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The Evolution of Avian Growth Rates in Variable Environments

A thesis presented in partial fulfillment of the requirements for the degree of

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in

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John Clive Ashton

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ERRATA

Chapter 1

- (i) Page 3, line 9, “glow growers” should be “slow growers”.
- (ii) Page 3, lines 30-31 imply that the Fieldfare is a ground nester, whereas it actually has cup nests in trees.
- (iii) Page 6, line 10, “that a the” should be “that the”
- (iv) Page 9, line 13, “ideals” should be “ideal”

Chapter 2

- (i) Equation 2.1 should be:

$$Mt = Ma - (Ma - Mo) \cdot \exp\left\{-\ln\left(\frac{1 - \frac{Mo}{Ma}}{0.5}\right) \cdot \left(\frac{t}{t_{50}}\right)^p\right\}$$

- (ii) In regard to the section in the methods that describes the use of phylogenetic contrasts, it should be noted that all regressions were forced through the origin.

Chapter 3

- (i) Table 3.3 legend, “all three independent variables. *V*, *FF* and *PD*...” should be “both independent variables. *V* and *FF*...”
- (ii) Fig. 3.3 legend, last sentence refers to an earlier draft.
- (iii) Page 54, second paragraph, reference to Fig. 2.2 should be to Fig. 2.1.

Chapter 4

- (i) In Fig. 4.9 *Junco hyemalis* is classified as a protected nester, whereas nest sites are in fact variable for this species, sometimes cavities and sometimes in the open.
- (ii) Page 57, line 20, “it not specify” should be “it does not specify”
- (iii) Fig. 4.5, “horizontal” should be “horizontal”.

Chapter 5

- (i) Page 82, 3rd paragraph “If energy is....periods of starvation” is a repeat of the previous paragraph.
- (ii) Fig. 5.6 legend, “horizontal” should be “horizontal”.

Chapter 6

Page 122, 2nd sentence, should read “With an ideal food supply, as the maximum fat deposition rate increases, *GRI* increases, and the probability of fledging decreases by a small amount”

Chapter 7

- (i) The methods should state the fact that approval from the Massey University Animal Ethics Committee was obtained for the brood swapping and deprivation experiments.
- (ii) “Control” chicks in the deprivation experiment are not controls in the sense that conditions are normal for those chicks (e.g., they may have increased food supply during the experiment) and should be referred to as “non-deprived” chicks.
- (iii) Table 7.4 legend, “Treatment chicks (C)...” should be “Treatment chicks (T)...”

Chapter 9

Page 179, paragraph 2; this argument applies to *case* probabilities only. The frequency interpretation of *class* probabilities is compatible with determinism and is an objective theory of probabilities.

Appendix 1

Parus major, *P. Montanus*, and *Sturnus vulgarus* are wrongly recorded as unprotected nesters in Table A1.2, whereas in fact they are protected nesters.

Abstract

Tubenoses and swifts develop slowly, and often have a variable food supply. Lack (1968) attributed this to convergent evolution, arguing that slow growth is an adaptation allowing survival in environments with a variable food supply. In this thesis, I test whether there is a general relationship among bird species between slow growth rate and variability in food supply. I analysed data on nestling period, growth rates for mass and wing length, and variability in food supply in birds using phylogenetically independent contrasts.

Variability in food supply may be correlated with feeding frequency, and growth rate is correlated with predation risk. I included these potential confounds in my analysis. Variability in food supply was correlated with nestling period, and negatively correlated with mass and wing growth rate, taking average feeding frequency and predation risk into account. I show that nest site preference is incompletely coadapted with growth rate. The correlations between growth rate and variability in food supply could also be explained by the proximate effect of environmental variability on growth. I therefore tested predictions of Lack's hypothesis, in comparison to those of growth models assuming facultative growth adjustments in response to variability in food supply. This further supported Lack's hypothesis.

While Lack proposed that slow growth is an adaptation to variability in food supply, he did not explain the underlying mechanism. I examined three possible mechanisms, along with two alternative explanations where slow growth is not an adaptation to a variable food supply, and tested them with comparative data. I developed two of these models using computer simulations which predicted that survival is increased by reducing maximum lean tissue growth rates and increasing maximum fat deposition rates when food supply is variable. I tested predictions from these models using experiments on the Welcome Swallow, corroborating a model that predicts that lean tissue growth is prioritised over fat deposition but that fat deposition is facilitated by reduced lean tissue growth rates. I also tested whether swifts and tubenoses are adapted to an unpredictably, or predictably, variable food supply, and discuss the degree to which chicks of swifts and tubenoses are well designed for survival in environments with a variable food supply.

Acknowledgments

The primary idea in this thesis that slow growth is an adaptation to a variable food supply belongs to Ed Minot. He played a major role in helping me to develop the ideas early on in my study. My doctoral supervisor Doug Armstrong has made more suggestions and provided me with more insights than I can count. I am deeply grateful for the enormous amount of time and effort he has devoted to the role of supervisor. I am also grateful for the confidence he has shown in me, especially in his support for my bid for a scholarship. My wife Louise has read passages of the thesis, helped me with field-work, took the photographs that appear in Chapter 7, and helped me in innumerable other ways. Most importantly I owe to her the opportunity that I have had to undertake a doctoral thesis at all. Her support has been immeasurable. This thesis would also have been impossible if it were not for the financial support I had from a Massey Doctoral Scholarship. Bob Jolly listened patiently to my early ideas and offered helpful advice. He and Aileen Jolly provided me with lodgings free of charge near Massey University, which was a tremendous help. Clare Veltman gave me valuable feedback on my thesis proposal and made numerous helpful suggestions. Ian Jamieson suggested the deprivation experiment that appears in Chapter 7. Discussions with Wayne Linklater ultimately lead to Chapter 3. Conversations with Dave Lambert made me consider more alternative hypotheses and interpretations than I would have otherwise. Many ideas in this thesis are direct responses to criticisms he raised in these discussions. Ian Henderson gave me useful advice on phylogenetic analysis. Suggestions by Brian Springett helped me to select the method that I used to sample insects in Chapter 7. My ideas on adaptation that appear in Chapter 9 have been improved with the help of suggestions and criticisms from G.C. Williams, D.C. Dennett, Richard Dawkins, and John Catalano. Professors Williams and Dawkins took the time to send me important references. Charles Sibley was kind enough to send me up-to-date phylogenies for the tubenoses and other taxa. Thanks are due also to the various orchard-owners of Twyford, Hawkes Bay, who not only tolerated my skulking about under their culverts and bridges in my pursuit of Welcome Swallow data, but also offered me observations on Swallow breeding sites and dates.

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