

# THE PRUDENT PARENT: ENERGETIC ADJUSTMENTS IN AVIAN BREEDING <sup>1)</sup>

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## CONTENTS

1. Introduction: the dilemma of the prudent parent.....	225
2. Condition thresholds for breeding .....	226
3. Laying date and clutch size in relation to food supply .....	228
4. Energetic implications of variation in growth rate....	233
5. Parental effort and optimal working capacity .....	241
6. Perspective .....	246
7. Summary .....	248
8. Acknowledgements .....	249
9. References .....	249
10. Appendix .....	252

### 1. INTRODUCTION: THE DILEMMA OF THE PRUDENT PARENT

We accept Lack's (1968) contention that features characterizing breeding in birds such as laying date, clutch size, growth rate and duration of the nestling period have all evolved so that in their natural habitat "the birds concerned produce, on average, the greatest possible number of surviving young". Lack identified the main selective pressures responsible as "the availability of food, especially to the young and to a lesser extent to the laying female, and the risk of predation on eggs, young and parents". He closed his book by deploring the circumstantial nature of his evidence (mainly comparisons drawn between closely related species) and urged future workers to engage in field experiments. This approach he considered more valuable than his speculative one, but he warned that experimentation would help to clarify interpretation of breeding adaptations only "if the experimenter is a naturalist capable of designing appropriate experiments and of appreciating the complexity of each situation".

In taking up this challenge we must first explore the context of the question. Implicit in Lack's approach is an emphasis on the pooled

wisdom of the species, that is the genetic component, explicable only in terms of the ultimate survival value of the trait. In this view field experiments are expected to demonstrate why the species has arrived at a favoured range of laying dates, clutch sizes, or some other breeding parameter. This can be done by comparing the fates of young born early or late, or originating from broods of various sizes. The difficulty in this approach is that this best of all possible worlds is not met with: most individual birds are cautious parents. The majority of parents delay laying to beyond the most favourable date *i.e.* beyond the date giving maximum probability of nestling survival for the population (Murton 1961, Lack 1966, Perrins 1970, Harris 1969) and produce a clutch smaller than the most productive one (Perrins & Moss 1975; Drent & Ward, in prep.). We are forced to the interpretation that achievement of the most productive laying date and clutch size must entail a substantial decline in subsequent survival were most parents to attempt this. The salient problem is thus that there is not one invariant answer to the question "when should I lay my first egg" or "how many eggs should I lay" but instead the answer appears to depend on some interplay between local environmental conditions and the state of the parent (general proficiency as influenced by experience and state of energy and nutrient balance). Differences between parents and among the same parents from year to year thus become the vital points demanding explanation rather than annoying uncertainties clouding the major issue of species patterns. In our opinion field experimentation aimed at evaluating the adaptedness of breeding patterns should place the question in the framework of individual selection. It should emphasize the adaptive significance of phenotypic variation, the fine adjustment allowing a continuously close fit to altering environmental conditions and equally shaped by natural se-

<sup>1)</sup> dedicated to Prof. dr. Lars von Haartman on the occasion of his 60th birthday.