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A blurring of life-history lines: Immune function, molt and reproduction in a highly stable environment

Loren Merrill [a,*], Paulina L. González-Gómez [b], Vincenzo A. Ellis [c], Iris I. Levin [d,e], Rodrigo A. Vásquez [f], John C. Wingfield [g]

[a] *Illinois Natural History Survey, University of Illinois, Urbana-Champaign, IL 61820, USA*
[b] *Instituto de Filosofia y Ciencias de la Complejidad (IFICC), Santiago, Chile*
[c] *Department of Biology, University of Missouri, St. Louis, MO 63121, USA*
[d] *Department of Biology, Grinnell College, Grinnell, IA 50112, USA*
[e] *Department of Ecology and Evolutionary Biology, University of Colorado at Boulder, Boulder, CO 80309, USA*[1]
[f] *Instituto de Ecología y Biodiversidad, IEB, Universidad de Chile, Santiago, Chile*
[g] *University of California Davis, Davis, CA 95616, USA*

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ABSTRACT

Rufous-collared sparrows (*Zonotrichia capensis peruviensis*) from valleys in the Atacama Desert of Chile, live in an extremely stable environment, and exhibit overlap in molt and reproduction, with valley-specific differences in the proportion of birds engaged in both. To better understand the mechanistic pathways underlying the timing of life-history transitions, we examined the relationships among baseline and stress-induced levels of corticosterone (CORT), testosterone, and bacteria-killing ability of the blood plasma (BKA), as well as haemosporidian parasite infections and the genetic structure of two groups of sparrows from separate valleys over the course of a year. Birds neither molting nor breeding had the lowest BKA, but there were no differences among the other three categories of molt-reproductive stage. BKA varied over the year, with birds in May/June exhibiting significantly lower levels of BKA than the rest of the year. We also documented differences in the direction of the relationship between CORT and BKA at different times during the year. The direction of these relationships coincides with some trends in molt and reproductive stage, but differs enough to indicate that these birds exhibit individual-level plasticity, or population-level variability, in coordinating hypothalamo–pitui tary–adrenal axis activity with life-history stage. We found weak preliminary evidence for genetic differentiation between the two populations, but not enough to indicate genetic isolation. No birds were infected with haemosporidia, which may be indicative of reduced parasite pressure in deserts. The data suggest that these birds may not trade off among different life-history components, but rather are able to invest in multiple life-history components based on their condition.

1. Introduction

Life-history theory proposes that organisms trade off between competing functions due to resource constraints (Stearns, 1992). The classic example is allocation of resources to current versus future reproduction, and the inherent trade-off between self-maintenance and reproductive effort (Stearns, 1992; Sheldon and Verhulst, 1996; Schmid-Hempel, 2003). Molt and immune function are the best-studied components of self-maintenance in birds. Molt quality influences thermoregulatory capacity (Nilsson and Svensson, 1996; Dawson et al., 2000), flight performance (Swaddle et al., 1996; Echeverry-Galvis and Hau, 2013), and plumage-based signal quality (Smith and Montgomerie, 1991; Serra et al., 2007), all of which have important fitness implications. Immune system function is also an integral factor shaping avian fitness (*sensu* Combes, 2001; Davison et al., 2008); it determines the ability to inhibit or limit parasite establishment and is responsible for the regulation or elimination of established infections (Davison et al., 2008 and references therein). Together, molt and immune function can have large-scale consequences for future reproductive capacity.

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* Corresponding author at: 1816 S. Oak St., Champaign, IL 61820, USA.
E-mail addresses: loren21@illinois.edu (L. Merrill), plgonzalezgomez@gmail.com (P.L. González-Gómez), vincenzoellis@mail.umsl.edu (V.A. Ellis), Iris.Levin@colorado.edu (I.I. Levin), rvasquez@uchile.cl (R.A. Vásquez), jcwingfield@ucdavis.edu (J.C. Wingfield).

[1] Current address.

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Molt and immune defenses demand energy and resources (-molt: Murphy, 1996; Hoye and Buttemer, 2011; immunity: Klasing, 2004), and there is a large body of work examining pair-wise trade-offs among molt, immunity, and reproduction (e.g., molt-immunity: Moreno-Rueda, 2010; Ellis et al., 2012; molt-reproduction: Barta et al., 2006; Johnson et al., 2012; reproduction-immunity: Deerenberg et al., 1997; Ardia, 2005; Kelly, 2011). There is evidence that most birds undergo seasonal changes in which they invest differentially among these three life-history functions (e.g., Nelson and Demas, 1996; Zera and Harshman, 2001; Wingfield, 2005). For example, most temperate birds exhibit discreet periods of breeding and molt, with molt typically occurring at the conclusion of breeding (Morton, 1992; Barta et al., 2006; Johnson et al., 2012). Immune function can also vary over the annual cycle (Nelson and Demas, 1996; Hegemann et al., 2012; Merrill et al., 2013), as organisms allocate resources between self-maintenance and current reproduction in response to resource limitation, or if parasite pressure changes over the course of the year (John, 1994; Horrocks et al., 2012a).

Organisms also use seasonal cues (e.g., photoperiod, rainfall) to initiate different life-history stages, and these life-history stages are typically regulated, at least in part, by circulating glucocorticoids and androgens (Wingfield, 2005). However, organisms that live in stable environments with little seasonal variation in resource availability, or little change in photoperiod, temperature or rainfall, may not need, or be able, to utilize seasonal cues. In these cases, what factors determine life-history stage, and do organisms exhibit trade-offs among different life-history stages? Birds that do exhibit overlap of multiple life-history stages, such as molt and reproduction, may attempt to reduce the costs of one or both processes. They can do this via reduced molt intensity (Echeverry-Galvis and Hau, 2012), smaller clutches (Foster, 1974), and extended incubation (Ricklefs and Brawn, 2013). However, little work has been conducted on measures of immune function, molt and reproduction concurrently, especially over an entire year. The goal of this study is to understand how birds balance immune function, molt and reproduction in two discrete populations in an environment with little seasonal variation. Additionally, we explore whether population differences might be attributed to differential parasite pressure or population genetic differences.

Previously, we examined the relationships among corticosterone (CORT), testosterone (T), reproduction and molt in rufous-collared sparrows (*Zonotrichia capensis peruviensis*) over the course of a year in the Atacama Desert of Chile (Gonzalez-Gomez et al., 2013). This desert is the driest and oldest desert on the planet (Hartley et al., 2005) and exhibits very little change in environmental conditions over the year. We studied sparrows living in two valleys (Azapa Canyon and Lluta Canyon) separated by 1000 m high canyon walls and 25 km of non-vegetated desert habitat, inhospitable to these birds. We documented most of the birds molting during March and breeding in October, indicating that the birds maintain some semblance of an annual cycle, although many of the sparrows diverge from the general trends. We found individuals molting or breeding year round, as well as individuals engaging in both breeding and molt in every sampling period during the year. We also found that the sparrows in the two valleys exhibited distinct patterns from each other. Among birds engaged in breeding, approximately five times as many birds overlap breeding and molting in Azapa as in Lluta (25% vs. 6%, Gonzalez-Gomez et al., 2013). We also found differences in body condition with relatively heavier birds in Azapa than in Lluta in January but the opposite pattern in December. In addition, stress-response levels are significantly higher in Lluta than in Azapa in January. Despite these differences, there were no data on the genetic structure of the two breeding groups to help determine whether the differences between the two sites were due to genetic or environmental reasons. Although 25 km is a relatively short distance, previous studies have found genetic differences between two populations of *Z. capensis* that live 25 km apart inhabiting benign environments that theoretically do not represent a dispersal barrier to this species (Moore et al., 2005) as could be the inhospitable Atacama Desert.

Here we expand upon previous work with these birds (Gonzalez-Gomez et al., 2013) and incorporate an aspect of immune function (bacteria-killing ability), prevalence of haemosporidian blood parasite infections, and preliminary data on the genetic structure of the two populations of *Z. capensis* to help better understand the factors that shape how and when these birds allocate resources among multiple life-history stages. We have also included levels of testosterone (T) as well as baseline and stress-induced levels of corticosterone (CORT). In our prior study we examined the relationships between T and life-history stage as well as between both baseline and stress-induced CORT levels and life-history stage to determine if the hormones are associated with regulation of life-history trade-offs in this minimally seasonal environment. We found that CORT varied with time of year and with life-history stage in these birds and that during the period in which most birds were engaged in molt to some degree (March), birds down-regulated their stress-response (Gonzalez-Gomez et al., 2013). Birds not engaging in molt at this time, however, still exhibited this down-regulation. Other populations of *Z. capensis* undergo molt at different times during the year (e.g., May/June for those in the nearest study locale, Lima, Peru; Davis 1971), suggesting that sparrows in these valleys may be fine-tuned to local conditions. If this is the period of peak molt for the population, perhaps down-regulation of the stress response has been set to some circannual (e.g., photoperiod) or environmental cue (e.g., slight variation in stream flow or food availability), but the actual molt stage has become decoupled from hypothalamo–pituitary–adrenal (HPA)-axis activity and depends on other factors such as reproductive stage, and/or individual condition.

In the current study we used BKA as a functional assessment of the birds' immune defenses against a bacterial pathogen. We have previously found BKA to vary seasonally in other species (e.g., Icterids, Merrill et al., 2013) and it may be traded-off against molt (Ellis et al., 2012, but see Buehler et al., 2008) and reproductive effort (Merrill et al., 2013). In addition, we have found BKA to be positively linked to baseline CORT, and negatively linked to stress-induced CORT levels (Merrill et al., 2012, 2014), and T levels (Merrill et al., 2015) in blackbirds. We were interested in whether T or CORT were linked to regulation of immune function in these sparrows, and if so, in what manner.

For parasite assessment we screened for both *Plasmodium* and *Haemoproteus* blood parasites because these are known to infect *Z. capensis* in South America (Durrant et al., 2006; Merino et al., 2008; Jones et al., 2013) and are capable of exerting strong selective pressure on their bird hosts (Allander, 1997; Ots and Hõrak, 1998; Atkinson et al., 2001; Knowles et al., 2009; Martinez-de la Puente et al., 2010; Lachish et al., 2011; Watson, 2013). However, animals in desert environments may have lower prevalence and intensity of both endo and ectoparasites (Little and Earlé, 1995; Tella et al., 1999; Moyer et al., 2002; Valera et al., 2003; Horrocks et al., 2012b), and could be under reduced parasite pressure. For example, recent work examining blood parasites in the cinereous conebill (*Conirostrum cinereum*) in the same region of the Atacama Desert found one trypanosome infection and no other blood parasites among the 30 individuals assessed (Martinez et al. unpublished data).

Previously, we found that body condition (residuals of body mass over tarsus) in these sparrows varied over time, and that there were differences among sampling periods and localities in the proportion of birds engaging in molt and/or reproduction