 2009; Post & Palkovacs 2009) — novel approaches also allow the incorporation of rapid evolution in phenomenological models (Hairston *et al.* 2005); it is clear that a mechanistic understanding of long-term population change across taxa requires estimates of demographic

rates, weather/climate and life-history traits; the pace with which ecologists are able to gather such data in a comparable fashion for a sizeable number of species (among other factors, see below) is likely to determine how long it might take before we can draw robust generalities about how populations work. And sixth, across the board, more studies of density feedback from tropical and arid regions are required to gain a better understanding of interactions between stochastic and deterministic drivers of population change across climatic gradients. The bias of research effort towards temperate regions of developed countries prevails in all ecological disciplines (Martin *et al.* 2012), and is notorious in the study of density feedback (**Chapter 1; Figure 2**).

1.41 Regulation overshadows density dependence

The integration of spatial and temporal population change in our understanding of population dynamics has generated a long-standing debate around rival concepts and hypotheses. Herein, I synthesise this debate and emphasise that ecologists on both sides of the dispute have not questioned the biological validity of density feedback, but the characterisation of population-dynamical properties (mostly persistence versus extinction) that can emerge with or without the operation of a density feedback. My discussion below is correspondingly dense, oozing the semantic density of the ecological literature about population dynamics.

The debate stemmed from the exchanges that Alexander Nicholson (Division of Entomology, CSIRO-Canberra, Australia) and Herbert Andrewartha (Department of Zoology, University of Adelaide, Australia) had in the 1950s under the watchful eyes of the world's ecological community. To Nicholson, populations were self-adjusted by compensatory density feedbacks (mainly driven by competition) that prevented or enhanced growth at high or low numbers, respectively, and such a mechanism of balance could explain the persistence of populations in nature. To Andrewartha, population persistence originated from chance environmental perturbation causing a spatial mosaic of population states from low- to high-variability in numbers. Nicholson's ideas evoked an axis of temporal population variation, as recreated in his laboratory experiments with blowflies, whereas Andrewartha based his views along an axis of spatial variation recreated in his field observations. Even though Nicholson's views aligned, and Andrewartha's were in discordance, with the general thinking of their contemporaneous ecologists (e.g., Elton, Haldane, Varley), the two authors were clearly ahead of their time, elaborating notions of demographic determinism/age-structure (Nicholson) and stochasticity/metapopulation (Andrewartha) that ecologists are still trying to quantify and tease apart in the 21st Century. I cite the most important primary-literature papers

by Nicholson and Andrewartha in **Table 17 (Appendix A1)**, and in the biographical notes at the end of **Appendix A1**.

Boundedness, spreading the risk, stabilisation

In the second half of the 20th Century, the Dutch ecologists Piet den Boer and Johannes Reddingius armed Andrewartha's theory with a mathematical and (modernised) conceptual framework (den Boer & Reddingius 1996; but see Gotelli 1998): "...models where there is exchange of individuals between subpopulations by 'migration' are more stable than populations consisting of isolated subpopulations. Letting the exchange between subpopulations be 'density-dependent' had some stabilising effect too, but not very conspicuously so" (Reddingius & Boer 1970). Following Andrewartha's postulates, den Boer (1968) reasoned that the uneven spatial spread of a population's widest fluctuations lead to *spreading the risk* [of extinction], so that the probability of persistence is relatively low locally and high regionally; that is to say that populations *gamble for existence* (Reddingius 1971). Spreading-the-risk dynamics were thus hypothesised to confine population numbers within limits (i.e., *boundedness*), evoking regulation as a one mode of *stabilization* (Reddingius & Boer 1970; Reddingius 1971) — such an hypothesis was used to revisit classic insect datasets (den Boer 1986b, a, 1988) and to test caveats (den Boer & Reddingius 1989; Reddingius & den Boer 1989; den Boer 1990), all unleashing considerable polemics (Roff 1974; 1986a; Strong 1986a; Latto & Hassell 1987; Pochke & Kirchberg 1987; 1988; Berryman 1991a). The mathematical treatment of population size as a 'first-order Markov process' further revealed that boundedness could be achieved irrespective of density feedback over relatively short periods of time, so that the chances for persistence or extinction would be a matter of the length of the time interval considered (Reddingius 1971). More simulation works also showed that populations might persist when undergoing feedback-free random walks (den Boer 1991; Murray 2000b), and all those works were also punctually criticised (Hanski *et al.* 1996; Murray 2000a; Tyre & Tenhumberg 2000).

Determination, metapopulation regulation, site-dependent regulation, vagueness

The concepts of spreading the risk and stabilisation were challenged by that of *metapopulation regulation*, whereby asynchrony of regulatory and chaotic dynamics geared to dispersal events can account for population persistence at broad spatial scales (Allen *et al.* 1993; Hanski *et al.* 1996): "Much confusion has been created by the claim (den Boer 1968, 1987) that metapopulation regulation or persistence requires no density dependence at the level of local populations. The claim is incorrect. Without any density dependence,

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populations would grow indefinitely large, or they would go rapidly extinct, and in the latter case no metapopulation would persist for long. Density dependence is required for metapopulation persistence; what is not needed is regulation of local populations” (Hanski 1990). *Site-dependent regulation* also proposed that, in territorial species, spatial resource heterogeneity generates population occupancy gradually from high- to low-quality patches, so demographic rates are mostly impacted in sites of poorest environmental quality but, arguably, free of the restraining effects of crowding (Rodenhouse *et al.* 1997); this hypothesis provoked additional debate (Hawkins & Berryman 2000; Hunt & Law 2000; Rodenhouse *et al.* 2000). Regulation was further contrasted with *determination*, by which demographic rates (e.g., *per capita* recruitment of marine fish) can correlate negatively with population density without the operation of demographic feedback (Sale & Tolimieri 2000), ensuing several criticisms (Berryman *et al.* 2002; Hixon *et al.* 2002); and with *vagueness* (Strong 1986a, b) by which density feedback might only effectively affect population growth rates at extreme low or high densities, leaving a density-vague range where density-independent migration determines persistence in a spreading-the-risk manner (see also Murray 1994; Cosner 1996), adding more papers to the debate collection (Lomnicki 1987; Strong 1987; Berryman 1991b).

Limitation

The semantic discrepancies between Andrewartha and Nicholson, historically epitomised by the distinction between the meanings of *population regulation* [process by which a population returns to its equilibrium density (what prevents population growth)] (Murdoch 1970; Sinclair 1989; Turchin 1995) and *population limitation* [process that set the equilibrium density (what limits population density in good and poor habitats)] (Osenberg & Mittelbach 1996; Sinclair & Pech 1996; Hunt & Law 2000; Krebs 2002a), and how population limitation and regulation relate to population persistence (Hanski 1990; Sinclair & Pech 1996), are still alive, yet dormant (Belovsky *et al.* 2004), as supported by my questionnaire survey (**Chapter 1; Appendix A2**). While experts such as Anthony Sinclair and Charles Krebs have attempted to clarify the definition of and how to measure both population properties, others (particularly Bertram Murray and Tom White versus Alan Berryman and Peter Turchin) have expressed their opposing views on whether the demographic relationship of populations with their environment are only limited by (stochastic) abiotic factors like weather, system shocks (e.g., wildfire, flood) and food availability (Murray 1982, 1999a, b, 2001; White 2004; White 2008), or *additionally* regulated by (deterministic) biotic interactions between individuals operating as compensatory density feedback (Turchin 1999; Turchin 2001; Berryman *et al.* 2002; Berryman 2004) — i.e., the same debate as that of Andrewartha and Nicholson. My

view on this matter might be radical (**Chapter 2**), but I think *population regulation* is no longer a useful concept in ecology — it is too vague and over-arching to capture the subtleties and complexities of the population dynamics it apparently embodies. Instead, I understand, from conceptual and mathematical principles, that there are factors that limit and enhance the demographic rates of individuals, that there are density feedbacks driven by biotic interactions among individuals as a demographic response to limitation, and that there are a finite number of population dynamics (stability, cycles, chaos, decline) emerging from the spatio-temporal interplay of limiting factors and biotic interactions. It is these latter concepts that should be explored, developed and inter-linked, rather than focussing on providing a biologically meaningful and universally accepted definition for *regulation* when none probably exists.

Outcomes from debates

It can be clearly seen how controversy boosts the branding of terms to confine the reasoning of confronting views (**Chapter 2**). Most importantly, the concepts defined above (up to nine!) have queried density feedback, not conceptually, but as a requirement for population regulation. Therefore I strongly argue that the semantic discussion about regulation has unfairly led density feedback to a corner of semantic darkness. I have emphasised in **Chapter 2** that regulation and density feedback are not synonymous, and that density feedback (or density dependence) has a clear definition and biological meaning.

Some experts opine that the ideas around the old debate might be ‘resolved’ (Murdoch 1994) and ‘outdated’ (Lundberg *et al.* 2000) because both sides addressed theoretical aspects that are complementary. So Lundberg *et al.* (2000) argued that “... the point of departure [from the debate] for understanding population variability is to acknowledge the mutual interaction... between environmental stochasticity and endogenous density-dependent processes”. Their optimism is much founded on the modern development of stochastic models that can capture complex dynamical features, such as temporally (‘colour’) and spatially (‘Moran effect’) auto-correlated noise, and these authors would probably sympathise with Bjørnstad and Grenfell (2001) that “... ironically, adding technical and methodological complexities greatly clarifies our biological understanding [of population variability]”.

I believe the field of population dynamics is indeed in an exciting moment of methodological development, but those elaborations still need to be integrated in a unified conceptual framework. A profound revision and stabilisation of the ecological terminology, as I propose in **Chapter 2** and below, could be instrumental in updating the definition of old concepts with what the new modelling tools tell us about what determines population numbers. Also, I have argued in my **Foreword** and in **Chapter 2** that an improvement in the

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quality and scope of statistical training, at least from the undergraduate stage, is mandatory for mathematics to become a language of communication among ecologists, instead of the alarming barrier they currently entrench between an elite of numerical ecologists and the majority of the ecological community.

1.42 A terminological advance for ecology

In **Chapter 2**, I reveal that ecologists have created an average of six terms of *density dependence* per decade since the beginning of the 20th Century, and have confused foundational terms and the concepts they represent, by apparently naïve matters such as the change in the sign of density-dependent statistical relationships relative to different types of measured demographic rates (**Chapter 2; Figure 8**). This prolific library of synonymies, polysemies and philosophically grounded lexicon illustrates the drift that ecological nomenclature is undergoing in the prevailing absence of regulatory rules. If I interpret lexical inconsistency as an indication of areas of research lacking broad consensus, then the conceptual and terminological issues presented in my questionnaire survey among ecologists (**Chapter 1; Appendix A2**), and in **Chapter 2**, suggest that the field of population dynamics is in a burgeoning mess and communication among scientists thereby jeopardised. The conundrum unfortunately extends to all ecological disciplines where lexical consistency has been analysed. Indeed, that the standards of ecological terminology are low was already recognised by Robert Whittaker (1957) on reviewing the second edition of Carpenter's (1956) glossary, noting that: "The field of ecology has a well-earned reputation for formidable, sometimes excrescent, terminology... there is a real need for a new glossary which will provide current, clearly stated definitions, preferably with citation of sources". No noteworthy progress has been made in the nearly 50 years since.

The silent rule

Synonymy and polysemy can stimulate areas of ecological research that might have not achieved optimal classification schemes (Hodges 2008). Yet in terminological reviews, it is essential to determine whether lexical inconsistencies can be identified by context or actually reflect a failure to understand the concepts for which they stand (Regan *et al.* 2002; Jax & Hodges 2008). Despite the inflation of the nomenclature of density dependence among ecologists, in most cases the terms can be correctly understood by context. But is that enough? Generally speaking, terms can lose their communicative power and their semantic frontiers when faced by a history of contrasting views or arbitrary adherences to different

topics. Scientists can pre-empt these loaded terms by resorting to other available ones which, in turn, potentially fall into conflict with existing lexicon. Other authors may perhaps not care, yet they can inadvertently influence terminological trends by the lexical attributes of their scientific discourse. Eventually, when using a key term in a publication, an author only needs another publication to refer to as the genesis of that term (or of the concept embedded in it). An the ‘silent rule’ in ecology seems to be that terminology is understood in the context of each publication, such that personal views or egocentric styles can end up superseding general understanding of words.

The silent rule is reinforced not only within single research papers or book chapters, but also within single publication outlets. Thus, some journals (e.g., ‘Trends in Ecology and Evolution’) and books (e.g., Jorgensen & Fath 2008; Levin 2009) include glossaries or encourage definitions to guide readers. Authors also refer to popular dictionaries of ecological terms [where definitions of identical terms do not match] (Carpenter 1956; Lincoln *et al.* 2003; Allaby 2005), which are proliferating for particular topics and broad taxa (e.g., fungi, birds, entomology, herpetology, zoology, plant pathology, environment, conservation, etc.). Or else authors follow the advice given by ‘terminological gourmets’, i.e., individual ecologists who review the ecological literature to bring order to particular mistreated lexicon, e.g., *fledging* (Middleton & Prigoda 2001), *floral larceny* (Inouye 1980), *fecundity* (Bradshaw & McMahon 2008), *carrying capacity* (Dhondt 1988; del Monte-Luna *et al.* 2004), *climax* and *succession* (Tansley 1935), *community* (Fauth *et al.* 1996), *eusociality* (Lacey & Sherman 2005), *niche* or *habitat* (Whittaker *et al.* 1973; Hall *et al.* 1997), or “...163 definitions of 70 different concepts of *stability*... to dispel the existing ‘confusion of tongues’” (Grimm & Wissel 1997).

On a different level, the English language is taken as the norm, but the complexity escalates if we consider the silent rules occurring in the native languages of ecological journals in non-English-speaking countries, in the translation of English ecology books [where meaning relies on context more than on a word-by-word translation], or in native-language, nation-based schools of thought and terminology (e.g., Dauvin *et al.* 2008b) which can even hamper implementation of cross-country environmental policies (Dauvin *et al.* 2008a).

Finally, colleagues have pointed out to me that terminology can become a ‘window dressing’ strategy in that “... connecting a study with Allee effects, density dependence, or a modish terminology gains a study more kudos”. Surely the former statement refers to the ornamentation of language to increase the chances of having manuscripts accepted in high-

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impact journals, but it applies equally when terminology is instrumental to seeking institutional support. Thus, Adams *et al.* (1997) described an ‘audience effect’ whereby both the frequency and definition of 30 broad ecological terms related to the potential readership in 43 peer-reviewed journals; for instance, the term *biodiversity* is clearly skewed towards a group of journals amenable to funding agencies, politicians and the general public. All the aforementioned actions must entwine into a complex chain of lexical variability, lacking unifying criteria of nomenclature.

So how would I recommend a terminological revision? Two extreme (and complementary) approaches are foreseeable: bottom-up and top-down, and both are doomed to fail if ecologists continue to be blasé about a lexicon, which is understandable only within a specialised field of research and among the peers. This is a call for a change in personal attitudes towards language, ideally commencing at the early stages of undergraduate training. The bottom-up approach implies the instigation of regulatory measures at the level of authors contributing to primary literature, while the top-down approach implies harnessing a ‘code of ecological nomenclature’.

Bottom-up approach

In the primary literature, the benchmark should be that a student can understand the main working concepts used in a publication, and the rule of thumb that all concepts named in the title and in the string of keywords are defined explicitly in the main text, and each definition is accompanied by at least one peer-reviewed reference. It might take two lines of the editorial policy of a peer-reviewed journal to achieve this. Even though some journals exemplify this practice, authors are nevertheless often given the freedom to make their own definitions to suit the content of their papers, without necessarily providing references, and this leads to semantic inflation and potential synonymy of existing terms. One word in or out of a definition can translate into a considerable change in meaning. Terminological standards could be lifted by a regular terminology-focused section in peer-reviewed journals, or preferably articulated through a *Journal of Ecological Nomenclature* — it is not difficult to foresee that papers published in such journal would often reach astronomical citation rates, so the journal would certainly be attractive to all authors, editors and scientific publishing companies. Such initiatives would certainly prompt a thorough review and updating of lexicon in ecology.

Top-down approach

The Ecological Society of America once pursued the only major attempt to forge a universal code in ecology by establishing a ‘Committee on Ecological Nomenclature’ (McGinnies *et al.* 1931; Shelford *et al.* 1931). I chronicle the history of this committee in **Appendix A3**. In a nutshell, it operated for more than 20 years and produced a glossary of 789 terms, and six basic principles of nomenclature, which I paraphrase in **Appendix A3**. The rationale of the committee reflects the recognition of a problem, the overall resolution of which would be worth revisiting.

To harness a universal ‘code’, broad actions need to be taken, and promoted with the awareness that language, as our way of expressing ideas, is at the core of any ecological theme. Thus, terminology could be proposed as the central theme of at least one of the major ecological congresses organised by long-running institutions embracing worldwide membership (e.g., British Ecological Society, International Association for Ecology, Ecological Society of America): ‘a global language for a global ecology’. Such a congress, could gather scientists from all fields across the environmental sciences to set the guidelines of the classification scheme of ecological terms and those of an updating protocol as ecological findings progress, and to nominate a committee of authors which would be given the statutory power to implement and look after those guidelines in key peer-reviewed journals, or in a *Journal of Ecological Nomenclature* (see above). The organisation and implementation of such a scheme is fraught with nuances and complexities which would require an entire monograph to describe, and I essentially want to emphasise here that the output would include two main components (*i*) mature terms with a single authorised definition on a central, open-access online database, and (*ii*) authors complying with the ‘code’ as a condition of manuscript acceptance in journals with a label for terminological excellence. Clearly, the efforts involved in getting those initiatives moving would be considerable, surely as much as the ensuing retribution would once the initiatives had been settled. If ecology is ever to become a unified science, a common nomenclature would be a pre-requisite of such an extraordinary and elegant achievement.

1.43 Final statement

It is telling that recent reviews of the determinants of population growth have classified ecological studies, not by intervening processes, population-dynamical types or any other ecological property, but by schools of thought and methods of investigation (Krebs 2002b; Sibly & Hone 2002). Hence concepts, terminology, hypotheses, theories and mechanisms are

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unfortunately subordinated to models, statistics and research protocols. I think that the established split among different and increasingly sophisticated methods to analyse population dynamics will not necessarily help in drawing generalities for population ecology, as pledged by Turchin (2001). If we are all aiming to quantify the relative roles of drivers of population change, we need to bring our research agenda to a more unified framework that is able to integrate readily across taxa, disciplines and schools of thought. Attempts to achieve so (e.g., Berryman 2004) might not initially agree with many, because any conceptual synthesis is indeed a simplification, or because they might be discipline-specific (e.g., fisheries, Rose et al. 2001). Certainly, unresolved matters such as “does age-structure matter in long-term signals of climate and density feedback?” (e.g., Stenseth *et al.* 2004; Berryman & Lima 2006; Coulson *et al.* 2008) leave behind the impression that mathematical development alone drives ecological knowledge at the expense of understanding the mechanisms driving population dynamics. If we acknowledge that “... there are not ten million kinds of population dynamics; rather there are a multitude of essentially trivial variations on a few common themes” (Lawton 1999), those initiatives seeking generalities seem not only worthwhile, but necessary. Science progresses by innovation, but innovation necessitates an ordered body of knowledge to progress.

I think that ‘Ecology’ would benefit from publications where disagreeing experts came together in co-authored publications. Density dependence is an iconic example of how ecological debate can result in confusion rather than clarification of points of view. I have queried authors involved in different disputes about density feedback, and the common understanding is that one party is right and the other is wrong. Colloquial language warns that “two wrongs do not make one right”. Indeed, the standard editorial approach is to give opposing authors the chance to write reciprocal responses, which leave readers (normally with much less insight into the specific matters at discussion than the published authors) with the option of adhering to either view, or staying indecisive. Alternatively, journal editors could give authors in dispute the choice between contentious (current standard) or cooperative papers. I believe journals should be proactive to create conditions for agreement, a feature missing in the editorial policy of all journals of which I am aware of.

Finally, many ecologists like me have chosen ecology as their area of research because our discipline clearly connects nature with us (humans). The modern incorporation into ecology of economic principles and concepts such as those of ‘ecosystem services’, ‘ecological footprints’ or ‘resource prioritisation’ exemplify the recognition of our reliance on natural resources for survival that needs to be internalised in how we globally manage our finances, our wastes and our own rates of population growth. We ecologists have the vast task of

informing the relevance of our findings and their inherent uncertainties to students, citizens, managers and politicians. Through my PhD research, I have found it disheartening that in the frenzy of publishing papers, and intellectually outperforming other schools of thought, we might be diluting our joint power to shift the ongoing trend of environmental degradation that threatens human survival in the long term. I want to reiterate that stronger emphasis on the comprehension, mathematical description and application of density feedback (as one example of many other concepts essential for each field of ecological research), from students to seasoned academics, is not only preferable, but absolutely necessary for ecology to become one of the most influential branches of modern science. Ecology, in seeking the ‘laws of nature’ as applied to biological systems, is a critical discipline for achieving these outcomes, and embodies the functions that science must have in contributing and sharing knowledge towards the improvement of the well-being of our society and the environment.

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APPENDIX A1 - HISTORICAL ACCOUNT

1.44 Chronicle of density dependence

Table 17. Papers on density dependence (DD) with emphasis on cross-discipline conceptual/statistical descriptions, reviews and debates (mostly) in the primary ecological literature. References are accompanied with a synthetic description of content. Sequences of connected papers are cited together as per the date of the last paper in the sequence..

Year	Statistics: tests, models and caveats	Concepts: applications, developments and caveats
1874	(von Nägeli 1874): first model accounting for DD (see Harper 1974)	
1924		(Elton 1924): animal cycles
1927		(Nicholson 1927): seminal conception of population balance
1928		(Chapman 1928): environmental resistance
1928		(Thompson 1929): populations are limited not regulated
1931		(Allee 1927, 1931a): animal aggregation and cooperation
1933		(Nicholson 1933): competition drives population balance
1935		(Smith 1935): <i>density-dependent</i> coined
1941		(Allee 1941): <i>inverse</i> and <i>direct</i> DD coined
1947		(Varley 1947): <i>delayed</i> DD coined
1953	(Nicholson & Bailey 1935; Andrewartha & Birch 1953): critique and expansion of Lotka-Volterra model	(Moran 1953): metapopulation synchrony (later known as ‘Moran effect’: spatially auto-correlated noise) (Neave 1953): <i>depensatory</i> DD coined
1954		(Nicholson 1954a): theory of population regulation (Nicholson 1950, 1954c, b): blowfly experiments
1956		(Reineke 1933; Shinozaki & Kira 1956): laws of plant self-thinning
1957		(Andrewartha 1957; Birch 1957; Hutchinson 1957; Milne 1957; Nicholson 1957): Cold Spring Harbor Symposium in ‘Quantitative Ecology’: face-to-face debate; distinction between fundamental and realised niches (DD-based)

Table 17. Continuation.

1958		(Milne & Solomon 1958; Solomon 1958; Varley 1958): DD jargon (Williamson 1957; Andrewartha & Browning 1958; Williamson 1958): competition challenged
1959	(Morris 1959): <i>k</i> -factor analysis proposed	(Andrewartha 1959; Nicholson 1959; Varley 1959): is DD biologically meaningful?
1960	(Varley & Gradwell 1960): <i>k</i> -factor analysis expanded	
1963	(Smith 1961; Andrewartha 1963; Cole 1963; Smith 1963): DD in apple blossom thrips questioned	
1964	(Watt 1964): different responses condition <i>k</i> -factor estimation	
1966	(Tanner 1966): DD correlation test	
1967	(Southwood 1967): delayed/overcompensatory DD affect <i>k</i> -factor slope	(Andrewartha & Birch 1960): 'theory of the environment' (Hairston <i>et al.</i> 1960; Murdoch 1966; Ehrlich & Birch 1967; Slobodkin <i>et al.</i> 1967): is population regulation universal?
1968	(Salt 1966; Solomon 1968): <i>k</i> -factors can be nonlinear	(den Boer 1968): population persistence equates with spreading the risk [of extinction]
1969	(Hassell & Huffaker 1969; Morris & Royama 1969): <i>k</i> -factors and delayed DD	
1970	(Eberhardt 1970): DD correlation implies no causality (Maelzer 1970): sample size/non-independence and <i>k</i> -factor slope (St. Amant 1970): DD from random numbers	(MacArthur & Wilson 1967; Pianka 1970): <i>r</i> - <i>K</i> natural selection (DD-driven) (Murdoch 1970): population regulation as a return to equilibrium density (Mackerras 1970; Hopper 1987): Nicholson's contribution to ecology (Varley & Gradwell 1970): <i>overcompensatory</i> DD coined
1971	(Kuno 1971): sampling error and <i>k</i> -factors (Luck 1971): mortality and DD mortality in <i>k</i> -factors (Reddingius 1971): DD likelihood ratio/simulation test	(Charlesworth 1971): DD drives natural selection
1973	(Itô 1972; Benson 1973): sampling error and <i>k</i> -factors	(May 1973): carrying capacity = 'probabilistic cloud' of population densities
1975	(Bulmer 1975): DD autoregressive test	
1976	(Anderson 1976; Bulmer 1976): serial correlation	
1977	(Slade 1977): trending affects type I error in <i>k</i> -factors	
1981	(Royama 1977, 1981): autoregressive models	(Gilpin & Ayala 1973; Fowler 1981): DD shape
1982		(Charlesworth 1981; Hassell 1981; Murray 1982): effective and ineffective DD

Table 17. Continuation.

1983		(Hassell 1985; Dempster & Pollard 1986): population regulation and spatial heterogeneity
1984	(Vickery & Nudds 1984): DD simulation test	(Westoby 1984): plant self-thinning reviewed
1985		(Antonovics & Levin 1980; Watkinson 1980; Vandermeer 1984; Pacala & Silander 1985): DD in plants
1987	(Pollard <i>et al.</i> 1987): DD randomization test	(Berryman 1987): carrying capacity = emergent property (Cole 1955; Richards 1955; Wiens 1986; Shorrocks 1987): critiques of Andrewartha's books (Hassell 1986; den Boer 1987; Hassell & Sabelis 1987): population persistence and spatial asynchrony
1988	(den Boer 1986b, a; Latto & Hassell 1987; Pochthke & Kirchberg 1987; den Boer 1988): classical insect DD dynamics revisited	(Mountford 1988): heterogeneity and population/subpopulation DD
1989		(Dennis 1989): Allee effects and extinction (May 1974; Hassell <i>et al.</i> 1976; May 1976, 1989): DD drives both population stability and instability in single-species models (Sinclair 1989): empirical evidence for regulation (book chapter)
1990	(Reddingius 1990; Solow 1990): sample size conditions Bulmer's test	(Hanski 1990): metapopulation regulation
1991	(Stiling 1987, 1988; Brown 1989; Hassell <i>et al.</i> 1989; Stiling 1989; Solow & Steele 1990; den Boer 1991): sample size, random walks and DD detection (Gaston & Lawton 1987; Vickery & Nudds 1991): DD tests revisited	(Reddingius & Boer 1970; den Boer 1974; Roff 1974; den Boer & Reddingius 1989; Reddingius & den Boer 1989; den Boer 1990; Berryman 1991a): population regulation is a case of stabilisation (Strong 1986a; Lomnicki 1987; Strong 1987; Berryman 1991b): population vagueness (Wolda 1989; Berryman 1991a; Wolda 1991): meaning and measurability of carrying capacity
1992	(Crowley 1992): DD attraction test (Turchin & Taylor 1992): DD autocorrelation test	
1993		(Birch & Browning 1993): Andrewartha's contribution to ecology (Hastings <i>et al.</i> 1993): chaos and Lyapunov exponents

Table 17. Continuation.

1994	(Dennis & Taper 1994): Likelihood ratio & bootstrapping DD test (Holyoak & Lawton 1992; Hanski <i>et al.</i> 1993; Holyoak & Lawton 1993; Wolda & Dennis 1993; Schaefer 1994; Wolda <i>et al.</i> 1994): DD detection and meaning (Woiwod & Hanski 1992; Holyoak 1994a, b): delayed DD detection [see 2003 below]	(Murdoch 1994): population regulation is widespread but hard to detect (Murray 1994): population limitation hypothesis
1995	(Fox & Ridsdillsmith 1995; Reddingius 1996): DD tests revisited	(Turchin 1995): population regulation as a long-term stationary probability (book chapter)
1996	(Holyoak & Baillie 1996): longevity and DD detection (Ray & Hastings 1996): spatial scale and DD detection	(Ferrière & Gatto 1993; Doebeli & Koella 1995; Ferrière & Fox 1995; Doebeli & Koella 1996): DD dynamics as an evolutionary output (Saether <i>et al.</i> 1996): reunion of life-history and demographic paradigms (Steele 1985; Halley 1996): coloured (temporally auto-correlated) noise; spectral analysis of time series (Sinclair & Pech 1996): population regulation as a net density effect; regulation does not mean persistence; compensation, harvesting and predation
1998	(Dennis <i>et al.</i> 1998): DD Likelihood ratio and bootstrapping test (metapopulations) (Shenk <i>et al.</i> 1998): sampling error in DD tests (Sibly & Smith 1998): <i>k</i> -factor analysis revisited	(Begon <i>et al.</i> 1986; Latto 1994; Fréchette & Lefavre 1995; Damuth 1998): self-thinning in animals
1999		(Courchamp <i>et al.</i> 1999; Stephens & Sutherland 1999): Allee effects and conservation (Murray 1999b; Turchin 1999): population regulation and hypothesis falsification (Stephens <i>et al.</i> 1999): component/demographic Allee effects (Wolda 1995; Murray 1999a): DD quantification versus testing
2000	(Hunter & Price 1998; Hunter & Price 2000; Turchin & Berryman 2000): delayed DD and auto-correlated environment (Murray 2000b, a; Tyre & Tenhumberg 2000): DD detection from random numbers	(Grant 1997; Benton & Grant 1999; Grant & Benton 2000): DD and elasticities (Koenig 1999; Lundberg <i>et al.</i> 2000): population variability in space and time (Rodenhouse <i>et al.</i> 1997; Hawkins & Berryman 2000; Hunt & Law 2000; Rodenhouse <i>et al.</i> 2000): site-dependent regulation
2001		(Bjørnstad & Grenfell 2001): the ‘noisy clock’, deterministic and stochastic factors in time-series analyses (Murray 2001): lack of evidence for population regulation

Table 17. Continuation.

2002	(de Valpine 2002): incorporating measuring error in state-space models (Montecarlo methods, likelihood, Bayes estimators)	(Beckerman <i>et al.</i> 2002): delayed life-history can cause apparent delayed DD (Boyce 1984; Mueller 1997; Reznick <i>et al.</i> 2002): <i>r/K</i> selection revisited (Eberhardt 2002): demographic paradigm for long-lived homeotherms (Haak 2002): review of the old debate (Hixon <i>et al.</i> 2002): population regulation in open populations (Krebs 1991; Krebs 1995, 2002b): DD versus mechanistic paradigms (Lande <i>et al.</i> 2002): total DD in the life history (Liermann & Hilborn 1997; Osenberg <i>et al.</i> 2002): DD in fish meta-analyses (Sibly & Hone 2002): density, demographic and mechanistic paradigms (Stenseth <i>et al.</i> 2002): DD and density-independence (NAO, ENSO) (Wright 2002): DD and plant-species coexistence
2003	(Turchin 1990; Hanski & Woiwod 1991; Williams & Liebhold 1995; Berryman & Turchin 1997; Williams & Liebhold 1997; Solow 2001; Jiang & Shao 2003): delayed DD and auto-correlated environment	(Lawton 1999; Turchin 2001; Berryman 2003): DD and demographic laws
2004		(Hastings 2004): transient population dynamics (Boyce 1992; Henle <i>et al.</i> 2004; Sabo <i>et al.</i> 2004): DD and population viability (May 1999; Belovsky <i>et al.</i> 2004): ‘what determines population numbers’ is an unanswered ecological question
2005		(Cooper 2001; Cuddington 2001; Jelinski 2005): balance of nature revisited (Coulson <i>et al.</i> 2005): decomposing population growth rates by their components
2006	(Brook & Bradshaw 2006): multi-model DD evidence (Dennis <i>et al.</i> 2006): incorporating process/measuring error in stochastic state-space modelling (likelihood) (Lele 2006): incorporating measuring error in stochastic modelling (composite-likelihood) (Freckleton <i>et al.</i> 2006): sampling error in DD detection and parameter estimation	

Table 17. Continuation.

2007	(Berec <i>et al.</i> 2007): Multiple Allee effects (Hairston <i>et al.</i> 2005; Saccheri & Hanski 2006; Metcalf & Pavard 2007; Pelletier <i>et al.</i> 2009; Post & Palkovacs 2009; Reznick & Ricklefs 2009): rapid evolution; eco-evolutionary dynamics (Kokko & López-Sepulcre 2007): ecogenetic feedback
2008	(Eberhardt <i>et al.</i> 2008): population growth curves (Jennings 2000; Rose <i>et al.</i> 2001; Lorenzen 2008): DD in fisheries (Lindström <i>et al.</i> 2001; Ims <i>et al.</i> 2008): animal cycles revisited (Sale & Tolimieri 2000; White 2001; Berryman <i>et al.</i> 2002; Krebs 2002a; Berryman 2004; White 2004, 2007; White 2008): population regulation versus limitation and determination
2009	(Holt 2009): Allee effects and the establishment/persistence niches
2010	(Ives <i>et al.</i> 2010): accounting for measuring error in times-series analyses (autoregressive moving average) (Sibly <i>et al.</i> 2005; Doncaster 2006; Getz & Lloyd-Smith 2006; Ross 2006; Sibly <i>et al.</i> 2006; Doncaster 2008; Polansky <i>et al.</i> 2009; Clark <i>et al.</i> 2010): DD shape in the theta-logistic model (Bassar <i>et al.</i> 2010): Density manipulations and eco-evo dynamics (Gascoigne & Lipcius 2004a, b; Gascoigne <i>et al.</i> 2009; Kramer <i>et al.</i> 2009; Gregory <i>et al.</i> 2010): evidence for Allee effects (Volkov <i>et al.</i> 2005; Comita <i>et al.</i> 2010): symmetric/asymmetric DD in plant species coexistence
2011	(Fagan <i>et al.</i> 2002; Tobin <i>et al.</i> 2011): DD in invasion theory and pest control (Kokko & Lindström 1998; Boyce <i>et al.</i> 1999; Ratikainen <i>et al.</i> 2008; Harrison <i>et al.</i> 2011): sequential DD, with implications for harvesting
2012	(Herrando-Pérez <i>et al.</i> 2012b): DD terminology revisited (Chapter 2)

1.45 Biogeographical notes on Nicholson and Andrewartha

Alexander John Nicholson was born in Blackhall (Ireland) in 1895. B.Sc. in zoology (1915) and M.Sc. in applied entomology (1920) at Birmingham University (England). Lecturer in entomology (1921) and D.Sc. in insect mimicry (1929) at Sydney University (Australia). And staff member of the CSIRO division of Entomology in Canberra (Australia, 1930), where he became chief (1936) and retired (1960) (see Mackerras 1970; Hopper 1987; Kingsland 1996; Waterhouse 2000).

The origin of Nicholson's views on population regulation sprang from his D.Sc. essay on insect mimicry, presented at his presidential address of the Royal Zoological Society of New South Wales (Nicholson 1927). He posited that the population size of mimetic species depended on compensatory density feedbacks ('success'), whereas mimicry was shaped by natural selection in response to predators ('adaptation'). He subsequently laid the ideas of a general theory of population dynamics, where competition was the main density-dependent factor driving populations towards a balance with their environment (Nicholson 1933). After a hiatus for the Second World War, Nicholson presented empirical evidence for population 'balance' or 'self-adjustment' through laboratory experiments (some lasting for more than two years), in which he subjected blowflies *Lucilia cuprina* to finite and unlimited sources of protein, water and carbohydrates, and to different levels of age-structured population culling (Nicholson 1950, 1954c, b). He presented the theory of population regulation in animals (Nicholson 1954a), with emphasis on insects (Nicholson 1958b). His liaison with the physicist Victor Bailey resulted in two publications describing models of competition (Nicholson & Bailey 1935), and spatial host-parasite interactions (Bailey *et al.* 1962), and a draft book in 1931 entitled: 'The natural regulation of animal abundance'. Kenneth Sisam (Editor for Clarendon Press) justified a delayed review of the book because "... very few biologists are competent to follow the mathematics, and very few mathematicians are competent to follow the biology". The publication of the book failed twice, with considerable intrigues in the review process involving Ronald Fisher, Charles Elton, Jack Haldane and an unknown reviewer for Cambridge University Press, among others (Hopper 1987). Nicholson died in 1969.

Appendix A1

Herbert George Andrewartha was born in Perth (Australia, 1907). B.Sc. in agriculture (> 1924) and assistant entomologist (1929) at the University of Western Australia. Assistant research officer at CSIRO in Melbourne (Australia, 1933). M.Sc. in agricultural science at the University of Melbourne (1935). Researcher at the Waite Agricultural Research Institute in Adelaide (Australia, 1935). And reader-in-charge in animal ecology (1954) and chair of zoology (1962) at the University of Adelaide, where he retired in 1972. Andrewartha died in 1992 (see Birch & Browning 1993).

Andrewartha focused his research on insect pests. He completed a major review on insect diapause (Andrewartha 1952), and provided compelling evidence that weather, food and spatial heterogeneity could govern the dynamics of the Australian plague grasshopper *Austroides cruciata* (Birch & Andrewartha 1945; Andrewartha & Birch 1948) and the apple-blossom thrips *Thrips imaginis* (Davidson & Andrewartha 1948a, b). In alliance with Charles Birch, those findings were integrated into a ‘theory of the environment’ in his first book (Andrewartha & Birch 1954) [later simplified and compacted into a textbook (Andrewartha 1961; Orians 1962; Andrewartha 1970)], further narrowed down to entomology (Andrewartha & Birch 1960). Like Nicholson, Andrewartha pursued a general and applied theory of population dynamics until his latest book ‘The ecological web’ (Andrewartha & Birch 1984) and papers (Andrewartha 1961, 1984). Disproving the demographic role of density dependence (Smith 1961; Andrewartha 1963; Smith 1963) [however restated in the second edition of ‘Introduction to the study of animal populations’ (Andrewartha 1970)], and dismissing competition when not identified with a discernible mechanism (Andrewartha & Birch 1953; Philip 1955; Andrewartha & Browning 1958; Williamson 1958), were fervent features in his writings. Experts said that his books overcooked the arguments and evidence (Richards 1955), were not recommended for undergraduates (Cole 1955; Shorrocks 1987), and “...so non-theoretical, so empirical, so detailed, and so reductionist that many ecologists who relish neat ideas might dismiss it as irrelevant” (Wiens 1986). Even after his death in 1992, Andrewartha’s views of population ecology have fared quixotically in ecology.

Although Nicholson and Andrewartha cited and rampantly criticised each other in their publications on demography, the two only direct confrontations in the ecological literature (clearly distilling their views on population dynamics) occurred in the “*Cold Spring Harbor Symposium on Quantitative Ecology*” (Andrewartha 1957; Nicholson 1957), and *Nature* (Andrewartha 1959; Nicholson 1959) (see **Chapter 6**, and **Table 17** in this appendix).

APPENDIX A2 - QUESTIONNAIRE

1.46 Statements

Table 18. Set of 58 closed statements, classified into 3 parts, as used in the questionnaire survey done by 136 ecologists. DD = density dependence or density-dependent

Regulation

1. Regulated populations show a tendency to return to equilibrium population size
 2. Predation and competition are the main causes of regulation
 3. Poorly regulated populations are likely to be subjected to unbounded fluctuations
 4. A positive relationship between mortality and population size is indicative of regulation
 5. Persistence is a feature of well-regulated populations
 6. Demographic Allee effects contribute to population regulation
 7. Regulation can be inferred by measuring the strength of density-dependent (DD) feedbacks
 8. Regulation involves the processes that prevent population growth
 9. Regulation can be proved if increasing population size reduces fecundity
 10. A population is regulated when the effect of density-dependent factors overrides that of compensatory factors
 11. Evidence for regulation derives from studies where a convergence to an equilibrium population size is found
 12. Regulation is a long-term stationary probability distribution of population densities
 13. Population structure across individuals (size, age, stage and/or sex) is required to determine the causes of regulation
 14. Well-regulated populations can go extinct when faced by extreme stochastic events
 15. Regulation can occur only where both reproduction and survival are affected by population size
-

Density dependence

16. Density dependence (DD) is a negative feedback of density on population growth rate
 17. Compensation and Allee effects are forms of inverse DD
 18. Population size cycles may result from DD feedbacks
 19. Predators and parasites are the main causes of delayed DD
 20. DD can never drive a population extinct
 21. Direct DD and negative DD represent the same type of density feedback
 22. DD is evidenced by a relationship between density and a demographic rate
 23. Within a given area, DD may be detectable only at one particular spatial scale
 24. DD is the main process contributing to the persistence of populations
 25. Overcompensation is not a type of DD
 26. Density dependence implies there is some dependence of per capita growth rate on present and/or past population densities
 27. The harvest of a population (e.g. hunting, fishing) can compensate for (i.e. reduce) DD mortality
 28. DD can stabilise population fluctuations around equilibrium population size
 29. The term density-dependent regulation is a tautology (i.e. redundant)
-

Table 18. Continuation

Regulation versus limitation

30. Limitation is the process which sets the equilibrium population size
31. Populations persist because density-independent factors are so spatially variable that at least one subpopulation is likely safe from extinction at any given time
32. Population limitation has been neglected in ecology because it is theoretically very dull
33. Competition determines which best competing individuals survive not how many
34. The success in investigating population limitation is that you do not need to determine whether a particular factor is density-dependent (DD) or not
35. Limitation has to do with the primary factor determining population size, while regulation is a population response to limitation
36. A long-term growth rate of zero need not indicate that population numbers are regulated
37. Weather-driven changes in the availability of food determine the changes in animal populations
38. All mortality factors acting on a population are necessarily DD
39. Researchers have been unable to identify mortality factors acting in the field in a negative feedback manner
40. The regulation/limitation controversy does not rest in the theory but in the application of both concepts to real populations
41. The controversy was unnecessary, scientists interested in abundance look at limitation while those interested in feedback mechanisms look at regulation
42. The magnitude of environmental factors (e.g. weather) is density-independent but the demographic response of populations to them can be DD
43. Predators are not effective enough to regulate prey numbers
44. Larger populations are more likely to hold individuals resistant to environmental harshness (e.g. weather extremes) than smaller populations
45. Populations are not regulated, but limited by the capacity of the environment to support only some individuals

Controversies

46. Density dependence (DD) is necessary but not sufficient for population regulation
 47. Testing for DD is unnecessary, since DD is derived through pure logical deduction from the persistence of populations
 48. Models for DD regulation of population size do not necessarily depend on the concept of equilibrium population size
 49. Density is not a close predictor of the main causes of population fluctuation (e.g. food supplies, social space or predation pressure)
 50. DD factors only operate at very high or at very low population densities
 51. Proving a relationship between density and population growth rates does not guarantee the existence of DD factors regulating a population
 52. Time series analysis of census data can be used to draw hypotheses about the causes of regulation but not to test those hypotheses
 53. Analysing DD in populations that show a limited range of densities is largely futile
 54. DD remains popular in ecology because it is amenable to modelling statistics
 55. The causes of regulation can solely be identified through manipulative experiments
 56. Theoretically, DD implies only the existence of an equilibrium, which need not be stable or regulated
 57. Equating regulation with balance is misleading
 58. Time series analysis of census data can provide a useful description of the relative strength of DD
-

1.47 Respondents

Table 19. The total of 136 ecologists who participated in the questionnaire survey.

Airoldi JPA	Switzerland	Griffen B	USA	Mueller LD	USA
Anderson KE	USA	Griffis-Kyle KL	USA	Muenkemueller T	Germany
Angulo E	Spain	Gunnarsson G	Sweden	Myers JH	Canada
Argasinski K	Poland	Haak C	Germany	Mysterud AM	Norway
Armstrong DP	New Zealand	Hagen SB	Norway	Obbard ME	Canada
Balbontín J	Spain	Hario MK	Finland	Oro D	Spain
Begon M	UK	Harmand J	France	Owen-Smith N	South Africa
Beja P	Portugal	Hassell MP	UK	Pauli JN	USA
Berec L	Czech Republic	Hawkins BA	USA	Penteriani V	Spain
Berryman AA	USA	Hernández MJ	Venezuela	Pimentel D	USA
Bjørnstad ON	USA	Hewison AJM	France	Rabie PA	USA
Botsford LW	USA	Hilker FM	Portugal	Ray C	USA
Bowman J	Canada	Hixon MA	USA	Reed AW	USA
Bravo R	Spain	Holt RD	USA	Reed DH	USA
Burgess MD	UK	Holyoak M	USA	Reluga TC	USA
Burrows MT	UK	Hunter MD	USA	Ridley J	UK
Butler MJ	USA	Ives AR	USA	Rodel HG	Germany
Cameron TC	UK	Jager HI	USA	Roland J	Canada
Cappuccino N	Canada	Jansen VAA	UK	Sale PF	Canada
Carrete M	Spain	Jeschke JM	Germany	Salvidio S	Italy
Chamaillé-Jammes S	France	Johnson DW	USA	Sarda R	Spain
Clark RA	USA	Johnson MTJ	USA	Satioh T	Japan
Coulson T	UK	Johst K	Germany	Sendra ED	Argentina
Courchamp F	France	Jonzén N	Sweden	Serrano D	Spain
Coyle DR	USA	Kisdi E	Finland	Serrano E	Spain
Damgaard C	Denmark	Kjellander P	Sweden	Shenbrot G	Israel
de Vladar HP	The Netherlands	Kluth C	Germany	Sletvold N	Norway
Del Piero D	Italy	Kohler SL	USA	Smith GC	UK
Denkinger J	Ecuador	Kokko H	Finland	Smith RH	UK
Dexter KG	USA	Krasnov BR	Israel	Solbreck C	Sweden
Donahue MJ	USA	Krebs CJ	Canada	Steen H	Norway
Eberhardt L	USA	Lafferty KD	USA	Sulkava RT	Finland
Ehrlén J	Sweden	Le Galliard JF	France	Testa JW	USA
Einum S	Norway	Lehikoinen EA	Finland	Tobin PC	USA
Ellner SP	USA	Lewis OT	UK	Todd CR	Australia
Etnier MA	USA	Lima M	Chile	Tremblay JP	Canada
Festa-Bianchet M	Canada	Lindberg WJ	USA	Tyre AJ	USA
Forrester GE	USA	Lindén TA	Finland	Valkenburg P	USA
Fowler CW	USA	Lloyd-Smith JO	USA	Vincenzi S	Italy
Fowler NL	USA	Lobón-Cervía J	Spain	Walde SJ	Canada
Fryxell JM	Canada	Lucero Y	USA	Ward DM	USA
Getz WM	USA	Lundberg P	Sweden	Ward EJ	USA
Gibson AJF	Canada	Marschoff ER	Argentina	White JW	USA
Girondot M	France	Matthysen E	Belgium	Williams DW	USA
Grant A	UK	Møller AP	France		
Greene CM	USA	Morita K	Japan		

1.48 **Comments on population limitation****Table 20.** Selected comments made by questionnaire respondents on the concept *limitation*.

-
- Berryman:** “The process of negative feedback (regulation) is called density dependence when talking about population dynamics; i.e., when population density decreases then growth increases and vice versa. When discussing the mechanism we generally call it regulation, but when discussing the fixed point, or more correctly the factors which determine it, we normally call it limitation. Thus limitation and regulation discuss different aspects of the same thing. This is the basics of feedback control of any first order system. In second of order feedback, the two variables (e.g., pest and parasitoid numbers) are mutually linked so limiting factors do not really apply”
- Cameron:** “What controversy? It was never really controversial, just a ‘few’ objectors”
- Coulson:** “A process can limit population growth by reducing survival or fertility rates. Predation, disease, culling can all do this. A limiting process does not need to be the dominant regulating process”
- Einum:** “Limitation of the environment to support only some individuals equals regulation... I would not consider limitation a ‘process’. One can talk about limiting factors, but not limiting processes”
- Fowler (NL):** “We [plant population ecologists] don't use limitation as a technical term much, so I didn't answer questions using it”
- Holyoack:** “All populations are limited by the environment” is trivially true”
- Jager:** “I wasn't aware of there being a controversy [limitation vs regulation]” (H. I. Jager, pers. com.)
- Jonzén:** “I do not use the term limitation, it adds to the confusion more than it helps researches in their work”
- Kjellander:** “Only those limiting factors that show density dependence have the theoretical capability to stabilize population size... There is no controversy in my field of knowledge any more [mammal population ecology]”
- Matthyesen:** “I am not very familiar with the concept of ‘limitation’. For me DD inherently leads to an equilibrium population size and in some conditions to an upper limit to population size”
- Lehikoinen:** “It depends on how equilibrium is defined. Limitation results in an average population size, which may look like an equilibrium size, but it is a secondary impression and not a true equilibrium size”
- Lima:** “Regulation is not a ecological property of natural populations, is just the emerging dynamics when there is a limiting factor and individuals must compete for the access to this factor, resource, etc.”
- Lindberg:** “Clarity in the relationship between limitation and regulation is needed, and the focus often depends on the interests of the researchers”
- Owen-Smith:** “Density dependence is necessarily associated with a population level at which the growth rate becomes zero but this limitation on abundance need not be a stable equilibrium”
- Reed:** “Some populations are regulated, some are limited”
- Sale:** “I do not know of any mechanisms other than density-dependent negative feedback that reliably control population density, but there are plenty of other mechanisms that drive population density (and sometimes these mechanisms will even drive it to remain apparently constant over relatively long periods of time)”
- Solbreck:** “I am uncertain about the exact meaning of limitation, for example to what extent it involves lagged feedback”
- Williams:** “I must confess that I am not familiar with the term ‘limitation’. It sounds like what we used to call ‘carrying capacity’.”
- Witting:** “Any study that attempts to explain changes in the abundance of a species by correlated changes in one or several ecological factor/s is in fact a study on limitation (although these studies may not have detected the true reason for the abundance change). Unlike regulation, studies on limitation do not have to detect density dependence. They only need to show that the abundance responds to changes in the limiting factor under study... Limitation is only part of the process [that sets the equilibrium population size]... Limitation is certainly not neglected in the literature; people just don't necessarily know that they study limitation”
-

1.49 Quotes on population regulation

Table 21. Selected quotations made by ecologists on the concept *regulation*

-
- Berryman (1991a):** "...there seems to be no fundamental conceptual differences between the notions of stabilization and regulation"
- Berryman *et al.* (2002):** "...populations being regulated within a basin of attraction will tend to exhibit one or more of the following behaviors in stochastic environments: 1. return tendency... 2. Stochastic boundedness... 3. Regular oscillations... 4. Trends and discontinuities"
- den Boer (1987):** "'Stability', in the sense of persistence, is not only promoted by processes that feed back upon the starting condition (norm) or some equilibrium value (regulation), e.g. by some kind of density dependence, but also by 'spreading of risk' (den Boer 1986b), i.e. statistical levelling of fluctuations, which may make a major contribution to 'staying longer within limits' (Reddingius & Boer 1970; Reddingius 1971) The latter kind of stability, in which feedback processes need not be involved, is here called 'range stability'"
- den Boer and Reddingius (1989):** "...staying between limits is called 'stabilization' and only when this results from density-dependent processes it is considered 'regulation'"
- Elliott (1994):** "...the term density dependent regulation is frequently used, even though it is a tautology, but the term density-independent regulation is a contradiction and should be avoided; density-independent persistence is more apt"
- Hanski (1990):** "...much confusion has been created by the claim (den Boer 1968, 1987) that metapopulation regulation or persistence requires no density dependence at the level of local populations"
- Hixon *et al.* (2002) :** "...by definition, a population is regulated when it displays three closely related phenomena: (1) persistence, (2) boundedness, and (3) return tendency (Murdoch 1994; Turchin 1995)"
- Murdoch (1994):** "Murdoch & Walde (1989) proposed as criterion for boundedness, and hence regulation, that the cumulative variance of logarithmic population densities should approach an upper bound... persistent species must consist of regulated single populations or regulated collections of subpopulations"
- Murdoch and Walde (1989):** "...regulation cannot occur in the absence of density dependence: such a population in a stochastic environment will drift at random to zero or infinity. Density dependence... prevents this drift by creating an equilibrium"
- Sale and Tolimieri (2000):** "...persistence equals density dependence at some time or place... suggests that density dependence will ensure that populations have both lower and upper bounds"
- Sinclair (1989):** "By far the most abundant evidence for regulation comes from measures of density dependence"
- Sinclair *et al.* (2006):** "...negative feedback imparts stability to the population"
- Sinclair and Pech (1996):** "...although noting the original definition of regulation, namely that populations are regulated when they experience density dependence (negative feedback), they prefer to argue that populations are regulated if they are kept within limits (den Boer & Reddingius 1989)... interpretations that equate regulation with persistence of populations (Reddingius & den Boer 1989; Hanski 1990; Krebs 1995) merely lead to confusion"
- Strong (1986a):** "...the model of stochastic boundedness (Chesson 1978) is a particular interesting alternative [to mathematical theory of equilibrium and stability] because it uses 'vague' density relationships"
- Royama (1977):** "...if a given population process is such that inequality 2.10 is satisfied, and hence the population is persistent, we may call such a state 'the regulation of the population' in the stronger sense"
- Turchin (1995):** "...if we define equilibrium broadly as a stationary probability distribution, then being regulated and having an equilibrium are one and the same thing. The whole issue of equilibrium versus nonequilibrium dynamics becomes a semantic argument (Berryman 1987)... this is the same as May's (1973) stochastic equilibrium probability distribution and Chesson's (1982) convergence in distribution to a positive random variable"
-

APPENDIX A3 - TERMINOLOGY: EXAMPLES AND COMMITTEE

1.50 Examples of proposed terminology

In the following examples (censuses and photos of species shown in **Figure 7**), my interest is in the terminology to name hypothesised density feedbacks irrespective of their reported evidence.

The Bay checkerspot butterfly (*Euphydryas editha bayensis*): McLaughlin *et al.* (2002) studied the effects of rainfall and ensemble density feedback on the checkerspot butterfly at the Jasper Ridge Biological Reserve (California, USA). The population of a ~ 3-ha patch of heterogeneous serpentine grassland (known as JHR) declined from the 1960s to extinction in 1998 (**Figure 7a**). These authors fitted models incorporating rainfall with and without immediate (first-order) and delayed (second-order) density feedback to explain change in population growth rate (modelled response). Most variation in population growth rate was accounted for by a model including rainfall in the precedent year and immediate feedback, giving statistical support for an Allee effect (therein referred to as ‘endogenous factor’). However, the authors posited that the Allee effect was only apparent, and that the observed dynamics resulted from the interaction of weather with topography.

The Dungeness crab (*Cancer magister*): Higgins *et al.* (1997a; 1997b) modelled the catch of Dungeness crabs for different ports of western USA between the 1950s and 1990s. These authors used a model framework allowing for environmental (stochastic) forcing and harvesting, and different component feedbacks where age-specific egg production and survival were compensatory for changes in the abundance of different age classes. Despite the observed erratic fluctuations of population numbers (see landings at Eureka and Crescent City in **Figure 7b**), Higgins *et al.* (1997b) asserted that there was no evidence for chaos, suggesting that density-dependent mechanisms were compensatory, not overcompensatory.

The stoat (*Mustela erminea*) and the lemming (*Dicrostonyx gorenlandicus*): Gilg *et al.* (2003) modelled the cyclic dynamics of lemmings in the tundra of Karup Valley (Greenland) through the numerical and functional responses of four predators [snowy owl *Bubo scandiaca*, long-tailed skua *Stercorarius longicaudus*, arctic fox *Alopex lagopus*, and stoat]. They observed a delayed compensatory feedback of the stoat’s numerical response on lemming density at snowmelt the year before (second-order lag). The authors concluded that stoats destabilise and the other three predators stabilise lemming populations, eliciting prey

density peaks every four years (**Figure 7c**). Since the modelled response was lemming population numbers, implicitly this study looks at ensemble density feedbacks originating from predation-driven mortality.

The Spanish imperial eagle (*Aquila adalberti*): Ferrer and Penteriani (2008) studied component density feedbacks on fertility rates of the Spanish imperial eagle in Mediterranean scrubland of the Doñana National Park (Andalucía, Spain). This population recovered from long-term poaching in the 1950s (**Figure 7d**). Since 1959, a compensatory density feedback on number of fledglings per pair was linked to competition for a gradually decreasing number of high-quality nesting sites; the observed phenomenon was that the population increased in numbers. The population experienced stability at around 15-16 pairs in the 1970s and 1980s. In the following decade, a decrease in population numbers coincided with a pronounced increase in adult mortality, and a depensatory density feedback (therein termed as ‘positive density dependence’) on fertility arose from less-fertile juvenile mates, triggering a reduction in the reproductive rate.

1.51 ESA committee on ecological nomenclature

Synthesis

In response to concerns on terminological issues of members of the Ecological Society of America (ESA) in several of the Society’s meetings prior to 1930, this institution appointed a *Committee on Ecological Nomenclature* which operated for over 20 years. The *Committee* was created in Cleveland in January 1931 (Shelford *et al.* 1931) and, only two months later in Pasadena, its rationale was formally stated: “...the Ecological Society cannot escape a considerable degree of responsibility for developing or promoting suitable terminology in its field and for encouraging accuracy and harmony in the use of particular terms and expressions throughout its membership. Furthermore, such encouragement tactfully applied might be expected to have helpful influence amongst biologists not directly affiliated with the Society, though using similar language at times...” (McGinnies *et al.* 1931).

The two principal aims of this committee were (i) to “serve as a clearing house, or discussion center, of ecological terms” (ESA 1933c), and (ii) to provide a list of terms including definitions, origin, synonymy, cross-references and equivalents in foreign languages (ESA 1936) which should be instrumental “to aid in the clarification of ecological terminology and to encourage more precise usage of terms” (ESA 1939). Crucial to this task was reaching terminological consensus among experts and disciplines, and a persistent

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challenge the slow communication among panel members located in distant states, and between those and the entire ESA membership. Three different provisional lists of definitions of terms were subsequently compiled, refined, and mimeographed by the panel members (ESA 1933a, 1934a, 1935c), and exhortations to enlarge the glossary of terms were actively disseminated across ESA members, discipline-focused subcommittees, and one note in the journal *Science* (Hanson *et al.* 1931). The final product was the monograph *Nomenclature*, which covered 789 terms and six basic principles of nomenclature (Eggleton *et al.* 1952). The *Committee* was dissolved shortly thereafter.

The Committee in time

The evolution of the enterprise can be traced through the pace of ESA meetings as prospected in the following [in the Bibliography, I cite the ESA references to the relevant proceedings, as well as to the issue of *Ecology* where part or all of the proceedings were reported]:

Cleveland, 1930-1931: Within the ‘Symposium on environmental units and their terminology’ Arthur S. Pearse pondered: “Ecology is often superficial and inaccurate. Environments and societies are so complex that they are not always clearly understood. At times standards for studying and for recording results are too low. In reports ecologists may use too few or too many technical terms, or coin new terms which never gain general acceptance. Ecological knowledge is at present not well organised. There are many indefinite or ambiguous terms in use. A standing committee which would consider terms and publish annual lists of new terms, limitations, and accepted usages might help the progress of ecology” (ESA 1930). Attending the later recommendation, such a committee was formally created in 1931 with a panel of five members featuring Herbert C. Hanson, James C. Needham, Walter P. Taylor, Arthur. G. Vestal, and Wynfred E. Allen (chairman) (Shelford *et al.* 1931).

Pasadena, 1931: A statement was made that “...the Committee is agreed, and probably most members of the Society concur, that it is not practicable or desirable to attempt to force improvement by legislation, but it does seem possible that improvement may follow responsible suggestions and formal recommendations if they can be offered in a form suited to existing needs” (McGinnies *et al.* 1931). The committee distributed a query among ESA members to provide (i) key terms with loose usage, (ii) views as to whether the terminology should be regulated uniquely across, or separately within, disciplines (e.g., botany, zoology, agronomy), (iii) suggestions about terms to distinguish between waxing and waning phases of environmental influences (McGinnies *et al.* 1931). The query was also disseminated in a paper published in *Science*: “The committee is trying to work in the interest of all who make

use of ecological terms, therefore it requests that any individual who cares to make a suggestion will give it to one of the members of the committee, preferably before the New Orleans meeting” (Hanson *et al.* 1931).

New Orleans, 1931: A list of nine generic categories into which terms could be classified into was compiled, i.e., ‘habitats’, ‘combinations of influences’, ‘items of influence’, ‘changing influence’, ‘control of influence’, ‘degree of influence’, ‘character of observation’, ‘direction of influence’, and ‘group of unrelated organisms of similar influence’ (ESA 1932). The New Orleans proceedings pointed out that “...on account of the wide geographical separation of the members of the Committee considerable time was consumed in its organisation and in communications necessary to its operation” (ESA 1932).

Atlantic City, 1932: The committee panel renewed five members, with Herbert C. Hanson as chairman (ESA 1933b), noting that “...the work of the committee on Nomenclature proceeds slowly, especially when the members are widely scattered” (ESA 1933c).

Boston, 1933: A mimeograph of ‘Tentative Glossary of Ecological Terms’ with 75 terms was presented (ESA 1933a), five basic principles of nomenclature were formulated (ESA 1934a; principles are listed below), and one committee member was replaced. The Committee had already targeted a consensual nomenclature across different disciplines in that “...the Committee is attempting to point out the usage of the same term in related fields as agronomy, soil science, forestry and meteorology in order to bring about greater uniformity. Where different terms are used for the same concept or where a term has different meanings in various fields the Committee points out such differences and attempts to harmonise them. Occasionally, it has seemed desirable that the Committee recommend to the Society the desirability or undesirability of certain terms, not with the idea of being dogmatic or arbitrary, but to aid in the development of ecological terminology. The Committee hopes that these definitions will stimulate discussion and correspondence” (ESA 1934c).

Pittsburgh, 1934: The Boston glossary was subjected to review (‘Revised List No. 1’), while the committee drafted definitions of a second glossary (‘Preliminary List No. 2’) (ESA 1934b, 1935b): “Members of the Ecological Society may obtain a mimeographed copy of each list from the chairman, at the North Dakota Agricultural College, Fargo. Please enclose a 3c stamp for each list”.

St. Louis, 1935-1936: A third list of terms was collected (‘Preliminary List No. 3’, 11 pages) and the second list had been revised (‘Revised List No. 2’, 17 pages), whereas another list of “soil terms useful in ecology and needing clarification” was also gathered [3 pages] (ESA 1935a, 1936). “References have frequently been given in the report for the purpose of

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showing the origin of the particular definition and to furnish leads to those interested in further study of the terms. No attempt has thus far made to give credit to the man who coined the term” (ESA 1936). Each list could be requested from the chairman for 6 cents in stamps.

Atlantic City, 1936-1937: The committee reflected upon aiming at a potential print-out of a single preliminary list of terms (ESA 1937), though “...this should not be done until the material has been thoroughly edited, and the forest soil terms included by a representative Committee member who have sufficient time and interest to devote to this” (ESA 1937).

Richmond, 1938: Some 650 terms had been classified whether defined or ‘suggested for defining’ in one single list (ESA 1938), the six principles of nomenclature were recovered from the 1933 Boston proceedings (see above), and further recommendations were made for a future printed publication (ESA 1939). “Many terms have been purposely omitted for various reasons. For instance: certain words have had such limited usage that their consideration by the committee did not seem justified” (ESA 1939). A Soil Science Subcommittee of 4 members, chaired by Joseph Kittredge, Jr., contributed most soil terms. By 1940, Frank E. Eggleton was appointed to replace Herbert C. Hanson as chairman (ESA 1940).

Dallas, 1941: The history and work of the committee were reviewed, with two new members being elected for a total panel of 7 committee members (ESA 1942). “A more ambitious program of intra-committee criticism and revision of definitions, which has been in effect during the past year, has greatly increased the amount of work and consequently slowed the progress” (ESA 1942).

After a decade of dedication, the enterprise had settled as “...one of the standing committees of the Society” (Dreyer *et al.* 1948), and members would further reflect on the slowness of communication among members by ordinary mail across USA states. The *modus operandi* mostly had consisted of panel members revising the list of terms, submitting it to the chairman and receiving replicate revised versions from the chairman (ESA 1943). New terms seemed to be incorporated to the glossary following continuous exhortations to the entire ESA society to contribute. A fourth list had been in preparation for 18 months by the end of 1943 (ESA 1943) and would be in the next few years (ESA 1944, 1945; 1946; Dreyer *et al.* 1947; 1948). A final monograph (Eggleton *et al.* 1952), presenting a glossary of 789 terms with definitions, was published for the Ithaca ESA meeting though, curiously, this is not mentioned in the proceedings from that meeting (see Test *et al.* 1953).

A new panel was elected in 1953 with F. Raymond Fosberg as chairman (Buell *et al.* 1954), and shortly after that, it was declared that “...in view of the reluctance of Dr. Eggleton to have an evaluation [of the glossary] made by this committee, I suggest that the Society

dissolve the Committee on Nomenclature as of no further utility” (Reed *et al.* 1956). I could only find one further quote to this committee in the proceedings of *The Bulletin of the Ecological Society of America*: “...in accordance with instructions from Council at its East Lansing meeting in September, 1955, the Secretary had the ‘Report of the Committee on Nomenclature 1947-1952’ reproduced by an offset process, and this is now being offered to anyone interested at cost” (Hodson *et al.* 1957). Clearly, the Committee on Ecological Nomenclature reached its peak with the publication of Eggleton *et al.*’s (1952) monograph and faded away thereafter.

Output

Along with the glossary, the six principles propounded by the *Committee on Ecological Nomenclature* to improve terminological standards in ecology would certainly be of use if that enterprise was to be re-tackled in the future, as I propose in **Chapter 2**. They are paraphrased below:

- Natural growth of ecological terminology should not be hampered by rules. The Committee has attempted, however, to serve as a clearing house and to point out, especially to beginners in the field, what is considered to be good usage. Precedent, and approval of authoritative bodies are important in the selection of terms and thereby in the development of any science.
- Restricted scientific usage should not violate common literary or general scientific usage.
- Words long used in a broad sense should not be given a new and arbitrarily restricted, or special, meaning.
- Uniformity of usage is desirable within any one field and in closely related fields, such as forestry, agronomy, ecology, physiology, soil science, meteorology and geography. If a relatively new word is commonly accepted in one branch of science it should be adopted in other branches when it is needed there.
- New words should be coined only when there is a distinct need. It is desirable that ecological literature be intelligible to as wide a field of readers as possible. It is not necessary to have a separate term for every slight difference of meaning.
- Words are tools of thought. An exact term may aid in establishing a clear-cut, distinct concept. On the other hand, the too-early coining of new terms or definitions may actually foster ambiguity and inaccuracy. Much care must be given to the choice of appropriate terms so that the writer or speaker may convey to others his exact shade of meaning. The Committee believes that the definitions given in this list will help to make ecological terms more efficient tools of thought.

APPENDIX A4 - LIFE HISTORY: DATA

1.52 Base data

In **Chapter 3**, I used the dataset from Brook & Bradshaw (2006) and Brook *et al.* (2006), including 1,198 time series of population abundance from primary scientific literature, books, and the GPDD. These included:

- NERC Centre for Population Biology, Imperial College. *The Global Population Dynamics Database* [GPDD]. <http://www.sw.ic.ac.uk/cpb/cpb/gpdd.html>.
- Patuxent Wildlife Research Center, USGS (USA), *Amphibian Count Database (ACD)*. <http://www.mp2-pwrc.usgs.gov/cvs/ampCV/>.
- United States Fish and Wildlife Service (USFWS), *Waterfowl Population Status, 2002* (Appendix F. p.46-47). <http://migratorybirds.fws.gov/reports/reports.html>.
- Cody, M.L. and Smallwood, I.A., eds. (1996). *Long-term Studies of Vertebrate Communities*. Academic Press, San Diego.
- Primary literature found by searching for key terms (e.g., ‘time series’) or known, well/studied species.

I report the number of time series per taxa and some descriptive statistics in **Table 6** and **Table 22**, respectively.

Table 22. Summary statistics (averages by taxonomical groups) of the population dynamics time-series dataset of 1,198 species, where n = number of species, q_t = number of annual observed transitions in population size, r_a = average rate of population change (log annual ratio of successive densities), σ_r^2 = variance of r_a , CVN = coefficient of variation in population size.

Taxonomic group	n	q_t	r_a	σ_r^2	CVN
All species	1,198	22	0.005	0.733	0.610
Invertebrates	639	19	0.010	0.719	0.604
Vertebrates	529	26	0.000	0.680	0.606
Aquatic invertebrates	36	19	0.019	1.155	0.833
Birds	225	27	0.002	0.412	0.497
Fish	115	21	-0.001	0.808	0.756
Herpetiles	37	14	-0.034	1.121	0.731
Insects	603	18	0.009	0.694	0.591
Mammals	152	31	0.005	0.873	0.625
Plants	30	13	-0.014	1.940	0.817

The GPDD is the largest database of population time-series data currently available (Inchausti & Halley 2001). It contains > 5,000 separate time series for over 1,400 animal and plant species. This database was used as my foundation data source, with additional time series being added for any species not already present in the GPDD, or where superior time series were available. For those intending to use resources such as the GPDD to make comparisons between species and across taxonomic groups, it is important that the data be brought into a common, consistent format, by considering caveats in data structure and content (**Table 23**) as well as stringent criteria for data selection (**Table 24**).

1.53 GPDD caveats

Table 23. Caveats considered in retrieving the fraction of time series from the GPDD.

Taxonomic bias. Some species or taxonomic groups were well-studied and had many long-term time series available and so were over-represented in the GPDD compared to more poorly studied taxa.

Broad taxonomic status. Many single-species time series had poorly specified taxonomy such that they were only identifiable to the level of family or genus.

Pooled data. Some time series gave the combined abundance of a number of different species within a loosely defined taxonomic group, e.g., deer, aphids.

Study period. Study lengths varied from several months to 151 years.

Sampling time scale. Sampling frequencies included daily, monthly, seasonal, annual or even generational (with time intervals unspecified).

Population-size types. Measures of abundance varied and included total population census, census of closed regional subpopulations, sampling within large open populations, counts of specific demographic segments (eggs, juveniles, adults, calling males, nesting females), measures of density, indirect measures of species presence (scats, tracks), trapping rates, number of individuals harvested, total mass of harvests, and many other indices.

Population-size transformations. Many abundance measures were transformations of population size, including various ratios, logarithms and power relationships.

Population-size ranges. Measures of abundance varied across ten orders of magnitude.

Zero population sizes. Many time series contained zero abundance measures, which may have reflected extinction, extirpation, migration, cryptic behaviour, inadequate sampling methods or insufficient sampling effort. The nature of zero values was usually unspecified.

Sampling corrections. Some abundance measures included corrections for sampling intensity, but many time series were uncorrected and provided no means of accounting for this.

Sampling methods. Sampling methodologies were diverse and difficult to classify without reference to the primary literature. Efforts by database managers to classify data type systematically, sampling units, and source units were clearly hampered by inconsistent reporting of such information in the source literature and the subjective nature of their classification system (leading to > 300 different classifications for the ~ 5,000 time series).

Data quality. Similarly, efforts by database managers to produce measures of the quality of each time series were also subjective.

1.54 Criteria for data selection

Table 24. Criteria fulfilled by each GPDD time series selected in this study.

Species identity. Attributable to a single, identifiable species. Time series of organisms identifiable only to the genus or family level and those which were a combined abundance of several species were excluded.

Multi-annual population-size estimates. If multiple abundance measures were provided within each year, then these were averaged to produce a single measure for each year.

Back-transformation. All transformed abundance measures (mostly logarithms) were back-transformed to produce values that were directly proportional to population size.

Zero population sizes. Where a single zero or sequence of zeros occurred in a time series, the first zero in each run of zeros was converted to the lowest non-zero abundance measure for that time series so that it could be included as a low value for analysis (i.e., to permit the calculation of overall population growth rates). This assumes that single zeros are indicative of low abundance, below the threshold for observation. Preserving them as a low, non-zero value allows the pattern of the data to be preserved, whether it was a decline to low abundance or recovery from it. Where there were two or more consecutive zeros, continued failure to observe the species may indicate migration, extirpation or inadequate sampling strategy. Given this uncertainty and the fact that successive zeros are uninformative for analyzing species' population dynamics, all remaining zeros in each run of zeros were treated as missing data. The sensitivity of my results to these zero-abundance observations is negligible (see Brook *et al.* 2006).

Time-series length. Time series were required to contain at least eight annual abundance transitions (at least nine years long if there were no years of missing data). For example, a ten year study with missing data for the sixth year would have been excluded because it contained only seven annual transitions.

Population-size variability. Abundance measures in each time series were required to fluctuate over at least four different values. Time series exhibiting just two or three abundance states (due to low abundance or coarse measurement indices) were excluded.

Time series per species. To overcome the over-representation of a small number of well-studied species, only a single time series was allowed for each species. However, this produced the challenge of selecting a single 'best' time series from those available. This was achieved by a systematic quality scoring system designed to select the time series that gave an optimal balance of reliability, length and population size. Reliability scores were assigned subjectively to each time series by the managers of the GPDD on a scale of 1 (harvest data for large with no indication of catch effort) to 5 (census data with accurate abundance values). Reliability scores were useful for identifying high-quality time series for each species, but many species had several time series with high reliability scores that varied substantially in duration, and/or number of individuals surveyed. To obtain a balance of reliability score, time-series length and size of the surveyed population, a quality index was calculated for each time series and only the highest-scoring time series was kept per species.

$Quality\ Score = [Reliability] + [TimeScore] + [PopScore] \div 2$, where:

- [Reliability] = subjective reliability score given in GPDD and similarly to new datasets, with values ranging from 1 (poor) to 5 (excellent).
- [TimeScore] = standardise (\log_e ([Timesteps] + [Changes])). Maximum and minimum values restricted to ± 2.5 standard deviations to reduce the influence of extreme outliers. Rescaled from 1 to 5.
- [PopScore] = standardised (\log_e [Average Population Size]). Maximum and minimum values restricted to ± 2.5 standard deviations to reduce the influence of extreme outliers. Rescaled from 1 to 5.

1.55 High-quality data subset

I replicated model contrasts on a high-quality subset of time series after assessing low sample size, extreme non-stationarity, missing values and outliers, as follows (summary shown in **Table 25**):

The statistical ‘detection’ of density feedback increases with time-series length (Woiwod & Hanski 1992; Holyoak & Lawton 1993; Wolda & Dennis 1993), which also alters variability in parameters estimated in models of population dynamics (Dennis *et al.* 2006); so we excluded the shortest 101 time series (i.e., < 14 time steps).

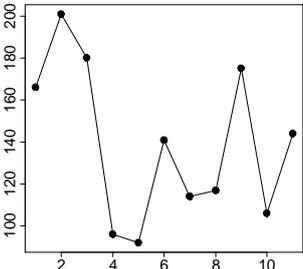
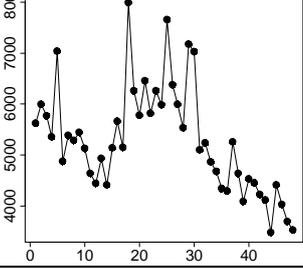
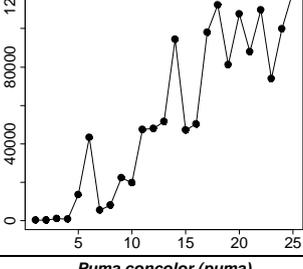
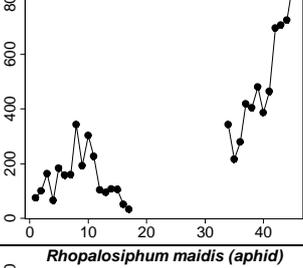
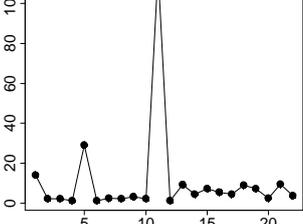
Stationarity implies that endogenous processes driving population dynamics, such as density feedback, vary around mean levels with constant variance (Turchin & Taylor 1992). This property allows reliable reconstruction of those processes through density-dependent models (Royama 1992; Turchin & Taylor 1992). I assessed stationarity through the variability in ‘return rate’, i.e., “...the time it takes [for a population] to return to equilibrium following disturbance” (Berryman 1999) in $\log_e(N)$ - t space. Given a time series, a variance considerably smaller than a mean of the ‘return time’ is indicative of a relatively constant period of oscillation (Berryman 1999, p. 99-100). Thus, I excluded 140 time series with a coefficient of variation of the return rate > 3 (i.e., > 75th percentile). Furthermore, stationary time series should show no temporal trending in population size, so I further excluded 93 time series for which linear trending of log-transformed population sizes had more AIC_c -support than an intercept-only model and slopes > |0.1| (< 25th and > 75th percentiles).

The frequency of missing values in a time series was regarded a sign of poor quality, so I removed those 14 stationary time series where missing-value frequency was ≥ 20 % of their length.

I detected time series with extreme outliers by studentising the residuals (Cook 1982) from the linear-trending model used above, and this resulted in a further exclusion of 38 time series with residuals > 3.4 (> 75th percentile).

For the high-quality time series, I report model rankings in **Table 28** and **Table 29**, and model-averaged fixed effects in **Figure 18** and **Figure 19**.

Table 25. Summary of stages used to obtain the high-quality time series with extreme departures from the assumptions of the Ricker-logistic and Gompertz models.

Criteria	Exclusion threshold	Time-series type removed
		y axis = abundance (N) x axis = years
Time-series length	< 14 time steps	<p data-bbox="979 456 1203 479"><i>Sceloporus graciosus</i> (lizard)</p> 
Variation of return rates	> 3	<p data-bbox="1011 770 1171 792"><i>Aythya affinis</i> (duck)</p> 
ln(N) trending	slope > 0.1	<p data-bbox="963 1084 1219 1106"><i>Acrocephalus scirpaceus</i> (warbler)</p> 
Missing values	> 20 % of data points	<p data-bbox="1011 1397 1171 1420"><i>Puma concolor</i> (puma)</p> 
Outliers	studentised residual > 3.4	<p data-bbox="979 1711 1203 1733"><i>Rhopalosiphum maidis</i> (aphid)</p> 

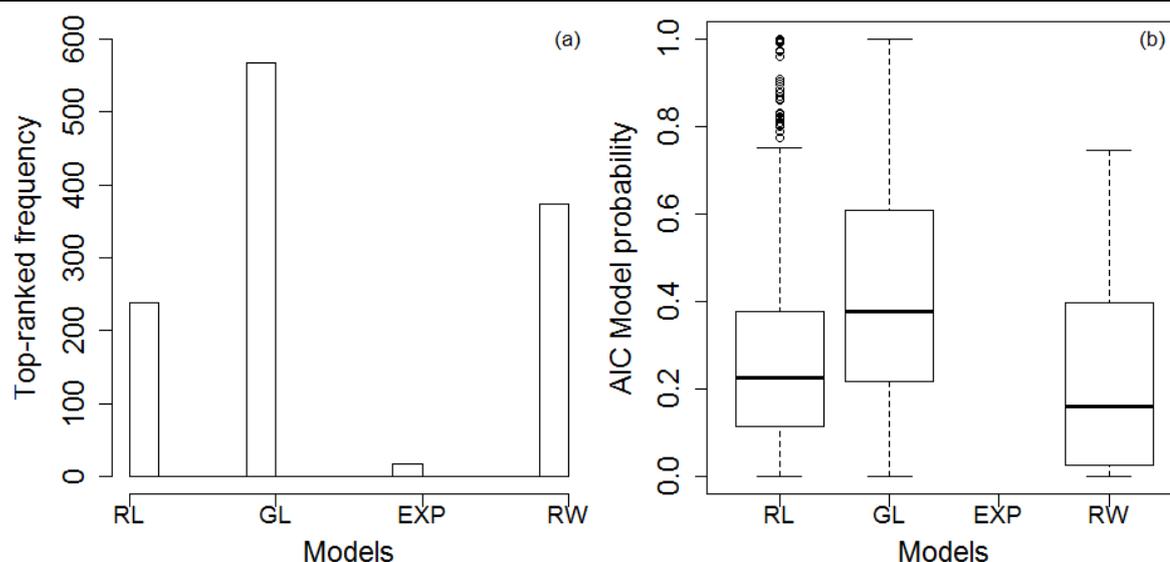
APPENDIX A5

- LIFE HISTORY: MORE RESULTS

1.56 Single-species population models

Top-ranked information-theoretical support occurred in 239 censuses (20 % of the dataset) for Ricker-logistic growth, 568 censuses (47 %) for Gompertz growth, 18 censuses (2 %) for exponential growth and 373 censuses (31 %) for random walk (**Figure 16**). Of the censuses supported for Ricker-logistic growth, 204 had considerable support for Gompertz growth ($\Delta AIC_c < 4$), so I found evidence for Gompertz growth in a total of 772 species' censuses (568+204, 65 %). I used those 772 species to relate life history and density feedback [after removing species with missing life-history traits and censuses showing depensatory density feedback] (see sample sizes in **Table 6**).

Figure 16. AIC_c support for four single-species population models across 1,198 species' time series of population abundance, quantified as (a) frequency with which each model was top-ranked, and (b) median model probability (bold line) of each model over all time series. Models are: RL = Ricker-logistic population growth, GL = Gompertz population growth [both accounting for density feedback], EXP = exponential growth and RW = random walk [both not accounting for density feedback]. I have formulated these models in **Table 4**.



1.57 Model support and effect sizes

I present in **Table 26** a summary of tables and figures reporting results of GLM/GLMM model fits presented in the main text and this appendix. See sample sizes in **Table 6**, model sets in **Table 7**, and rationale for selecting high-quality time series in **Table 25 (Appendix A4)**.

Table 26. Summary of content of figures and tables for model sets accounting for life-history effects on strength of compensatory density feedback. Control variables are time-series length (q) and number of generations monitored ($G = q/\text{age at first reproduction}$).

Control variable	All time series	High-quality time series
q	Table 8	
	Figure 9	Table 28
	Table 30 (measurement error)	Figure 18
G	Table 27	Table 29
	Figure 17	Figure 19

Top-ranked models

All time series, number of monitored generations (G) as control

Table 27. Bayesian information criterion (BIC) support for the top-ranked models¹ derived from GLMM relating life history to strength of compensatory density feedback (EN) for all time series supported for Gompertz growth, including all major groups (aquatic invertebrates, amphibians, birds, fish, insects, mammals, plants, reptiles), and the subsets of mammal and bird species. $wBIC$, %DE and %DE_{LH} are medians (in bold) from 100 bootstrapped samples (95th percentile ranges)². I show samples sizes in **Table 6**, model sets in **Table 7**, and effect sizes in **Figure 17**.

Dataset	Control variable	Top-ranked model per model set	$wBIC$	%DE	%DE _{LH}	ER	Top rank
All taxa	G	$EN \sim G + Long$	1.00 [0.00 to 1.00]	20.6 [13.1 to 31.7]	20.5 [12.8 to 30.0]	> 1000	79 (5)
All taxa	$G, Body$	$EN \sim G + Body + Long$	1.00 [0.35 to 1.00]	25.6 [18.5 to 34.9]	25.1 [17.9 to 34.2]	> 1000	96 (4)
Mammals	G	$EN \sim G + Body$	0.87 [0.19 to 0.90]	43.0 [25.3 to 61.0]	34.0 [12.2 to 51.2]	> 1000	93 (5)
Mammals	$G, Body$	$EN \sim G + Body$	0.72 [0.15 to 0.81]	43.0 [25.3 to 61.0]	34.0 [12.2 to 51.2]	> 1000	89 (9)
Birds	G	$EN \sim G + Long$	0.60 [0.03 to 0.91]	17.6 [8.5 to 29.4]	15.8 [7.0 to 28.0]	> 1000	66 (27)
Birds	$G, Body$	$EN \sim G + Body + Long$	0.42 [0.04 to 0.91]	18.9 [9.1 to 32.2]	17.1 [7.2 to 30.7]	> 1000	56 (38)

¹ **Model sets:** 1 single response [Strength of compensatory density feedback (EN)], and 1 or 2 life-history predictors [$Body$ = Body size (mm), $Fert$ = Fertility (number of young per year) and $Long$ = Longevity (maximum age attained in the wild, months)], and 1 or 2 control variables [G = number of generations monitored, and $Body$].

² **BIC metrics:** $wBIC$ = BIC Model probabilities given each data and model set, %DE = % Deviance in EN explained by each model within each model set, %DE_{LH} = % Deviance in EN explained by each model minus % Deviance in EN explained by the model including only G (i.e., Deviance in EN explained by life history conditional on q), ER = Evidence ratio of the top-ranked model $wBIC$ to only- G model $wBIC$ within each model set (i.e., times support for top-ranked model equating life-history traits was larger than for only- G), and **Top rank** = times each model was top-ranked over the 100 bootstrapped samples (in brackets: times each model was not the top ranked model yet received considerable support [$\Delta BIC < 4$]).

High-quality time series, length of the time series (q) as control

Table 28. Bayesian information criterion (BIC) support for the top-ranked models¹ derived from generalised linear mixed modelling relating life history to strength of compensatory density feedback (EN) for high-quality time series supported for Gompertz growth, including all major groups (aquatic invertebrates, amphibians, birds, fish, insects, mammals, plants, reptiles), and the subsets of mammal and bird species. w BIC, %DE and %DE_{LH} are medians (in bold) from 100 bootstrapped samples (95th percentile ranges)². I show samples sizes in **Table 6**, model sets in **Table 7**, and effect sizes in **Figure 18**.

Dataset	Control variable	Top-ranked model per model set	w BIC	%DE	%DE _{LH}	ER	Top rank
All taxa	q	$EN \sim q + Long$	0.83 [0.00 to 1.00]	27.2 [16.9 to 39.5]	16.5 [5.8 to 27.5]	> 1000	67 (15)
All taxa	$q, Body$	$EN \sim q + Body$	0.55 [0.00 to 0.98]	25.8 [15.5 to 37.5]	15.5 [4.4 to 26.6]	> 1000	55 (22)
Mammals	q	$EN \sim q + Long$	0.28 [0.00 to 0.85]	39.8 [22.3 to 67.0]	30.5 [12.9 to 61.1]	> 1000	41 (41)
Mammals	$q, Body$	$EN \sim q + Body$	0.41 [0.00 to 0.63]	39.8 [22.3 to 67.0]	30.5 [12.9 to 61.1]	> 1000	65 (28)
Birds	q	$EN \sim q + Long$	0.61 [0.02 to 0.89]	20.8 [8.1 to 38.1]	14.4 [2.3 to 27.8]	> 100	72 (18)
Birds	$q, Body$	$EN \sim q + Body + Long$	0.31 [0.0 to 0.89]	21.8 [9.6 to 39.7]	16.0 [4.5 to 27.8]	19	50 (30)

¹ **Model sets:** 1 single response [Strength of compensatory density feedback (EN)], and 1 or 2 life-history predictors [Age = Age at first reproduction (months), $Body$ = Body size (mm), $Fert$ = Fertility (number of young per year) and $Long$ = Longevity (maximum age attained in the wild, months)].

² **BIC metrics:** w BIC = BIC Model probabilities given each data and model set, %DE = % Deviance in EN explained by each model within each model set, %DE_{LH} = % Deviance in EN explained by each model minus % Deviance in EN explained by the model including only q (i.e., Deviance in EN explained by life history conditional on q), ER = Evidence ratio of the top-ranked model w BIC compared to q -only model w BIC within each model set (i.e., times support for top-ranked model equating life-history traits was larger than for the only- q model), and **Top rank** = times each model was top-ranked over the 100 bootstrapped samples (in brackets: times each model was not the top ranked model yet received considerable support [Δ BIC < 4]).

High-quality time series, number of monitored generations (G) as control

Table 29. Bayesian information criterion (BIC) support for the top-ranked models¹ derived from generalised linear mixed models relating life history to strength of compensatory density feedback (EN) for high-quality time series supported for Gompertz growth, including all major groups (aquatic invertebrates, amphibians, birds, fish, insects, mammals, plants, reptiles), and the subsets of mammal and bird species. $wBIC$, %DE and %DE_{LH} are medians (in bold) from 100 bootstrapped samples (95th percentile ranges)². I show samples sizes in **Table 6**, model sets in **Table 7**, and effect sizes in **Figure 19**.

Dataset	Control variable	Top-ranked model per model set	$wBIC$	%DE	%DE _{LH}	ER	Top rank
All taxa	G	$EN \sim G + Long$	0.98 [0.01 to 1.00]	23.1 [11.8 to 34.4]	20.0 [10.2 to 32.4]	> 1000	75 (7)
All taxa	$G, Body$	$EN \sim G + Body$	0.55 [0.21 to 0.98]	25.8 [15.5 to 37.5]	15.5 [4.4 to 26.6]	> 1000	55 (22)
Mammals	G	$EN \sim G + Long$	0.35 [0.00 to 0.84]	40.6 [21.6 to 63.5]	24.2 [7.9 to 42.3]	> 1000	50 (25)
Mammals	$G, Body$	$EN \sim G + Body$	0.37 [0.01 to 0.73]	38.3 [21.0 to 66.61]	24.6 [8.5 to 40.4]	> 1000	49 (35)
Birds	G	$EN \sim G + Long$	0.62 [0.01 to 0.89]	21.8 [10.5 to 37.6]	19.0 [6.3 to 33.7]	> 900	74 (15)
Birds	$G, Body$	$EN \sim G + Body + Long$	0.47 [0.02 to 0.88]	23.5 [11.6 to 38.5]	20.5 [8.8 to 34.1]	> 200	58 (28)

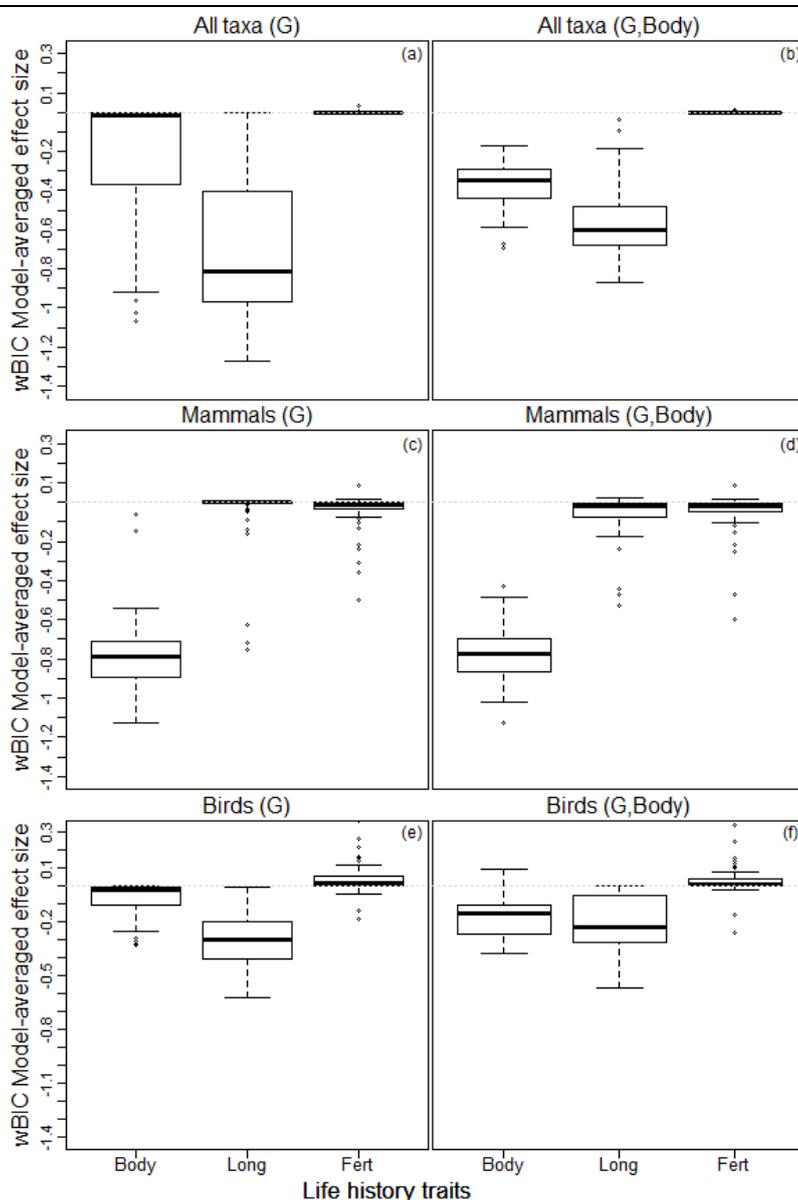
¹ **Model sets:** 1 single response [Strength of compensatory density feedback (EN)], and 1 or 2 life-history predictors [$Body$ = Body size (mm), $Fert$ = Fertility (number of young per year) and $Long$ = Longevity (maximum age attained in the wild, months)], and 1 or 2 control variables [G = number of generations monitored, and $Body$].

² **BIC metrics:** $wBIC$ = BIC Model probabilities given each data and model set, %DE = % Deviance in EN explained by each model within each model set, %DE_{LH} = % Deviance in EN explained by each model minus % Deviance in EN explained by the model including only G (i.e., Deviance in EN explained by life history conditional on q), ER = Evidence ratio of the top-ranked model $wBIC$ to only- G model $wBIC$ within each model set (i.e., times support for top-ranked model equating life-history traits was larger than for only- G), and **Top rank** = times each model was top-ranked over the 100 bootstrapped samples (in brackets: times each model was not the top ranked model yet received considerable support [$\Delta BIC < 4$]).

Model averaging

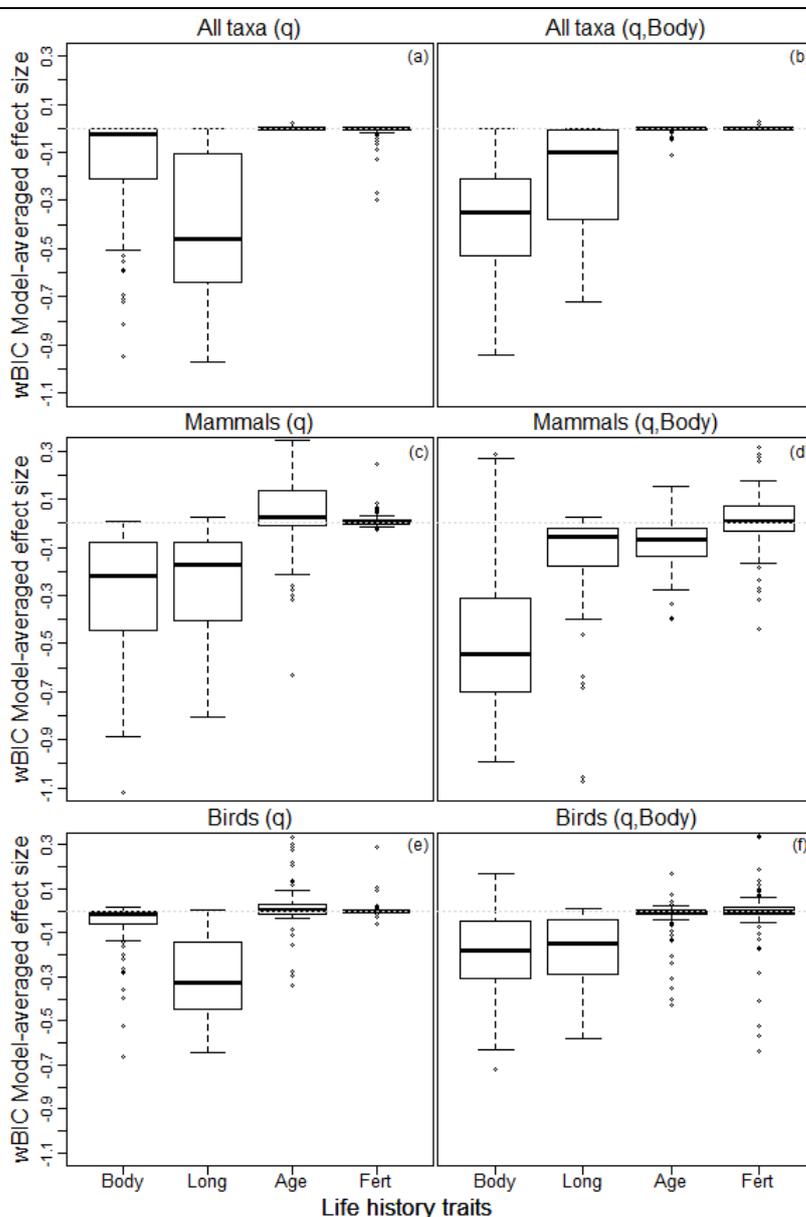
All time series, number of monitored generations (G) as control

Figure 17. Standardised BIC-weighted effect sizes for four life-history traits (*Body size* [*Body*], *Longevity*, *Fertility*) as predictors of variation in census-derived strength of compensatory density feedback (response), high-quality time series supported for Gompertz growth: (i) all taxa (a,b: aquatic invertebrates, amphibians, birds, fish, insects, mammals, plants, reptiles), and the subsets of (ii) mammal (c,d) and (iii) bird (e,f) species. Left panels (a,c,e) come from a model set controlling for number of generations monitored (G), and right panels (b,d,f) from a model set controlling for G and *Body*. Bold lines represent w BIC medians as obtained from 100 bootstrapped samples. Fits were obtained using GLMM which accounted for phylogenetic non-independence at the Linnean taxonomical level of *Class*, and GLM for the subset analyses of mammals and birds. I show sample sizes in **Table 6**, model sets in **Table 7**, and BIC metrics in **Table 27**.



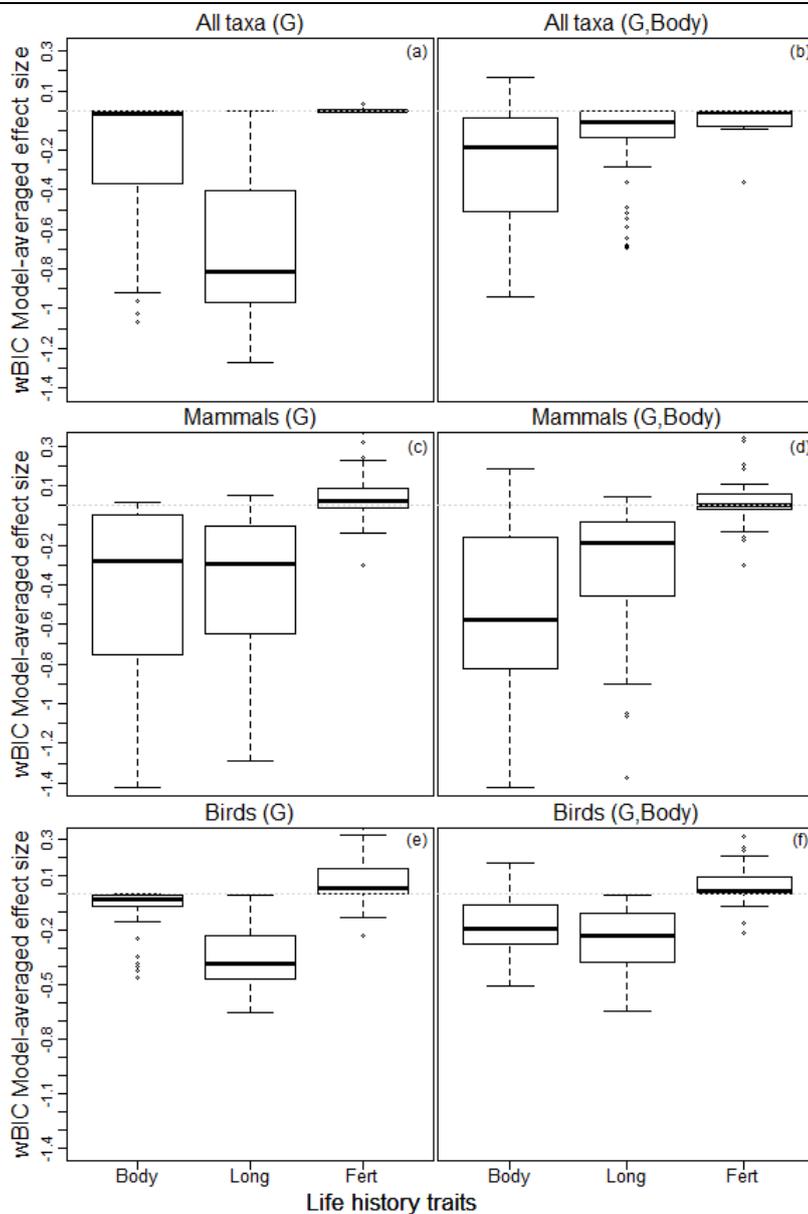
High-quality time series, length of the time series (q) as control

Figure 18. Standardised BIC-weighted effect sizes for four life-history traits (*Body size* [*Body*], *Longevity*, *Fertility*) as predictors of variation in census-derived strength of compensatory density feedback (response), over all time series supported for Gompertz growth: (i) all taxa (a,b: aquatic invertebrates, amphibians, birds, fish, insects, mammals, plants, reptiles), and the subsets of (ii) mammal (c,d) and (iii) bird (e,f) species. Left panels (a,c,e) come from a model set controlling for number of generations monitored (G), and right panels (b,d,f) from a model set controlling for G and *Body*. Bold lines represent w BIC medians as obtained from 100 bootstrapped samples. Fits were obtained using GLMM which accounted for phylogenetic non-independence at the Linnaean taxonomical level of *Class*, and GLM for the subset analyses of mammals and birds. I show sample sizes in **Table 6**, model sets in **Table 7**, and BIC metrics in **Table 28**.



High-quality time series, number of monitored generations (G) as control

Figure 19. Standardised BIC-weighted effect sizes for four life-history traits (*Body size* [*Body*], *Longevity*, *Fertility*) as predictors of variation in census-derived strength of compensatory density feedback (response), high-quality time series supported for Gompertz growth: (i) all taxa (a,b: aquatic invertebrates, amphibians, birds, fish, insects, mammals, plants, reptiles), and the subsets of (ii) mammal (c,d) and (iii) bird (e,f) species. Left panels (a,c,e) come from a model set controlling for number of generations monitored (G), and right panels (b,d,f) from a model set controlling for G and *Bod*. Bold lines represent w BIC medians as obtained from 100 bootstrapped samples. Fits were obtained using GLMM which accounted for phylogenetic non-independence at the Linnean taxonomical level of *Class*, and GLM for the subset analyses of mammals and birds. I show sample sizes in **Table 6**, model sets in **Table 7**, and BIC metrics in **Table 29**.



1.58 Examination of measurement error

Methods

I examined the potential effect of measurement error in my correlates of density feedback and life history in four stages. First, I simulated 772 time series using the parameters (intercept, slope, sigma, carrying capacity) for the 772 time series supported for Gompertz growth (**Table 6**: 326 core + 446 redundant species). Second, I introduced measurement error in each observation of each time series — to do so, I summed up the raw (simulated) value of each observation and a value obtained randomly from a normal distribution (q, σ), where q = length of time series and σ = measurement error/100. I repeated the simulation with three values of relatively high measurement error in census data: 5, 10 and 15 %. Third, I fitted the Gompertz model to the simulated time series with added measurement error. Lastly, I contrasted the models in my set (i.e., strength of density feedback as function of life history with controls for q and for body size, see models in **Table 7**) through GLMM (all taxa) and GLM (mammals and birds) and using strength of density feedback from simulated time series with each of the three magnitudes of added measurement error.

Results

Top-ranked models (highest $wAIC_c$ in the model set) remained the same and the deviance in strength of compensatory density feedback explained by life history was of the same magnitude for the original and simulated time series for 5 % measurement error in all taxa, mammals and birds, and for 10 % measurement error with a relative reduction in explained deviance only in mammals (**Table 30**). For the same dataset, Brook & Bradshaw (2006) had found that the most variable time series (potentially having the highest measurement errors) tended to have more information-theoretic support for density feedback yet contributed < 3 % to underlying variation in parameter estimates across species.

Table 30. Bayesian information criterion (BIC) support for the top-ranked models derived from GLMM (all taxa: aquatic invertebrates, amphibians, birds, fish, insects, mammals, plants, reptiles) and GLM (birds and mammals) relating life history to strength of compensatory density feedback (EN) for time series supported for Gompertz growth. $wBIC$, %DE and %DE_{LH} are medians (in bold) from 100 bootstrapped samples (95th percentile ranges). Models included time series length (q , years) and body size ($Body$, mm) as controls and three further life history traits, and I present results for observed (as in **Table 8**) and simulated (below) time series with incorporation of 5 %, 10 % and 15 % of measurement error. Samples sizes and model sets are given in **Table 6** and **Table 7**, respectively. See note below for predictors and BIC metrics.

Measurement error	Dataset	Control	Top-ranked model	$wBIC$	%DE	%DE _{LH}	Top rank
Observed time series	All taxa	q	$EN \sim q + Long$	0.57	30.7	9.5	54
5 %	All taxa	q	$EN \sim q + Long$	0.95	22.4	4.1	78
10 %	All taxa	q	$EN \sim q + Age$	0.90	22.1	3.3	75
15 %	All taxa	q	$EN \sim q$	0.73	14.7	-	66
Observed time series	All taxa	$q, Body$	$EN \sim q + Body + Long$	0.64	29.0	8.2	63
5 %	All taxa	$q, Body$	$EN \sim q + Body + Long$	0.69	22.4	7.8	65
10 %	All taxa	$q, Body$	$EN \sim q + Body$	0.38	21.1	2.4	47
15 %	All taxa	$q, Body$	$EN \sim q$	0.97	14.7	-	81
Observed time series	Mammals	q	$EN \sim q + Body$	0.79	45.2	28.9	85
5 %	Mammals	q	$EN \sim q + Body$	0.67	40.3	14.1	79
10 %	Mammals	q	$EN \sim q + Body$	0.24	38.8	3.3	35
15 %	Mammals	q	$EN \sim q$	0.23	21.3	-	40
Observed time series	Mammals	$q, Body$	$EN \sim q + Body$	0.59	45.2	28.3	80
5 %	Mammals	$q, Body$	$EN \sim q + Body$	0.61	40.3	14.1	74
10 %	Mammals	$q, Body$	$EN \sim q + Body$	0.27	38.8	3.3	39
15 %	Mammals	$q, Body$	$EN \sim q$	0.34	21.3	-	52
Observed time series	Birds	q	$EN \sim q + Long$	0.60	19.4	10.0	75
5 %	Birds	q	$EN \sim q + Long$	0.67	18.7	8.7	72
10 %	Birds	q	$EN \sim q$	0.24	10.1	-	42
15 %	Birds	q	$EN \sim q + Body$	0.25	9.8	3.9	40
Observed time series	Birds	$q, Body$	$EN \sim q + Body + Long$	0.29	21.1	11.0	43
5 %	Birds	$q, Body$	$EN \sim q + Body + Long$	0.32	19.7	9.0	47
10 %	Birds	$q, Body$	$EN \sim q$	0.44	10.1	-	58
15 %	Birds	$q, Body$	$EN \sim q + Body$	0.31	9.8	3.9	44

Traits: Age = Age at first reproduction (years), $Body$ = Body size (mm), $Fert$ = Fertility (young/year), $Long$ = Longevity (years); $wBIC$ = BIC Model probabilities given each data and model set, %DE = % Deviance in EN explained by each model within each model set, %DE_{LH} = % Deviance in EN explained by each model minus % Deviance in EN explained by the model including only q (i.e., Deviance in EN explained by life history conditional on q), and **Top rank** = times each model was top-ranked over the 100 bootstrapped sample

APPENDIX A6 - DEMOGRAPHIC RATES: DATA

I list below (**Table 31**) the species identities, study localities and data sources used in **Chapter 5** (and also **Chapter 4**).

Table 31. Dataset consisting of long-term censuses of population size, and fertility and survival rates. In ‘Ownership’, I distinguish data retrieved directly from the literature, or shared personally by those ecologists cited. ‘Authors’, ‘Year’, ‘Source’ and ‘Vol.’ (Volume) refer to the literature reference each population dataset is linked to. The full dataset includes 109 populations of birds and mammals.

Common name	Scientific name	Study Area	Data ownership	Authors	Year	Source	Vol.
Snow petrel	<i>Pagodroma nivea</i>	Terre Adélie, Antarctica	Christophe Barbraud and Stephanie Jenovrier (Project IPEV N° 109, French Polar Institute IPEV)	Jenouvrier S, Barbraud C, Weimerskirch H	2005	<i>Ecology</i>	86
Bonelli's eagle	<i>Hieraetus fasciatus</i>	Beja, Faro and Setúbal Districts, Portugal	Literature	Beja P, Palma L	2008	<i>Journal of Animal Ecology</i>	77
Vicuña	<i>Vicugna vicugna</i>	Parinacota Province, Tarapaca, Chile	Literature	Bonacic C, Macdonald DW, Galaz J, Sibly RM	2002	<i>Oryx</i>	36
Eurasian badger	<i>Meles meles</i>	Wytham Woods, Oxford, UK	David MacDonald	Macdonald DW, Newman C, Nouvellet M, Buesching CD	2009	<i>Journal of Mammalogy</i>	90
Wild dog	<i>Lycaon pictus</i>	Laikipia, Samburu, Isiolo and Baringo Districts, Kenya	Rosie Woodroffe	Woodroffe R	2011	<i>Journal of Mammalogy</i>	92
Osprey	<i>Pandion haliaetus</i>	Corsica, France	Literature	Bretagnolle V, Mougeot F, Thibault JC	2008	<i>Journal of Animal Ecology</i>	77
Weddell seal	<i>Leptonychotes weddellii</i>	Ross Island, Antarctica	Literature	Cameron MF, Siniff DB	2004	<i>Canadian Journal of Zoology</i>	82
Bearded vulture	<i>Gypaetus barbatus</i>	Pyrenees, Spain	Literature	Carrete M, Donazar JA, Margalida A	2006	<i>Ecological Applications</i>	16

Table 31. Continuation.

Common eider	<i>Somateria mollissima</i>	Coquet Island, UK	Literature	Coulson JC	2010	<i>Bird Study</i>	57
Black-legged kittiwake	<i>Rissa trydactyla</i>	River Tyne, UK	Literature	Coulson JC Thomas CS	1985	<i>Journal of Animal Ecology</i>	54
Wandering albatross	<i>Diomedea exulans</i>	Possession Island, Crozet Archipelago, Southern Ocean	Literature	Delord K, Besson D Barbraud C, Weimerskirch H	2008	<i>Biological Conservation</i>	141
Common guillemot	<i>Uria aalge</i>	Farallon Island, California, USA	PRBO Conservation Science and United States Fish and Wildlife Service	California Avian Data Center	2010	<i>www.prbo.org</i>	
Atlantic yellow-nosed Albatross	<i>Thalassarche chlororhynchos</i>	Gough Island, South Atlantic	Literature	Cuthbert R, Ryan P Cooper J, Hilton G	2003	<i>The Condor</i>	105
Emperor penguin	<i>Aptenodytes forsteri</i>	Terre Adélie, Antarctica	Henri Weimerskirch (Project N° 109, French Polar Institute IPEV)	Jenouvrier S, Caswell H Barbraud C, Holland M Stroeve J, Weimerskirch H	2005	<i>Ecology</i>	86
Southern fulmar	<i>Fulmarus glacialisoides</i>	Terre Adélie, Antarctica	Literature	Micol T Jouventin P	2001	<i>Polar Biology</i>	24
South polar skua	<i>Catharacta maccormicki</i>	Terre Adélie, Antarctica	Literature	Micol T Jouventin P	2001	<i>Polar Biology</i>	24
Black-browed albatross	<i>Diomedea melanophris</i>	Bird Island, South Georgia, Southern Ocean	Literature	Prince PA, Rothery P Croxall JP, Wood AG	1994	<i>Ibis</i>	136
Grey-headed albatross	<i>Diomedea chrysostoma</i>	Bird Island, South Georgia, Southern Ocean	Literature	Prince PA, Rothery P Croxall JP, Wood AG	1994	<i>Ibis</i>	136
White-tailed deer	<i>Odocoileus virginianus</i>	Nova Scotia, Canada	Literature	Patterson BR Power VA	2002	<i>Oecologia</i>	130
Seychelles Warbler	<i>Acrocephalus sechellensis</i>	Cousin Island, Seychelles, Indian Ocean	Lyanne Brouwer	Brouwer L, Tinbergen JM Both C, Bristol R Richardson DS, Komdeur J	2009	<i>Ecology</i>	90
Yellow-belly marmot	<i>Marmota flaviventris</i>	Picnic colony, East River Valley, Rocky Mountains, Colorado, USA	Kenneth Armitage	Oli MK Armitage KB	2004	<i>Ecology</i>	85

Table 31. Continuation.

Snow goose	<i>Anser caerulescens</i>	St Lawrence Estuary, Canada	Gilles Gauthier and Anna Calvert	Reed ET Calvert AM	2007	<i>Canadian Wildlife Service</i>	
Brandt's Cormorant	<i>Phalacrocorax penicillatus</i>	Farallon Island, California, USA	PRBO Conservation Science and US Fish and Wildlife Service	California Avian Data Center	2010	<i>www.prbo.org</i>	
Soay sheep	<i>Ovis aries</i>	Kilda Archipelago, Scotland	Tim Clutton-Brock, Bryan Grenfell, Josephine Pemberton, Tim Coulson, Loeske Kruuk and Mick Crawley	Coulson T Gaillard JM Festa-Bianchet M	2005	<i>Journal of Animal Ecology</i>	74
Red deer	<i>Cervus elaphus</i>	Isle of Rum, Scotland	Tim Clutton-Brock, Bryan Grenfell, Josephine Pemberton, Tim Coulson, Loeske Kruuk and Mick Crawley	Coulson T, Guinness F Pemberton J, Clutton-Brock T	2004	<i>Ecology</i>	85
Montagu's Harrier	<i>Circus pygargus</i>	Marche, Apennines, Italy	Literature	Pandolfi M Tanferna A	2009	<i>Journal of Raptor Research</i>	43
Cassin's auklet	<i>Ptychoramphus aleuticus</i>	South-east Farallon Island, California, USA	PRBO Conservation Science and United States Fish and Wildlife Service	California Avian Data Center	2010	<i>www.prbo.org</i>	
Pigeon guillemot	<i>Cephus columba</i>	Farallon Island, California, USA	PRBO Conservation Science and United States Fish and Wildlife Service	California Avian Data Center	2010	<i>www.prbo.org</i>	
Western gull	<i>Larus occidentalis</i>	Farallon Island, California, USA	PRBO Conservation Science and United States Fish and Wildlife Service	California Avian Data Center	2010	<i>www.prbo.org</i>	
Common loon	<i>Gavia immer</i>	New Hampshire, USA	Jason Grear and New Hampshire Loon Preservation Committee	Grear JS, Meyer MW Cooley JH, Kuhn A, Piper WH Mitro MG, Vogel HS Taylor KM, Kenow KP Craig SM, Nacci DE	2009	<i>Journal of Wildlife Management</i>	73
Common guillemot	<i>Uria aalge</i>	Isle of May, Scotland	Scottish Natural Heritage	Frederiksen M, Edwards M Richardson AJ, Halliday NC Wanless S	2006	<i>Journal of Animal Ecology</i>	75
Razorbill	<i>Alca torda</i>	Isle of May, Scotland	Scottish Natural Heritage		2006	<i>Journal of Animal Ecology</i>	75
European shag	<i>Phalacrocorax aristotelis</i>	Isle of May, Scotland	Scottish Natural Heritage		2006	<i>Journal of Animal Ecology</i>	75
Wigeon	<i>Anas penelope</i>	Lake Myvatn, Iceland	Arnthor Gardarsson and Arni Einarsson	Poysa H Pesonen M	2003	<i>Oikos</i>	102

Table 31. Continuation.

Harlequin ducks	<i>Histrionicus histrionicus</i>	Upper Laxa, Iceland	Literature	Gardarsson A Einarsson A	2008	<i>Waterbirds</i>	31
Bison	<i>Bison bison</i>	Delta population, Wood Buffalo National Park, Canada	Kindopp, R., Vassal M. and Andrews D., 2010. Wood Buffalo National Park Bison Survey, February 2009	Bradley M Wilmshurst J	2005	<i>Canadian Journal of Zoology</i>	83
Grey partridge	<i>Perdix perdix</i>	Plateau Aigre, France	Francois Reitz, Réseau National Perdrix-Faisan ONCFS - FNC - FDC	Bro E, Deldalle B, Massot M, Reitz FO, Selmi S	2003	<i>Wildlife Biology</i>	9
Common sandpiper	<i>Actitis hypoleucos</i>	Ashop River, Peak Discript, England	Derek W Yalden and PK Holland	Dougall TW, Holland PK Mee A, Yalden DW	2005	<i>Bird Study</i>	52
Grey wolf	<i>Canis Lupus</i>	Isle Royale, Michigan, USA	John Vucetich and Rolf Peterson: www.isleroyalewolf.org	Vucetich L	2009	www.isleroyalewolf.org	
Moose	<i>Alces alces</i>	Isle Royale, Michigan, USA	John Vucetich and Rolf Peterson: www.isleroyalewolf.org	Vucetich L	2009	www.isleroyalewolf.org	
Reindeer	<i>Rangifer tarandus</i>	Nordenskiold Peninsula, Svalvard, Norway	Erling Solberg	Solberg EJ, Jordhoy P Strand O, Aanes R, Loison A Saether BE, Linnell JDC	2001	<i>Ecography</i>	24
Common noddy	<i>Anous stolidus</i>	Lancelin Island, Perth, Australia	Literature	Dunlop JN	2005	<i>Emu</i>	105
Mallard	<i>Anas platyrhynchos</i>	Evo, Finland	Literature	Elmberg J	2003	<i>Wildlife Biology</i>	9
Spanish imperial eagle	<i>Aquila adalberti</i>	Doñana Nature Park, Huelva, Spain	Literature	Ferrer M Penteriani V	2008	<i>Journal of Applied Ecology</i>	45
Common eider	<i>Somateria mollissima</i>	Soderskar Bird Sanctuary, Finland	Literature	Hario M Mazerolle MJ Saurola P	2009	<i>Oecologia</i>	159
Barn Swallow	<i>Hirundo rustica</i>	Kraghede, Denmark	Anders Møller	Moller AP	2001	<i>Journal of Applied Ecology</i>	38
Greater kudu	<i>Tragelaphus strepsiceros</i>	Central Kruger National Park, South Africa	Norman Owen-Smith	Owen-Smith N	2006	<i>Ecological Monographs</i>	76
Greater kudu	<i>Tragelaphus strepsiceros</i>	Pretorius Kop, Kruger National Park, South Africa	Norman Owen-Smith	Owen-Smith N	1990	<i>Journal of Animal Ecology</i>	59
Wildebeest	<i>Connochaetes taurinus</i>	Central Kruger National Park, South Africa	Norman Owen-Smith	Owen-Smith N	2006	<i>Ecological Monographs</i>	76

Table 31. Continuation.

Tule elk	<i>Cervus canadensis</i>	Point Reyes National Seashore, California, USA	Literature	Howell JA, Brooks GC Semenoff-Irving, M Greene C	2002	<i>Journal of Wildlife Management</i>	66
Brambling	<i>Fringilla montifringilla</i>	Lake Tjulträsk, Sweden	Literature	Lindstrom A, Enemar A Andersson G, von Proschwitz T Nyholm NEI	2005	<i>Oikos</i>	110
Pigmy possum	<i>Burramys parvus</i>	Blue Cow, Snowy Mountains, Sydney, Australia	Literature	McCarthy MA Broome LS	2000	<i>Journal of Animal Ecology</i>	69
African elephant	<i>Loxodonta africana</i>	Amboseli National Park, Kenya	Literature	Moss CJ	2001	<i>Journal of Zoology</i>	255
Black-throated blue warbler	<i>Dendroica caerulescens</i>	New Hampshire, USA	Scott Sillett	Sillett TS Holmes RT	2005	<i>Greenberg R, Marra PP, Eds. Birds of Two Worlds: The Ecology And Evolution of Temperate-Tropical Migration. Baltimore: Johns Hopkins University Press</i>	
Song sparrow	<i>Melospiza melodia</i>	Palomarin Study Area, Point Reyes National Reserve, California, USA	Literature	Chase MK Nur N Geupel GR	2005	<i>The Auk</i>	122
Audouin's gull	<i>Larus audouinii</i>	Columbretes Islands, Castellón, Spain	Literature	Oro D, Martínez-Abraín A Paracuellos M, Nevado JC Genovart M	2006	<i>Proceedings of The Royal Society B-Biological Sciences</i>	273
Audouin's gull	<i>Larus audouinii</i>	Ebro Delta, Spain	Literature	Oro D, Martínez-Abraín A Paracuellos M, Nevado JC Genovart M	2006	<i>Proceedings of The Royal Society B-Biological Sciences</i>	273
Pied flycatcher	<i>Ficedula hypoleuca</i>	Forest of Dean, Gloucestershire, England	Literature	Stenning MJ Harvey PH Campbell B	1988	<i>Journal of Animal Ecology</i>	
Great tit	<i>Parus major</i>	Pilis Mountains, Budapest, Hungary	Literature	Sasvári L Torok J Toth L	1987	<i>Oecologia</i>	72

Table 31. Continuation.

Blue tit	<i>Parus caeruleus</i>	Pilis Mountains, Budapest, Hungary	Literature	Sasvári L Torok J Toth L	1987	<i>Oecologia</i>	72
Collared flycatcher	<i>Ficedula albicollis</i>	Pilis Mountains, Budapest, Hungary	Literature	Sasvári L Torok J Toth L	1987	<i>Oecologia</i>	72
Island fox	<i>Urocyon littoralis</i>	Tdams grid, San Clemente Island, California, USA	Gary Roemer and Elena Angulo	Angulo E, Roemer GW Berec L, Gascoigne J Courchamp F	2007	<i>Conservation Biology</i>	21
Montagu's harrier	<i>Circus pygargus</i>	Planiol colony, Castellón, Spain	Grupo de Investigación "Zoología de Vertebrados" (Universidad de Alicante, Spain)	Soutullo A, Liminana R Urios V, Surroca M Gill JA	2006	<i>Oecologia</i>	149
Mute swan	<i>Cygnus olor</i>	Aasla Island, Finland	Lennart Saari	Nummi P, Saari L	2003	<i>Journal of Avian Biology</i> 3	34
Wood Stork	<i>Mycteria americana</i>	South Carolina State, USA	South Carolina Department of Natural Resources	Murphy TM Coker JW	2008	<i>Waterbirds</i>	31
Moose	<i>Alces alces</i>	Nelchina, Alaska	Literature	Testa JW	2004	<i>Ecology</i>	85
Adelie penguin	<i>Pygoscelis adeliae</i>	Signy Island, Orkney Island, Antarctica	Literature	Trathan PN Croxall JP Murphy EJ	1996	<i>Polar Biology</i>	16
Chinstrap penguin	<i>Pygoscelis antarctica</i>	Signy Island, Orkney Island, Antarctica	Literature	Trathan PN Croxall JP Murphy EJ	1996	<i>Polar Biology</i>	16
Peregrine falco	<i>Falco peregrinus</i>	South-west Castellón, Spain	Literature	Verdejo J López-López P	2008	<i>Ardea</i>	55
Zino's petrel	<i>Pterodroma madeira</i>	Central Mountain Massif, Madeira, Portugal	Literature	Zino F, Oliveira P King S, Buckle A, Biscoito M, Costa Neves H Vasconcelos A	2001	<i>Oryx</i>	35
White-tailed eagle	<i>Haliaeetus albicilla</i>	Western Scotland	Literature	Evans RJ, Wilson JD Amar A, Douse A MacLennan A, Ratcliffe N Whitfield DP	2009	<i>Ibis</i>	151
Booted eagle	<i>Hieraaetus pennatus</i>	Doñana Nature Park, Huelva, Spain	Literature	Casado E, Suárez-Seoane S Lamelin J Ferrer M	2008	<i>Ibis</i>	150

Table 31. Continuation.

Southern elephant seal	<i>Mirounga leonina</i>	Marion Island, Prince Eduard Archipelago, Indian Ocean	Literature	Pistorius PA, Taylor FE Bester MN Hofmeyr GJG Kirkman SP	2008	<i>African Zoology</i>	43
Golden eagle	<i>Aquila chrysaetos</i>	Argyll and Bute, Scotland	Literature	Whitfield DP, Fielding AH Gregory MJP, Gordon AG McLeod DRA, Haworth PH	2007	<i>Ibis</i>	149
Tawny owl	<i>Strix aluco</i>	Kielder Forest, England	Literature	Petty SJ Fawkes BL	1997	<i>Duncan, James R.; Johnson, David H.; Nicholls, Thomas H., Eds. Biology And Conservation of Owls of The Northern Hemisphere: DAFS, MN, USA</i>	
Great cormoran	<i>Phalacrocorax carbo sinensis</i>	Horsens Fjord, Vorskø, Denmark	Thomas Bregnballe, National Environmental Research Institute, Aarhus University, Denmark	Bregnballe T	-	<i>Unpublished Data</i>	
Great bustard	<i>Otis tarda</i>	Villafáfila Wildelife Reserve, Zamora, Spain	Literature	Morales MB Alonso JC Alonso J	2002	<i>Ibis</i>	144
Stone curlew	<i>Burhinus oedicephalus</i>	Porton Down, Wiltshire, England	Literature	Bealey CE, Green RE Robson R, Taylor CR, Winspear R	1999	<i>Bird Study</i>	46
Great grey owl	<i>Strix nebulosa</i>	Norbotten, Sweden	Literature	Hipkiss T Stefansson O Hornfeldt B	2008	<i>Canadian Journal of Zoology</i>	86
Rock Ptarmigan	<i>Lagopus muta</i>	Canigou Massif, Pyrenees, France	Claude Novoa, ONCFS (ONCFS means office National de la Chasse et de la Faune Sauvage)	Novoa C, Besnard A Brenot JF, Ellison LN	2008	<i>Ibis</i>	150
African elephant	<i>Loxodonta africana</i>	Addo National Park, South Africa	Katie Gough: Gough, K.F. (2012). Relatedness, social behaviour, and population dynamics of elephants (<i>Loxodonta africana</i>) in Addo Elephant National Park, South Africa. PhD thesis, Nelson Mandela Metropolitan University, South Africa	Gough KF Kerley GIH	2006	<i>Oryx</i>	40
Greater flamingo	<i>Phoenicopterus roseus</i>	Fangassier Lagoon, Camargue, France	Arnaud Béchet, Centre de recherche Tour du Valat, France	Bechet A Johnson AR	2008	<i>Ibis</i>	150

Table 31. Continuation.

Northern goshawk	<i>Accipiter gentilis</i>	Eastern Westphalia, Germany	Oliver Krüger	Kruger O	2007	<i>Oecologia</i>	152
Common buzzard	<i>Buteo buteo</i>	Eastern Westphalia, Germany	Oliver Krüger	Kruger O	2001	<i>Oikos</i>	93
Booted eagle	<i>Hieraaetus pennatus</i>	Sierras de Burete, Lavia and Cambrón, Murcia, Spain	José Calvo and José Enrique Martínez, Universidad de Murcia, Spain	Martínez JE, Pagán I, Calvo JF	2006	<i>Journal of Ornithology</i>	147
Tawny owl	<i>Strix aluco</i>	Lahti, Finland	Kari Ahola and Teuvo Karstinen	Karell P, Ahola K, Karstinen T, Zolei A, Brommer JE	2009	<i>Journal of Animal Ecology</i>	78
Short-tailed shrew	<i>Blarina brevicauda</i>	Appalachian Plateau, Pennsylvania, USA	Mauricio Lima	Lima M, Merritt JF, Bozinovic F	2002	<i>Journal of Animal Ecology</i>	71
Mouse opossum	<i>Thylamys elegans</i>	Reserva Nacional Las Chinchillas, Chile	Mauricio Lima	Lima M, Stenseth NC, Yoccoz NG, Jaksic FM	2001	<i>Proceedings of The Royal Society B-Biological Sciences</i>	268
Leaf-eared mouse	<i>Phyllotis darwini</i>	Reserva Nacional Las Chinchillas, Chile	Mauricio Lima	Lima M, Stenseth NC, Leirs H, Jaksic FM	2003	<i>Proceedings of The Royal Society B-Biological Sciences</i>	270
Tree Pipit	<i>Anthus trivialis</i>	Thetford Forest, Norfolk/Suffolk, UK	Niall Burton, British Trust for Ornithology	Burton NHK	2009	<i>Ibis</i>	
Montagu's Harrier	<i>Circus pygargus</i>	Rocherort, Deux-Sèvres, France	Alexandre Millon	Millon A, Bretagnolle V	2008	<i>Oikos</i>	117
Eastern kingbird	<i>Tyrannus tyrannus</i>	Upland population, Charlotte Valley, Delaware, NY, USA	Michael Murphy	Murphy MT	2001	<i>Ecology</i>	82
Black-legged kittiwake	<i>Rissa trydactyla</i>	Bumburgh Head, Shetland, UK	Sullom Voe Association Ltd, collected by University of Aberdeen on behalf of the Shetland Oil Terminal Environmental Advisory Group	Heubeck M	-	<i>Unpublished Data</i>	
Northern lapwing	<i>Vanellus vanellus</i>	Västerfärnebo, Sweden	Literature	Berg A, Jonsson M, Lindberg T, Kallerink K-G	2002	<i>Ibis</i>	Online
Barrow's goldeneye	<i>Bucephala islandica</i>	Myvtan Lake, Iceland	Literature	Gardarsson A, Einarsson A, Gislason GM, Gudbergsson G	2006	<i>Hydrobiologia</i>	567
Piping plover	<i>Charadrius melodioides</i>	New England, USA	Literature	Hecht A, Melvin SM	2009	<i>Waterbirds</i>	32

Table 31. Continuation.

Barnacle goose	<i>Branta leucopsis</i>	Laus Holmar Islands, Sweden	Literature	Larsson K Forslund P	1994	<i>Journal of Animal Ecology</i>	63
Black-tailed deer	<i>Odocoileus columbianus</i>	King Creek, Washington, USA	Literature	Gilbert BA Raedeke KJ	2004	<i>Journal of Wildlife Management</i>	68
Griffon vulture	<i>Gyps fulvus</i>	Crete	Literature	Xirouchakis SM	2010	<i>Bird Study</i>	57
Common waterbuck	<i>Kobus ellipsiprymnus</i>	Kruger National Park, South Africa	Scientific Services Division, Kruger National Park	Ogutu JO, Owen-Smith N	2006	<i>Ecology Letters</i>	6
Impala	<i>Aepyceros melampus</i>	Kruger National Park, South Africa	Scientific Services Division, Kruger National Park	Ogutu JO Owen-Smith N	2006	<i>Ecology Letters</i>	6
Burchell's Zebra	<i>Equus burchelli</i>	Kruger National Park, South Africa	Scientific Services Division, Kruger National Park	Ogutu JO Owen-Smith N	2006	<i>Ecology Letters</i>	6
Warthog	<i>Phacochoerus aethiopicus</i>	Kruger National Park, South Africa	Scientific Services Division, Kruger National Park	Ogutu JO Owen-Smith N	2006	<i>Ecology Letters</i>	6
Sable antelope	<i>Hippotragus niger</i>	Kruger National Park, South Africa	Scientific Services Division, Kruger National Park	Ogutu JO Owen-Smith N	2006	<i>Ecology Letters</i>	6
Roan antelope	<i>Hippotragus equinus</i>	Kruger National Park, South Africa	Scientific Services Division, Kruger National Park	Ogutu JO Owen-Smith N	2006	<i>Ecology Letters</i>	6
Tsessebe	<i>Damaliscus lunatus</i>	Kruger National Park, South Africa	Scientific Services Division, Kruger National Park	Ogutu JO Owen-Smith N	2006	<i>Ecology Letters</i>	6
Giraffe	<i>Giraffa camelopardalis</i>	Kruger National Park, South Africa	Scientific Services Division, Kruger National Park	Ogutu JO Owen-Smith N	2006	<i>Ecology Letters</i>	6
Degu	<i>Octodon degus</i>	Bosque Fray Jorge National Park, Chile	Peter Meserve, Douglas Kelt and Andrea Previtali	Previtali MA, Meserve PL Kelt DA, Milstead WB Gutiérrez OR	2009	<i>Conservation Biology</i>	24
Peregrine falco	<i>Falco peregrinus</i>	Coastal population, California, USA	Matthew Kauffman	Kauffman MJ Frick WF Linthicum J	2003	<i>Ecological Applications</i>	13

APPENDIX A7 - DEMOGRAPHIC RATES: MORE RESULTS

1.59 Frequencies of compensatory and depensatory feedbacks

$ER_{CF} > 4$

Table 32. Frequency (%) of occurrence of compensatory and depensatory component density feedbacks on survival rates in bird and mammal populations supported or not for compensatory ensemble density feedback (Gompertz growth). Frequencies are given for survival rates showing evidence (evidence ratio = $ER_{CF} > 1$, $n = 106$ rates) or strong evidence ($ER_{CF} > 4$, $n = 56$ rates) for component feedback, split by whether the populations show different levels of statistical evidence for ensemble density feedback (ER_{EN}). Median ENs of component density feedback with 95th percentile ranges also reported.

Rate	Component feedback type	Demographic feedback support (ER_{EN})	Component-feedback frequency (%)		Component-feedback EN	
			$ER_{CF} > 1$	$ER_{CF} > 4$	$ER_{CF} > 1$	$ER_{CF} > 4$
Survival	Compensatory	> 4 (Yes)	46	53	-1.1 [-4.3 to -0.1]	-1.7 [-6.8 to -0.5]
		1-4 (Yes)	9	8	-1.1 [-5.8 to -0.1]	-2.0 [-5.7 to -1.7]
		< 1 (No)	6	8	-2.3 [-3.2 to -0.2]	-3.2 [-3.2 to -1.9]
	Depensatory	> 4 (Yes)	19	13	0.6 [0.0 to 2.6]	0.8 [0.4 to 3.0]
		1-4 (Yes)	6	5	1.1 [0.2 to 2.8]	2.3 [1.8 to 2.9]
		< 1 (No)	14	15	0.6 [0.2 to 4.6]	2.2 [1.1 to 5.2]

ER_{CF} > 4

Table 33. Frequency (%) of occurrence of compensatory and depensatory component density feedbacks on survival rates in bird and mammal populations supported or not for compensatory ensemble density feedback (Gompertz growth). Frequencies are given for survival rates showing evidence (evidence ratio = ER_{CF} > 1, *n* = 176 rates) or strong evidence (ER_{CF} > 4, *n* = 70 rates) for component feedback, split by whether the populations show different levels of statistical evidence for ensemble density feedback (ER_{EN}). Median ENs of component density feedback with 95th percentile ranges also reported.

Rate	Component feedback type	Demographic-feedback support (ER _{EN})	Component-feedback frequency (%)		Component-feedback EN	
			ER _{CF} > 1	ER _{CF} > 4	ER _{CF} > 1	ER _{CF} > 4
Fertility	Compensatory	> 4 (Yes)	22	24	-0.8 [-5.3 to -0.1]	-1.8 [-5.4 to -0.5]
		1-4 (Yes)	14	20	-0.7 [-3.6 to -0.0]	-1.4 [-8.4 to -0.5]
		< 1 (No)	15	11	-0.8 [-3.6 to -0.0]	-1.8 [-3.8 to -0.5]
		> 4 (Yes)	17	20	0.8 [0.1 to 2.4]	1.0 [0.6 to 2.4]
	Depensatory	1-4 (Yes)	10	9	0.8 [0.1 to 8.8]	1.7 [0.8 to 11.2]
		< 1 (No)	22	16	0.6 [0.1 to 2.5]	2.0 [0.5 to 4.4]

1.60 Model support

 $ER_{EN} > 4$ and $ER_{CF} > 1$

Table 34. Compensatory ensemble feedback EN (EN) fitted as a function of sample size in the time series (q , years), body size ($Body$ = body length, mm), and component feedback EN (CF) in birds and mammals [n = number of demographic rates included in each model contrast]. $wAIC_c$ are model probabilities (shown only top-ranked models in a set), and DE is % deviance explained (total and broken down by predictors). Model fits were done using all demographic rates, split by fertility or survival rates; and all types of component feedback, split by compensatory or depensatory feedbacks. Included demographic rates from populations with strongest AIC_c -evidence ratio for ensemble feedback ($ER_{EN} > 4$). See model set in **Table 12**.

Rates	n	Component feedback type	Top-ranked models	$wAIC_c$	DE_{total}	DE_q	DE_{BL}	DE_{CF}
All	137	All	$EN \sim q + Body$	0.70	8.1	2.1	6.0	-
Fertility	68	All	$EN \sim q + Body$	0.40	7.1	1.2	5.9	-
Survival	69	All	$EN \sim q + Body + CF$	0.69	18.7	2.7	11.0	5.0
All	87	Compensatory	$EN \sim 1$	0.36	0.0	-	-	-
Fertility	38	Compensatory	$EN \sim 1$	0.45	0.0	-	-	-
Survival	49	Compensatory	$EN \sim q + Body + CF$	0.59	17.3	1.4	6.1	9.8
All	50	Depensatory	$EN \sim q + Body$	0.69	17.5	3.7	13.7	-
Fertility	30	Depensatory	$EN \sim 1$	0.56	-	-	-	-
Survival	20	Depensatory	$EN \sim q + Body$	0.46	34.0	7.1	26.9	-

 $ER_{EN} > 4$ and $ER_{CF} > 4$

Table 35. Compensatory ensemble feedback EN (EN) fitted as a function of sample size in the time series (q , years), body size ($Body$ = body length, in mm), and component feedback EN (CF) in birds and mammals [n = number of demographic rates included in the contrast of each model set]. $wAIC_c$ are model probabilities (shown only top-ranked models in a set), and DE is % deviance explained (total and broken down by predictors). Model fits were done using all demographic rates having strong support for component feedback ($ER_{CF} > 4$), split by fertility or survival rates; and all types of component feedback, split by compensatory or depensatory feedbacks. Included demographic rates from populations with strongest AIC_c evidence ratio for ensemble feedback ($ER_{EN} > 4$). See model set in **Table 12**.

Rates	n	Component feedback type	Top-ranked models	$wAIC_c$	DE_{total}	DE_q	DE_{BL}	DE_{CF}
All	57	All	$EN \sim 1$	0.57	0.0	-	-	-
Fertility	31	All	$EN \sim 1$	0.45	0.0	-	-	-
Survival	26	All	$EN \sim 1$	0.51	0.0	-	-	-
All	38	Compensatory	$EN \sim 1$	0.69	0.0	-	-	-
Fertility	17	Compensatory	$EN \sim 1$	0.62	0.0	-	-	-
Survival	21	Compensatory	$EN \sim 1$	0.51	0.0	-	-	-
All	19	Depensatory	$EN \sim q + Body$	0.58	37.1	15.6	21.5	-
Fertility	14	Depensatory	$EN \sim q$	0.51	32.8	32.8	-	-
Survival	5	Depensatory	$EN \sim q + Body + CF$	1.00	74.3	11.0	58.9	4.4