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Avian adaptation along an aridity gradient

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PART I

Introduction

CHAPTER 1

General introduction

B. Irene Tieleman

Incentive for this thesis

This thesis was inspired by my interest in the causation and function of the variation in physiology, behavior and life history of birds in relation to environmental conditions. The large diversity in physiological parameters, behavioral strategies and demographic variables found among endotherms of similar size has puzzled many biologists. Yet, few comprehensive studies exist that explore these three components in a single system. Traditional life history theory focuses on demographic parameters, such as growth, reproduction and survival, that optimize the match between organism and environment (Stearns 1992; Roff 1993). Studying the physiological and behavioral mechanisms that constitute adaptations to the environment may well provide insights into the evolutionary forces and constraints that underlie variation in these traditional life history parameters. In this thesis I treat physiological and behavioral traits that give insights into how phenotypes are designed for reproduction and survival in specific environments as additional important attributes of life history. I hope that this approach further advances our understanding of the connections between physiology, behavior and demography in the context of environmental conditions.

Deserts and birds

Biologists have long been aware that organisms living in extreme environments provide good examples of evolutionary adaptation (Bartholomew 1986). With scant rainfall, low primary productivity and high ambient temperatures, arid environments combine extreme thermal conditions with a low availability of food and water for their inhabitants. Especially for birds, with their high mass-specific energy and water requirements, occupying deserts may require substantial adjustments in energy and water balance (Dawson 1984; Williams 1996). Because energy and water are potential currencies that underlie life history trade-offs, such adjustments may have far-reaching implications for reproduction and survival of birds in deserts. Chapter 2 provides an introduction to the deserts of the world and a general review of the physiological and behavioral adjustments used by desert birds to survive in their environment. This chapter summarizes the literature up to 1998, questions previous studies that suggest that birds have not evolved physiological specializations for desert life, and presents hypotheses to be tested. Chapter 3 collates literature data to specifically compare the energy and water balance of desert and non-desert birds, in the field and in the laboratory.

A comparative approach

The comparative method is a powerful tool that establishes correlations among phenotypic traits and between phenotypes and environments to develop and test hypotheses about ecological and evolutionary processes (Harvey & Pagel 1991;

Schmidt-Nielsen 1997). Comparative studies of desert versus non-desert birds have encountered a number of problems that may have obscured useful biological information. First, species have been categorized as desert or non-desert, whereas in reality natural environments form a continuum that depends on the interaction of meteorological and geographical factors, including temperature, amount and timing of rainfall, latitude, altitude, and continentality. Second, comparative work typically includes a large variety of species and has the inherent interpretational problem that species differ not only in habitat, but also in phylogenetic background, diet and behavior. Third, comparisons among species from different studies may be complicated by the use of a variety of methods to measure different physiological and behavioral characters at diverse times of the year. Restricting comparative analyses to a single clade of closely related species occurring in different habitats along an environmental continuum provides the opportunity for a detailed examination of adaptation of physiology, behavior, and life history. Such an approach potentially limits complications due to markedly different evolutionary history, dissimilar current life styles or varying methodological techniques.

Larks along an aridity gradient: a study model

My study model comprised a number of species of larks that occur in habitats along an aridity gradient. The family of larks (Alaudidae) is one of few avian families that has representatives living in environments ranging from hyperarid deserts, through arid, semi-arid and mesic areas, to even arctic habitats (Cramp 1988; Pätzold 1994). Environmental aridity is directly related to primary productivity (Emberger 1955) and provides a proxy for the selection pressures that animals experience with increasing aridity, including decreasing water and food availability and increasing temperatures. Because all larks are ground-foraging and ground-nesting birds that eat similar foods, a mixture of seeds and insects, diet and behavior do not confound comparisons of physiogical, behavioral and demographic traits among species (McNab 1988). The lark family has a number of additional characteristics that make it an attractive study model. First, all species are active during the day and lend themselves to behavioral observations. Second, larks readily adjust to captivity and are therefore suitable for laboratory studies. Third, larks can be captured and recaptured in the field enabling repeated measurements on the same individual as required by techniques such as the doubly labeled water method. Fourth, we have constructed a phylogeny of the lark family and can take into account phylogenetic relationships in analyses when appropriate (Chapter 4). Finally, most species are year-round residents or short-distance migrants and therefore live within a single characteristic geographical area.

Patterns in physiology and behavior of larks

Part II contains a series of comparative studies that explore the variation in the physiological and behavioral performance among and within species and individuals of larks from different environments in the laboratory and in the field. Chapter 4 presents a study to test the hypothesis that lower levels of basal metabolic rate (BMR) and total evaporative water loss (TEWL) in larks are correlated with increasing aridity. Along with several other investigators, I construct a phylogeny of larks based on two mitochondrial genes and investigate if evolutionary history can explain the present-day variation in BMR and TEWL along an aridity gradient. The physiological variation among larks along an aridity gradient could result from genetic adaptation to the environment by natural selection or from phenotypically plastic adjustments by acclimatization. Chapter 5 explores whether the interspecific differences in physiology among larks can be attributed to acclimation to temperature. In addition, this chapter investigates the hypothesis that in deserts, where the selection pressures on the energy and water balance might be stronger and the temporal heterogeneity of the environment larger, birds show less interindividual variation and more intra-individual flexibility in their physiology than do species from moderate climates. An overview of the physiological performance over a range of environmental conditions, with an emphasis on high temperatures, of larks from the extremes of the aridity gradient is given in chapter 6. Chapter 7 discusses the roles of cutaneous and respiratory water loss in reducing TEWL at moderate ambient temperatures in desert larks compared with mesic species, and in maximizing the potential for evaporative cooling when birds are heat stressed. It also investigates the intra-individual phenotypic flexibility of these avenues of evaporative water loss for four species in response to acclimation to different climates. The final chapter of part II, chapter 8, integrates the laboratory physiology of the previous chapters with data on the energy and water balance of a number of larks in the field during the reproductive season. A combination of information about parental effort, brood size, nestling energy and water budgets, and nestling growth rates enables establishment of energy and water budgets for complete families. This integrative approach provides fuel for a discussion of behavioral, physiological and environmental constraints on annual reproductive efforts in light of life history theory.

Physiological mechanisms

Identifying the physiological mechanisms that determine the performance of phenotypes in diverse environments could provide insights into selection pressures and evolutionary constraints. In part III I examine a number of physiological mechanisms and explore which of these are responsible for the variation in whole-organism traits among species and individuals from different environ-

ments. Chapter 9, in combination with chapter 5, explores if the reduced BMR and TEWL in desert species can be explained by phenotypically plastic adjustments of these traits to low thermoregulatory requirements, and if phenotypic plasticity itself varies with environment. These chapters investigate if the sizes of internal organs provide a mechanistic explanation for the variation in BMR between and within species. The subsequent three chapters examine the quantitative contributions of three mechanisms that have been proposed to reduce TEWL in desert birds. Chapter 10 describes an experiment to measure the water saving effect of counter-current heat exchange in the nasal passages at a variety of temperatures in two species of larks. Chapter 11 models the effect of hyperthermia, an increase in body temperature, on components of the water balance of birds that vary in body size. Predictions based on this chapter are evaluated in chapter 6 for lark-sized birds, and in chapter 12 for a large desert bird, the Houbara Bustard.

Behavioral strategies

How behavioral strategies of desert birds point to environmental and physiological constraints is the topic of part IV. Chapter 13 describes a study of the microsites selected by larks in the Arabian Desert to ameliorate the thermal environment during the hot summers. To investigate how time budgets of desert birds are affected by the thermal environment and by low availabilities of water and food, chapter 14 reports results of a food supplementation experiment on Hoopoe Larks. These birds optimized time spent on foraging and thermoregulation based on a combination of physiological state variables, indicating the presence of both environmental and physiological constraints on the behavior of desert birds.

Physiology, behavior and life history: a synthesis

Part V presents an integrative perspective of avian adaptation along an aridity gradient and discusses physiology and behavior in the context of life history variation. In chapter 15 I point out links between physiological adaptations, behavioral strategies, and demographic parameters, such as reproduction and survival, in light of environmental and ecological constraints. In addition, I indicate some directions for future work: Although this thesis is an end product that marks the completion of four years of research, it is also a way station that shows how far along we are on our road of discovery.

The diversity of life has inspired generations of biologists to explore, describe and experiment in an attempt to understand origin, mechanism and function of the living world around us. Early naturalists made careful observations upon which they based the foundation for Biology as a discipline, the Theory of Natural Selection (Darwin 1859; Wallace 1858). Their work structured later research that added to the levels of ecosystems and organisms the study of organs, cells and molecules, but still pursued the same questions: What makes up the diversity of life? From where do organisms come? How do they work? Why do they work the way they do? Modern biologists face the extra challenge of integrating the knowledge of the diverse levels of study, from ecosystems to molecules. More than ever it appears that the more we discover, the more questions remain. In pursuit of some answers I have had the opportunity to travel and work in remote areas where I encountered exceptional species, experienced amazing habitats and learned about different cultures, but also to marvel at nature close to home. What a privilege and a joy to be part of this search for knowledge.