VALIDATING BODY CONDITION INDICES AS INDICATORS OF INDIVIDUAL QUALITY: DOES CONDITION EXPLAIN INTRASPECIFIC VARIATION IN REPRODUCTIVE SUCCESS AND SURVIVAL AMONG CRIMSON FINCHES (*NEOCHMIA PHAETON*)?

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Dissertation submitted to the faculty of the Virginia Polytechnic Institute and State University in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

In

Biological Sciences

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03 September 2013

Blacksburg, Virginia

Keywords: conservation, fitness, life-history theory, physiology, repeatability

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ABSTRACT

Body condition is expected to reflect individual quality because high quality individuals should be better at acquiring and using resources, resulting in higher fitness. However, the hypothesis that condition indices are meaningful indicators of individual quality has been questioned. I monitored a population of crimson finches (*Neochmia phaeton*) for reproductive success and survival over four breeding seasons. My study population is well suited for this research because individuals forage in common areas and do not hold territories such that variation in condition between individuals is not confounded by differences in habitat quality. Because little is known about crimson finches in the wild, I first describe their breeding biology and life-history traits (Chapter I). Next, I sampled them for commonly used condition indices including mass adjusted for body size, muscle and fat scores, packed cell volume, hemoglobin concentration, total plasma protein, and heterophil to lymphocyte ratio. I describe the variation in these indices and find that many vary by sex and breeding stage, and to a lesser extent by year, age and time of day, concluding that these covariates need to be controlled for when examining intraspecific variation in condition (Chapter II). If condition indices reflect inherent individual

quality, then condition indices should be (a) repeatable within individuals, and (b) predictors of realized fitness. I test these two predictions in Chapters III and IV, respectively, and I find that condition indices are repeatable within individuals over short, but not long, time periods and that some indices predict reproductive success, while others do not, and that none predict survival. Both findings only partially support the hypothesis that condition indices are meaningful indicators of individual quality, raising concerns over this common interpretation. In Chapter V, I glean insights from the ecological and poultry science literature and discuss further complications with the use of condition indices as proxies for individual quality and fitness. I conclude that condition indices indicate how well an individual is currently acquiring resources as well as its likely physiological state over the next few months, but that they do not reflect individual quality and are not reliable proxies for fitness.

DEDICATION

To my teachers.

ACKNOWLEDGEMENTS

I am thankful to my advisor and mentor, Jeffrey R. Walters, for being particularly patient and trusting. Asking to join his lab was one of the best decisions I have ever made. Ignacio T. Moore, Dana M. Hawley and William A. Hopkins served on my advisory committee and greatly contributed to this dissertation and to my professional development. They engaged me in thoughtful discussions and found the perfect balance in both challenging and supporting me. I could not have asked for a better committee.

It was my pleasure to work with several phenomenal collaborators. Sarah Legge and Stephen Murphy initiated the research that became my dissertation work. Sarah Legge and the Australian Wildlife Conservancy made the research possible by supporting me at my field site with logistical support, accommodation, transportation, field equipment, and advising. This study was funded by the Australian Wildlife Conservancy and was based out of the WildlifeLink Centre for Research and Conservation at Mornington Wildlife Sanctuary. Nicole Weinstein advised me on hematological condition indices and taught me how to perform white blood cell differentials. I greatly appreciate Daniel Catlin for working with me on survival analyses.

I am thankful to my field technicians, Roy Churchwell, Evan Rehm and Jennifer Bruce. They worked long hours under challenging conditions to collect these data, without which I could not have addressed the research questions in this dissertation. I am grateful to Roy for being my first field technician which meant that his job was made more difficult than necessary by my lack of experience in managing people. I thank him for his patience. To Evan, I am forever indebted for his positive attitude, great communication skills and phenomenal work

ethic; all of which made that field season exceptionally successful and fun. I greatly appreciate Jennifer because despite the medical challenges that she endured, she persevered and was 100% committed to her work. Thank you.

Numerous other people also helped me in the field including all of the personnel, volunteers, and researchers at Mornington Wildlife Sanctuary. Kimberley Maute helped tremendously with advice, assistance in the field, thoughtful discussions on condition, and friendship. Michelle Hall was an outstanding mentor and teacher. Thanks to Alicia Young for helping in the field and trying to keep me sane, and to Stephen Murphy, John Pass, Jessica Bolton, Julie and Richard Kingswood, Joanna Axford, Malcolm Kennedy, Taegan Calnan, and Benjamin L. Phillips for their support. In particular, I am indebted to Butch and Robin Maher for their friendship and who, with their hospitality, warmth, and generosity, taught me so much about the region and about humanity more broadly.

Thanks to the Avian Ecology Lab at Virginia Tech for their support. In particular, thanks to Michelle Jusino for her friendship throughout, to Victoria Garcia for being my mentor, statistical adviser and therapist, and to Jonathan Moore for showing me what a great teacher can do. I am grateful to Robert Gunter, Sue Rasmussen and the other administrative and book keeping staff at the Department of Biological Sciences at Virginia Tech for being tremendously helpful over the last five years.

I thank my friends for supporting me, and in particular, my mother, Lena Kolesnikova, for instilling in me a love of nature and for encouraging me to pursue my interests. I am grateful to my partner, James Lindley McKay, for his love, patience and unwavering commitment. He is my inspiration.

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ATTRIBUTION

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Dr. Sarah Legge, National Conservation and Science Manager, Australian Wildlife Conservancy, Derby, Western Australia 6728, Australia. Dr. Sarah Legge initiated the research that became my dissertation work and was my advisor while I was in the field. She is a coauthor on the publications resulting from Chapters I and II and the manuscripts resulting from Chapters III and IV.

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Dr. Daniel Catlin, Research Assistant Professor, Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, Virginia 24061, USA. Dr. Daniel Catlin advised me on survival analyses and is a coauthor on the manuscript resulting from Chapter IV.

CHAPTER I. BREEDING BIOLOGY AND LIFE-HISTORY TRAITS OF AN AUSTRALASIAN TROPICAL GRANIVORE, THE CRIMSON FINCH (*NEOCHMIA PHAETON*)

Olga Milenkaya, Sarah Legge, and Jeffrey R. Walters

This article has been published as: Milenkaya, O., Legge, S., and Walters, J.R. (2011). Breeding biology and life history traits of an Australasian tropical granivore, the Crimson Finch *Neochmia phaeton*. *Emu* **111**(4), 312–320. Used with permission of CSIRO Publishing. http://www.publish.csiro.au/paper/MU10088.htm

Abstract. The evolutionary basis of the latitudinal gradient in clutch-size is a major, unresolved question in life-history theory, the resolution of which is hampered by the lack of proportionate study of southern passerines. Here, we present detailed data on breeding biology and life history for an Australasian tropical granivore, the Crimson Finch (*Neochmia phaeton*), emphasising aspects of their life history that are atypical of southern passerines. We collected data over three breeding seasons at Mornington Wildlife Sanctuary in north-western Australia. Apparent annual survival of adults was high, at 70–96%. Crimson Finches were multi-brooded and laid 5.08 ± 0.07 eggs per clutch. The rate of nest predation was high, with 59.7% of clutches lost to predation. Thus, Crimson Finch life history contradicts the leading explanation of the clutch- size gradient – that higher rates of nest predation and higher adult survival in southern species select

for smaller clutch-sizes. Our findings are more consistent with other explanations of the clutch-size gradient, specifically those involving post-fledging parental care, diet, seasonality and phylogeny. Exploring life histories that differ from the norm may be particularly helpful in understanding latitudinal differences in these strategies.

Keywords: clutch size; latitudinal gradient; life-history theory; reproduction; survival

INTRODUCTION

The clutch-size of passerines has been widely recorded to increase with latitude (Moreau 1944; Rowley and Russell 1991; Martin *et al.* 2000; Ghalambor and Martin 2001; Jetz *et al.* 2008). Tropical and southern-hemisphere temperate passerines (hereafter referred to as 'southern passerines') average just over two eggs per clutch, whereas northern-hemisphere temperate passerines (hereafter referred to as 'northern passerines') average over four eggs (Jetz *et al.* 2008). In addition to clutch-size, southern passerines differ from their northern counterparts in having higher adult survival (Yom-Tov *et al.* 1992; Johnston *et al.* 1997; Ghalambor and Martin 2001; Peach *et al.* 2001) and higher rates of nest predation (Lack 1949; Skutch 1985; Griebeler *et al.* 2010).

Moreau (1944) was one of the first to document the latitudinal gradient in clutch-size. Since then, various ecological hypotheses have been proposed to explain this pattern. Lack (1947) championed the idea that clutch-size is an evolutionary adaptation driven by natural selection to maximise fitness. The optimal clutch-size corresponds to the maximum number of

young that the parents can feed (Lack 1947), given an appropriate level of investment in current reproduction. Abundance of food or the ability of parents to collect the food is therefore the primary factor limiting clutch-size (Lack 1947). This food-limitation hypothesis predicts that clutch-size increases with latitude because food availability also increases with latitude (Lack 1947, 1948; Roff 1992). Similarly, Ashmole's (1963) seasonality hypothesis predicts small clutch-sizes in the south because the south lacks the spring food peaks and the harsh winters of the north. He hypothesised that the lack of a harsh winter contributes to the high adult survival observed among southern passerines. Mediated through density-dependent effects, this high adult survival creates food limitation and thereby also favours small clutch-sizes among southern passerines (Ashmole 1963).

Reproduction is costly and organisms face trade-offs between current reproduction and survival (Stearns 1992). As predicted by life-history theory, adult survival in passerines is negatively correlated with clutch-size (Ghalambor and Martin 2001; Peach *et al.* 2001). Northern passerines experience high rates of mortality and uncertainty about surviving to the next breeding season, favouring a large investment in current reproduction (Skutch 1985). In contrast, high adult survival in southern passerines may select for a small clutch-size because future reproductive potential is high (Skutch 1985).

Nest predation varies by latitude (Griebeler *et al.* 2010, and references therein) and may also be a selective pressure on clutch-size (Slagsvold 1982; Skutch 1985; Martin 1995; Ferretti et al. 2005). Either through proximate or ultimate mechanisms, higher nest predation may favour smaller clutch-sizes (Martin and Briskie 2009). For example, nest predation may result in food limitation to the young as adults trade off their provisioning rate with survival through perceived

predation risk (Skutch 1985). Juvenile survival may also affect clutch-size (Lack 1949), especially if juveniles require extensive parental care (Styrsky *et al.* 2005). Indeed, southern passerines generally have longer times to independence and remain with parents longer than do northern passerines (Russell *et al.* 2004).

Despite a long history of research, the reason for the evolution of different clutch-sizes across the latitudinal gradient remains unresolved (Ricklefs 2000). An informed discussion is hampered by the disproportionate study of northern passerines and a general lack of information about southern-hemisphere birds (Martin1996, 2004).

The Crimson Finch (Estrildidae: *Neochmia phaeton*; Figure A1.1), occupies the tropical savannas of northern Australia and New Guinea (Higgins *et al.* 2006). Its breeding biology and life-history traits are known primarily from aviculture (Shephard 1989; Vriends and Heming-Vriends 2002) and anecdotal field notes (Webb 1902; Storr 1977; Johnstone and Smith 1981; Immelmann 1982), with the exception of studies on diet (Todd *et al.* 2003), mouth markings of nestlings (Payne 2005) and nesting sites and timing of breeding (Todd 2002). A detailed description of life-history traits and breeding biology of wild Crimson Finches, however, is lacking.

Here we present empirical data on the breeding biology of wild Crimson Finches. Our expectation was that this species would follow the southern passerine pattern of small clutch-size, high adult survival and high rates of nest predation. Instead we document aspects of their life-history that are atypical of southern passerines, and discuss the implications of our findings for the evolution of clutch-size across the latitudinal gradient.

METHODS

Study site

A population of Crimson Finches was studied at the Australian Wildlife Conservancy's Mornington Wildlife Sanctuary in the Kimberley region of north-western Australia (17°30′49″S, 126°06′39″E, elevation 200 m). Breeding activity was monitored from 15 November 2006 to 11 April 2007, 5 December 2007 to 31 May 2008, and 9 December 2008 to 29 May 2009. Rainfall was measured at the site throughout the year with a standard rain gauge that was read daily. The climate was monsoonal, with a distinct wet season (annual rainfall = 847.7 ± 56.6 mm, of which 94.2 ± 3.4% fell between November and April over the 3 years of this study). The study site was a 2 km-long strip of riparian habitat along Annie Creek, a narrow zone dominated by River Pandanus (*Pandanus aquaticus*), *Melaleuca leucadendra*, River Red Gum (*Eucalyptus camaldulensis*) and figs (*Ficus* spp.). Non-native herbivores have been excluded from the area since 2004. Fire was actively managed in the surrounding tropical savanna, with prescribed burns during the late-wet and early-dry seasons. The site had 87.0 ± 6.1 breeding pairs of Crimson Finches each year (a minimum of 79 pairs in 2007, 83 in 2008 and 99 in 2009).

Searching for and monitoring nests

Nests were found by observing behavioural cues. Nest-building males were conspicuous, and 89% of nests were found during the building stage; 9% were found during laying or

incubation and 2% during the nestling stage (n = 852 nests over 3 years). We found most nests within the study area: across three breeding seasons, we found only 11 groups of fledglings that were not from previously known nests (9% of all fledged groups; n = 118). The status of nests (active or inactive) was determined on approximately every fourth day by unobtrusive behavioural observations. Contents of nests were checked to determine the start of laying and size of the complete clutch. Brood size was determined during nestling banding at ~6–10 days after hatching. The length of the breeding season was calculated as the number of equally good months for breeding (MacArthur 1964).

Morphology and moult

Adults were captured in mist-nets between 27 May 2004 and 20 May 2009 as part of this and another study. Birds were banded with a metal band (Australian Bird and Bat Banding Schemes, Canberra, ACT) and up to three plastic colour-bands for individual recognition. Sex was determined based on their sexually dimorphic plumage (Higgins *et al.* 2006). Mass, flattened wing-chord and head-bill length (distance from the back of the skull to the tip of the bill) were measured. The head-bill measurement reflects structural size. Mass, wing-length and head-bill measurements were compared between the sexes to test for sexual dimorphism. Mass is reported here from adults captured during the pre-breeding stage (2006–08) to avoid the effects of breeding on mass owing to, for example, eggs and the development of brood-patches. The cloacal protuberance and brood-patch were examined in males captured in 2008. Female brood-patches were routinely examined during all three breeding seasons. Any retained juvenile body

plumage was noted and the right wing was examined for retained juvenile greater primary coverts.

Social organisation

We determined group size for Crimson Finches in the dry and wet seasons based on resighting records. We also determined their rate of divorce, as the proportion of divorced pairs to the total number of pair-years. We considered a pair divorced if both individuals were found to be alive but no longer socially paired with each other.

Survival

Apparent annual adult survival (φ) and detection probabilities (ρ) were estimated to fit Cormack–Jolly–Seber models in Program MARK (White and Burnham 1999). Both recapturing and resighting events were used to build the encounter histories. Individuals that were resighted for the last time outside of the study site were excluded from the analysis because birds were not systematically monitored after dispersal. Six encounter occasions (one for each year from 2004 to 2009), two groups (male and female) and the sine-link function were used to assess survival based on 432 individuals. Goodness of fit was tested by parametric bootstrapping (1000 simulations) from the global model. The global model included sex, year and their interaction ($\varphi(sex \times year)$ $\rho(sex \times year)$). The variance-inflation factor ($\hat{c}$) was calculated as the observed deviance of the global model divided by the mean deviance of the simulated model. A $\hat{c} \leq 3$ suggests that there is little over-dispersion in the data. The global model and all nested models

were assessed using Akaike's information criterion corrected for sample size (AICc) and AICc weights. The effect of year on survival was tested with a likelihood ratio test in Program MARK. Estimates of apparent adult survival and detection probabilities were averaged across all models.

Juvenile survival and detection probabilities were also estimated to fit Cormack–Jolly–Seber models in Program MARK. A fully time-dependent model ($\varphi(t)$ $\rho(t)$) and the sine-link function were used. Both recapturing and resighting events were used to build the encounter histories. Five encounter occasions were used (one for banding and one for each of the 4 weeks after fledging). All nestlings that were banded and subsequently fledged (n = 253) were used for estimating survival into their first, second and third week after fledging.

Nesting

Height of nests was measured with a tape measure to 5 cm and the mean compared to the mean height of nests reported by Todd (2002). Nest-substrate and whether the nest was over land or water were recorded. The distance from each nest to the centre of a creek was calculated in ArcMap (ESRI, Redlands, CA, USA) using Google Earth 4.3 satellite imagery (Google, Mountain View, CA, USA; see www.earth.google.com, accessed April 2007) and GPS coordinates of each nest.

A fertility synchrony index was calculated following Kempenaers (1993). The analysis included 55 breeding females from the 2009 breeding season because this season had the most complete data on clutch initiation, and therefore the best estimate of synchrony for the population. As females can store sperm for more than 10 days before the first egg is laid

(Birkhead and Møller 1992), we calculated the fertility period for a given female to be 10 days before the laying of the first egg until the penultimate egg was laid.

The number of nests built, clutches initiated and eggs laid per pair annually were calculated by only considering pairs that were together for the duration of the breeding season and for which we know the exact number of nests, clutches and eggs.

Outcomes of nests, clutches and broods were calculated using only nests that were found during the building stage. Nests were considered abandoned if the male began building a new nest before initiation of a clutch or if the nest contents were unharmed when a new nest was initiated. Nests were considered destroyed if they were missing, broken, made inaccessible to the pair or if the contents were flooded by rising creeks. Nests were considered depredated if laying had begun and the contents were missing during subsequent checks. Nests were considered to have fledged young if at least one young was observed outside of the nest and identified to belong to that nest by resighting the fledgling (which was banded as a nestling) or the adults feeding the young. The size of clutches and broods, and the number of young fledged per successful nest or per successful pair were not always known (e.g. because nests were inaccessible) and were therefore excluded from analyses where appropriate. The percentage of pairs that fledged zero, one, two or three broods annually, and the number of fledglings per successful pair, were calculated using only pairs from the 2008 and 2009 seasons because they contained a more complete dataset for pairs.

Statistical analyses

With the exception of survival analyses (see above), statistical analyses were performed with JMP 8.0 (SAS Institute Inc., Cary, NC, USA) and significance levels were set at 0.05. Mass, wing-length and head-bill measurements were compared between the sexes with a two-sample *t*-test. The mean height of nests was compared to the mean nest-height reported by Todd (2002) with a one sample *t*-test. In all cases, the test assumptions were met. Means are presented as mean ± s.e.

RESULTS

Morphology and moult

Males were heavier than females and also larger in both wing-length and head-bill measurements (Table 1.1). Males did not exhibit swollen cloacal protuberances during nest building or laying (n = 35) and did not develop brood-patches during the laying, incubation or nestling stages (n = 36).

First-year Crimson Finches were moulting into adult plumage as early as 23 days after fledging. This moult was partial, with juvenile greater primary coverts and, rarely, some body plumage being retained. Of the birds known to be in their first year, 100% had at least one retained greater primary covert in their first breeding season (n = 22), compared to 3% of the adults older than 1 year (n = 110).

Social organisation

Crimson Finches formed flocks during the non-breeding season, comprising a mean 13.16 ± 0.48 individuals (median 10, n = 457), and were generally in pairs or small groups during the breeding season, comprising a mean 4.20 ± 0.05 individuals (median 2, n = 9506). They did not establish territories and sometimes nested very closely (<1 m) to other active nests. With 79–99 breeding pairs at the site each year, the population density was 4–5 pairs per 100 m of creek.

Crimson Finches bred in their first year, and always bred as socially monogamous pairs. Divorce occurred within seasons but not between seasons: all pairs remained together across years until one of the individuals disappeared. Within seasons the divorce rate was 2.9% (n = 173 pair-years). Five cases of divorce occurred, all in 2009, and all involving a recent, rather than ongoing, partnership. In four of the five cases of divorce, the pairs included a 1-year-old inexperienced bird and a mature bird in at least his or her third breeding season. The fifth case included an unbanded female of unknown age and a male 5+ years old. After divorce, two of the 1-year-old birds paired with another 1 year old, one remained alone and one paired with a 3+ year old. After the divorce, all of the older birds found partners of at least 2 years of age.

Survival

The goodness-of-fit test suggested that our data adequately fitted the model ($\hat{c}$ = 1.68) and adjustment for over-dispersion was not necessary. The top three of the 16 models had 99.0% of the support from the data (Table 1.2). All three of these models included an effect of year on

survival and no effects of sex or sex × year. The effect of year was highly significant (χ^2 = 22.322, d.f. = 4, $P < 0.001$). Survival and detection probabilities by year were averaged across all models and are summarised in Table 1.3. Estimates of both apparent annual adult survival and detection probability were high, at 70–96 and 89–93% respectively. Of the 64 individuals banded in 2004, 12.5% (n = 8) were still alive at the end of the breeding season in 2009.

Only successfully fledged young were included in the analysis of juvenile survival, so that 100% of individuals survived into their first week outside of the nest. The proportion of juveniles that survived into their second and third weeks were 0.74 ± 0.04 and 0.74 ± 0.07 respectively. Therefore, only ~55% of fledglings survived to independence (defined below). Detection probabilities for juveniles were 0.92 ± 0.02 in their first week, 0.63 ± 0.05 in their second and 0.63 ± 0.06 in their third week after fledging.

Nesting

Nesting activity occurred during the wet season (Figure 1.1) and lasted 3.7 months. The fertility synchrony index for the population was 35.3 ± 6.4% (range 22.3–52.5%, n = 55).

Crimson Finches nested nearly exclusively in the riparian River Pandanus (98% of nests, n = 870). Other substrates included artificial structures (n = 9), Fan Palm (*Livistonia eastonii*) (n = 4), Fitzroy Wattle (*Acacia ancistrocarpa*) (n = 1) and *Melaleuca leucadendra* (n = 1). Average height of nests was 2.86 ± 0.05 m (range 0.03–12 m, n = 519) and was marginally higher than height reported for the same subspecies of the Crimson Finch by Todd (2002) (mean ± s.d. = 2.45 ± 2.18 m, $P < 0.02$). Excluding nests located in artificial structures, 99.6% of nests (n = 838)

were within 20 m of the centre of a creek, with the rest located in River Pandanus up to 40 m from a creek, although still within the flood plain of the creek. The nine nests located in human structures were up to 90 m from a creek. About one-third (32.6%) of all nests were located directly over water when found (n = 585).

Reproductive effort and selected life-history traits, including clutch-size are summarised in Table 1.4. Clutch-size ranged from 1 to 7 and averaged 5.08 ± 0.07 eggs per completed clutch (Table 1.4). Nest building was primarily carried out by males that were opportunistically observed carrying nesting material and building nests on 957 occasions (O. Milenkaya, pers. obs.). By comparison, females were observed carrying nesting material on only 30 occasions but were sometimes observed sitting inside the nest rearranging the material (O. Milenkaya, pers. obs.). After the clutch was started, the dome nests were lined with white feathers and, rarely, also with other feathers, snake skin, pieces of white plastic bags, plant down and grass seed-heads. Males and females incubated the eggs and brooded and provisioned the offspring at similar rates (O. Milenkaya, pers. obs.). Fledglings became independent at ~3 weeks after fledging but adults were occasionally resighted feeding young up to 41 days after fledging.

Outcomes of nests, clutches and broods are summarised in Figure 1.2. Many nests were abandoned before laying, with 48.6% of all nests being abandoned, of which 91.1% were during the building stage. In contrast, only 4.8% of clutches and 1.6% of broods were abandoned. Of nests in which eggs had been laid (n = 290), 59.7% were depredated, 24.5% fledged, 9.0% were destroyed, 4.8% were abandoned and 2.1% failed in other ways (e.g. infertile clutch). Of nests in which young hatched (n = 127), 39.4% were depredated, 55.9% fledged, 2.4% were destroyed, 1.6% were abandoned and 0.8% failed in other ways (e.g. starved young). Nearly half of pairs

(49.4%) failed to raise any broods in a season, 42.7% of pairs fledged one brood, 7.3% fledged two broods and 0.6% fledged three broods annually (n = 164).

DISCUSSION

Our study is the first to describe the breeding biology and life-history traits of wild Crimson Finches in detail. Many aspects of the breeding biology and life history of the species are consistent with those of other members of the family Estrildidae. However, some aspects are inconsistent with the expectations for southern passerines in general.

Morphology and moult

The sexual dimorphism we found in Crimson Finches complements the results of Higgins *et al.* (2006), who reported differences between the sexes in length of tail and bill, with males larger than females. Our combined results show that Crimson Finch males are structurally larger and heavier than females.

Only females developed a brood-patch even though both sexes incubated and brooded. This may be uncommon (Gill 2003) but not wholly unique (Auer *et al.* 2007). Incubating male Chestnut-vented Warblers (*Parisoma subcaeruleum*) lack brood-patches but heat their eggs at a higher temperature than their female partners (Auer *et al.* 2007). This is a compelling example of males investing significantly in their clutches despite not developing a brood-patch. It remains unclear whether Crimson Finch males similarly incubate their clutch or simply occupy the nest during the female's absence. Whether or not they thermoregulate the clutch, Crimson Finch

males invest considerably in their clutches by contributing to parental care during both incubation and nestling stages.

Males were never observed to have swollen cloacal protuberances, even during the nest-building and laying stages. Small cloacal protuberances suggest low levels of sperm competition and low extrapair paternity (EPP) (Briskie 1993; Garamszegi *et al.* 2005), which would be unusual for a socially monogamous passerine (Griffith *et al.* 2002). Crimson Finches have high fertility synchrony compared with other tropical birds, which should favour extrapair mating (Stutchbury 1998). Traits exhibited by Crimson Finches, specifically high breeding synchrony, high breeding density and granivory, have been considered possible reasons for the observed high rate of EPP in another socially monogamous tropical passerine, the Blue-black Grassquit (*Volatinia jacarina*) (Carvalho *et al.* 2006). In contrast, Griffith *et al.* (2002) found little evidence for a role of breeding density or breeding synchrony in explaining interspecific variation in EPP, but male contribution to parental care and adult survivorship did correlate with rate of EPP: species in which males contribute to parental responsibilities have lower rates of EPP and species with high annual mortality have higher rates of EPP (Griffith *et al.* 2002). Thus high parental investment by male Crimson Finches and high adult survival may explain the low rates of cloacal protuberance observed. Losing male parental investment may be too high a cost for the female to pay for the opportunity to pursue extrapair copulations, as suggested by Arnqvist and Kirpatrick (2005). The role of male parental investment in rates of EPP, however, is not always consistent across species and remains unresolved (Griffith 2007). Also, our argument is contingent on the lack of swollen protuberances being indicative of low rates of EPP, which remains to be verified in this species.

In this study, first-year adults retained juvenile greater primary coverts and, rarely, some body plumage contrary to the observations of M. K. Todd presented in Higgins *et al.* (2006), in which the first pre-basic (post-juvenile) moult is described as complete. Adults in their first breeding season may therefore be precisely aged based on the presence of a moult limit (the boundary between replaced and retained feathers, see Pyle 1997) between the greater primary coverts and adjacent feathers. Further research into the moult patterns of young Crimson Finches is warranted in light of the contradicting results between Higgins *et al.* (2006) and this study.

Social organisation

Crimson Finches congregated in flocks during the dry season, were non-territorial year-round and bred at high densities. Our observed breeding density, although high, is an underestimate because unbanded pairs were not counted although some were resident at the site. Long-term pair-bonds have not previously been reported in Crimson Finches. We suggest that the few cases of divorce we observed occurred owing to the inexperience of the younger partner (Choudhury 1995).

Survival

Determining survival rates is essential for assessing the status of populations (Anders and Marshall 2005). We found that Crimson Finches have high adult survival and may live to be at least 5 years old and likely even older. The oldest known wild Crimson Finch before our study was 13 months old (Higgins *et al.* 2006) but captive Finches can live for 5 years (Shephard

1989). The evidence for an influence of sex on survival was very weak, whereas the effect of year was strong. Apparent annual adult survival decreased across years in our study, but the mechanism behind this trend is unclear.

Our high survival rates (70–96%) are consistent with estimates for other southern passerines, for example rates of 55–87% from Australia, New Zealand and South Africa (Rowley and Russell 1991; but see Karr *et al.* 1990). It is unclear whether our estimates are representative of the Estrildidae because published survival rates for species in this family are few, and range widely from 21% for the Zebra Finch (*Taeniopygia guttata*) (Yom-Tov *et al.* 1992) to 89% for the Red-billed Firefinch (*Lagonosticta senegala*) (McGregor *et al.* 2007). Crimson Finches have high adult survivorship, lay large clutches and are multi-brooded, a combination of traits that is inconsistent with trade-offs predicted by life-history theory.

We report juvenile survival rates in a tropical passerine, data that are particularly lacking and rarely reported (Anders and Marshall 2005). We estimate that juveniles become independent 3 weeks after fledging, but that only 55% survive to that stage. Juvenile survival is generally higher in the tropics and the southern hemisphere than in the temperate northern hemisphere, and this is attributed to extended parental care among southern passerines (Russell *et al.* 2004). Our estimates of juvenile survival are slightly lower than other estimates for southern passerines (61–67%), but are considerably higher than estimates for northern passerines (13–42%) (Sankamethawee *et al.* 2009 and references therein). Factors other than parental care may influence juvenile survival because, despite having a short period of parental care, Crimson Finches have a juvenile survival rate comparable to that of other southern passerines with a

longer period of parental care. Owing to the paucity of data it is not clear how our juvenile survival rates compare to those of other estrildids.

Nesting

Todd (2002) suggested that the Crimson Finch breeding season is not rigid but is possibly linked to rainfall. Although he showed that brood-patches on captured females were present during the wet season, ours is the first study to show the association between rainfall and nesting activity (Figure 1.1). Rainfall varied from year to year and nest-building activity tracked this annual variation (Figure 1.1), suggesting that the proximate cue for breeding is rainfall. The length of the breeding season (3.7 months) was short compared to other Australian birds (Wyndham 1986; Yom-Tov 1987) and we suggest that this is because the wet season is of fairly short duration.

Before our study, 88 nests of wild Crimson Finches had been recorded (Todd 2002 and references therein). We found over 800 nests, adding depth to knowledge of Crimson Finch nesting. Consistent with previous reports (Webb 1902; Storr 1977; Johnstone and Smith 1981; Immelmann 1982) this species is a riparian specialist. Although many of the nests located in artificial structures were far from a creek, all were close to human plantings of riparian vegetation (River Pandanus, reeds and sedges), suggesting that the vegetation is an important component of nest-site selection. We found Crimson Finches nested higher and more often in natural substrates than previously reported (Todd 2002). These differences may result from

differences in availability of nesting sites rather than nesting preferences between the studied populations.

Evolution of clutch-size

The evolution of different clutch-sizes across the latitudinal gradient has been a major theme in life-history theory but why such differences evolved remains unresolved (Ricklefs 2000). Various hypotheses have been proposed to explain why southern passerines generally lay small clutches whereas northern passerines typically lay large clutches. Here we discuss some of these hypotheses and how they may apply to the large clutch-size we observed in the Crimson Finch.

Rates of nest predation are generally higher in the tropics and southern hemisphere (49.4–78.5%) than in the temperate northern hemisphere (27.6–57.6%) (Griebeler *et al.* 2010, and references therein), and this may select for small clutch-sizes in southern passerines (Martin and Briskie 2009). The effect of nest predation on the evolution of clutch-size may, however, be overstated (Martin 1996) and cannot always explain latitudinal differences in clutch-size (Martin *et al.* 2000; Griebeler *et al.* 2010). Our results support these latter conclusions because the high rate of nest predation of Crimson Finches has not selected for small clutches.

In the Americas, annual adult survival is negatively correlated with clutch-size, with South American birds having high survival and small clutch-sizes compared to North American birds (Ghalambor and Martin 2001). The same trends are found between southern African and European passerines (Peach *et al.* 2001). Also, southern African granivores tend to have larger

clutches and lower survival compared to other southern African birds (Peach *et al.* 2001), further suggesting that clutch-size and adult survival are inversely related. However, Crimson Finches have high adult survival whereas southern African granivores have low survival, despite both having large clutch-sizes. This discrepancy suggests that annual adult survival alone cannot explain the evolution of clutch-size.

Lack (1949) suggested that juvenile survival may be important to the evolution of clutch-size. Small clutch-sizes in southern passerines may be driven by the need for extensive parental care during the post-fledging period (Styrsky *et al.* 2005). Unlike other tropical passerines, but consistent with other estrildid finches (Higgins *et al.* 2006), Crimson Finches have a short period of parental care after fledging, which might favour the evolution of large clutch-sizes. Further, unlike the species studied by Styrsky *et al.* (2005), adult Crimson Finches do not split the brood between parents and each parent can support more than one young at a time, thus allowing them to support large broods to independence.

The clutch-size of Crimson Finches we observed, although larger than expected for southern passerines, is consistent with other granivores (Yom-Tov 1987; Peach *et al.* 2001), including other members of the Estrildidae (Higgins *et al.* 2006). Yom-Tov (1987) found Australian finches to have a mean clutch-size of 4.6 eggs whereas the mean for other Australian passerine clutches was 2.7 eggs. Dietary guild has been proposed as a correlate of clutch-size in the past (Skutch 1985) and has been recently confirmed by Jetz *et al.* (2008). Their analysis of global variation in clutch-size among >5000 avian species found that granivores and omnivores have larger clutches than fruigivores and nectarivores. Dietary guild alone does not determine clutch-size, but may be one of several factors influencing its evolution (Jetz *et al.* 2008).

Ashmole's (1963) seasonality hypothesis predicts small clutch-sizes in southern passerines owing to the lack of harsh winters, and subsequent high adult survival, and the lack of a spring food peak. The food-limitation hypothesis similarly predicts that the number of young that can be fed optimises clutch-size (Lack 1947, 1948; Roff 1992). An underlying assumption of these two hypotheses is that tropical and southern regions lack seasonality. However, not all such habitats are aseasonal. The abundance of grass seed, for example, is highly seasonal in tropical savannas (Flores and Dezzeo 2005; Williams *et al.* 2005). If this is true at our site, then the release from the food-limitation and seasonality hypotheses may explain the large clutches we observed in Crimson Finches. If the provisioning stages of granivores are timed to match the peak in abundance of high-quality food in tropical savannas, then this may have selected for the large clutch-sizes observed among southern finches. Although Ashmole's hypothesis has been previously questioned (Martin *et al.* 2000; Martin 2004; Ferretti *et al.* 2005), modeling techniques have recently provided support (Griebeler and Böhning-Gaese 2004; Griebeler *et al.* 2010).

The influence of granivory and seasonality on the evolution of clutch-size in Crimson Finches is confounded by phylogeny because all native Australian finches are members of the Estrildidae (Arnaiz-Villena *et al.* 2009) are granivorous and have moderate to large clutches (Higgins *et al.* 2006). Furthermore, Australian estrildids belong to the wave of colonizers and their descendants that immigrated to Australia from Afro-Eurasia and are therefore phylogenetically separate from the old endemic passerines of Australia. The influence of phylogeny cannot be understated because 90% of the variation in life-history traits in birds is found at the level of family and higher (Owens and Bennett 1995). Exploring the ecological

reasons for the latitudinal gradient in clutch-size remains relevant, but should be examined at the family, as well as the species level.

Our study has shown that the Crimson Finch does not adhere to the typical southern passerine pattern: although they do indeed have high rates of nest predation and high adult survival, their clutch-sizes are not small. Our findings suggest that rates of nest predation and adult survival are not the primary drivers of latitudinal variation in clutch-size and support clutch-size hypotheses involving post-fledging parental care (Styrsky *et al.* 2005) and food availability (Lack 1947). They are consistent with Ashmole's (1963) hypothesis only if effects of seasonality on food availability outweigh those of adult population density. We suggest that the exploration of life histories that differ from the norm, such as southern passerines that lay large clutches (Yom-Tov 1987; Peach *et al.* 2001; this study) may be particularly helpful in understanding latitudinal differences in life history.

ACKNOWLEDGMENTS

We are especially grateful to our field assistants Roy Churchwell and Evan Rehm for helping to collect these data. We thank the personnel at Mornington Wildlife Sanctuary and members of the Avian Ecology Laboratory at Virginia Tech. Michelle Hall, Stephen Murphy, Benjamin Phillips, Graeme Armstrong and two anonymous reviewers provided comments on earlier drafts of the manuscript. This study was funded by supporters of the Australian Wildlife Conservancy and based out of the WildlifeLink Centre for Research and Conservation at Mornington Wildlife Sanctuary.

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Tables

Table 1.1: Sexual dimorphism in mass and length of wing and head-bill in Crimson Finches

Measurements are presented as the mean ± s.e. (sample size)

Measurement	Male	Female	*P*
Mass (g)	10.0 ± 0.09 (92)	9.65 ± 0.09 (80)	0.003
Wing-length (mm)	53.6 ± 0.08 (347)	52.5 ± 0.08 (295)	<0.0001
Head-bill length (mm)	24.4 ± 0.03 (346)	23.8 ± 0.03 (300)	<0.0001

Table 1.2: Model rankings and criteria of apparent annual adult survival (φ) and detection probability (ρ) from Program MARK

Listed here are the top five models, including the global model (in bold). The remaining 11 models are not included here because their $\Delta AIC_c > 12$ and their AIC_c weights < 0.001. Included are the deviance, number of parameters (K), Akaike's information criterion corrected for sample size (AIC_c), the difference in AIC_c values between models (ΔAIC_c), and the probability that the model is the best among all other candidate models (AIC_c weights) for each model

Model	Deviance	K	AIC_c	ΔAIC_c	AIC_c weights
[φ(year)ρ(.)]	115.9067	6	1178.0109	0	0.46585
[φ(year)ρ(year)]	110.3336	9	1178.5539	0.543	0.35509
[φ(year)ρ(sex)]	115.8978	7	1180.0358	2.0249	0.16926
[φ(year)ρ(sex × year)]	107.8822	14	1186.3951	8.3842	0.00704
[φ(sex × year) ρ(sex × year)]	102.5464	18	1189.3837	11.3728	0.00158

Table 1.3: Estimates of apparent annual adult survival (φ) and detection probability (ρ) of Crimson Finches

Estimates of apparent annual adult survival and detection probability were averaged across all models from Program MARK and are presented by year as the mean ± s.e.

Parameter	2004	2005	2006	2007
φ	0.96 ± 0.03	0.82 ± 0.04	0.81 ± 0.03	0.70 ± 0.03
ρ	0.89 ± 0.05	0.92 ± 0.02	0.92 ± 0.02	0.93 ± 0.03

Table 1.4: Breeding effort and selected life-history traits of Crimson Finches

Breeding effort and selected life-history traits	Mean ± s.e.	Median	Range	*n*
Number of nests built per pair per year	4.59 ± 0.19	5	1–8	78
Number of clutches initiated per pair per year	2.39 ± 0.10	2	1–5	77
Number of eggs laid per pair per year	11.93 ± 1.05	11	1–27	30
Clutch size (number of eggs per completed clutch)	5.08 ± 0.07	5	1–7	227
Brood size (number of nestlings per hatched clutch)	4.54 ± 0.10	5	1–7	114
Number of young fledged from successful nests	3.43 ± 0.15	4	1–7	96
Number of young fledged per successful pair per year	4.12 ± 0.22	4	1–10	78
Duration of incubation stage (days)	17.65 ± 0.31	18	13–21	40
Duration of nestling stage (days)	16.00 ± 0.26	16	12–20	47

Figure legends

Figure 1.1: On the right scale are the number of nests built (black line), clutches initiated (grey line), and broods fledged (dotted line) by a population of Crimson Finches at Mornington Wildlife Sanctuary. On the left scale is rainfall (mm, grey bars) during the breeding seasons of (*a*) 2006–2007, (*b*) 2007–2008, and (*c*) 2008–2009.

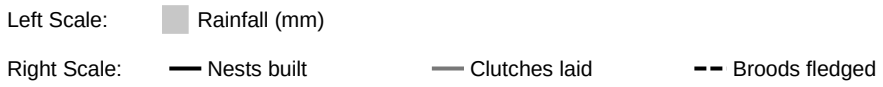
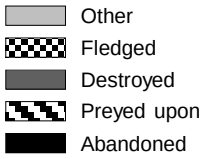


Figure 1.2: Proportion of Crimson Finch nests (*n* = 655), clutches (*n* = 290), and broods (*n* = 127) which were abandoned (black), preyed upon (diagonal lines), destroyed (dark grey), fledged (cross-hatched), or had another outcome such as starvation of nestlings, usurpation or clutch infertility (light grey).



Figures

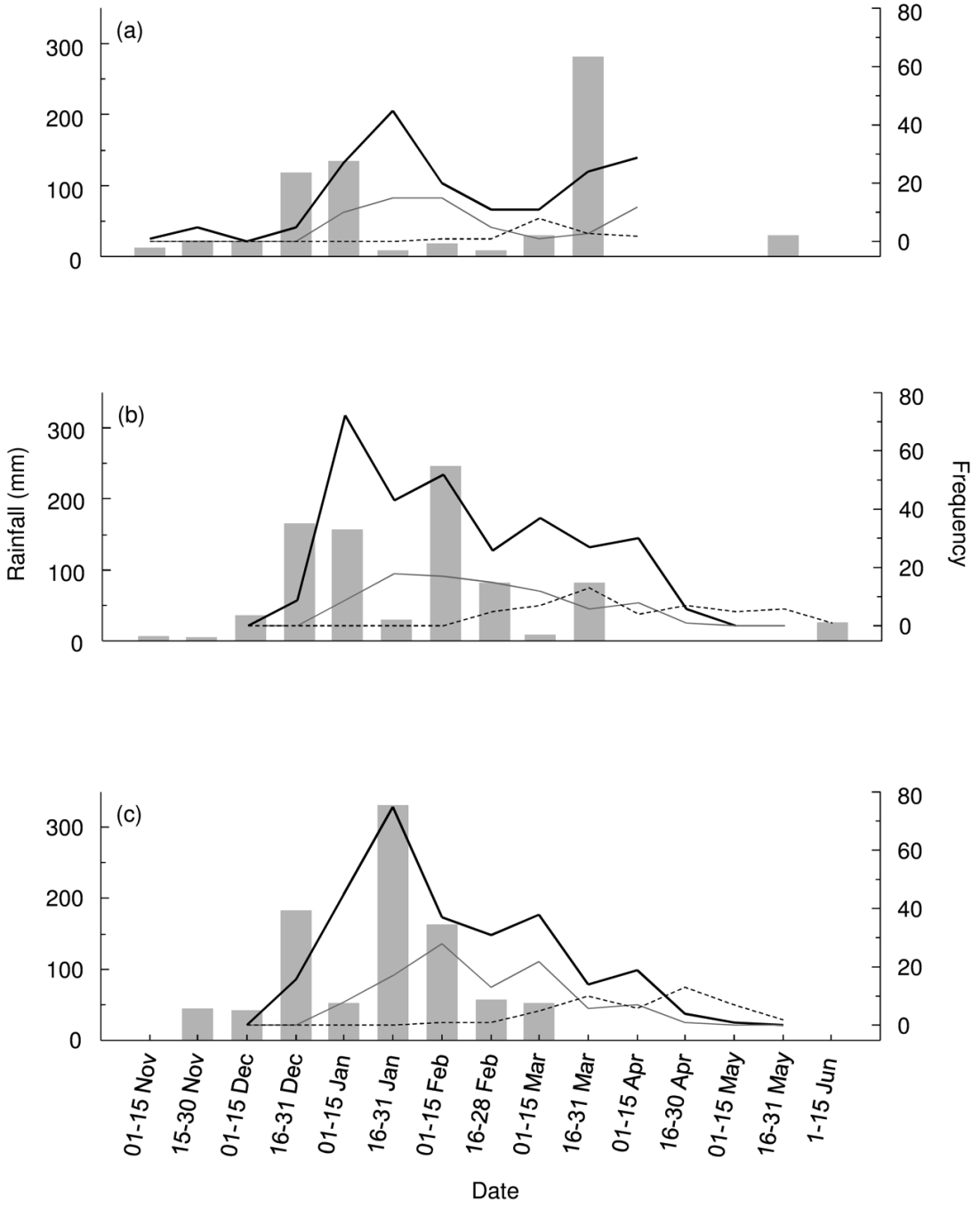


Figure 1.1: Rainfall and breeding activity of Crimson Finches at Mornington Wildlife Sanctuary, Australia

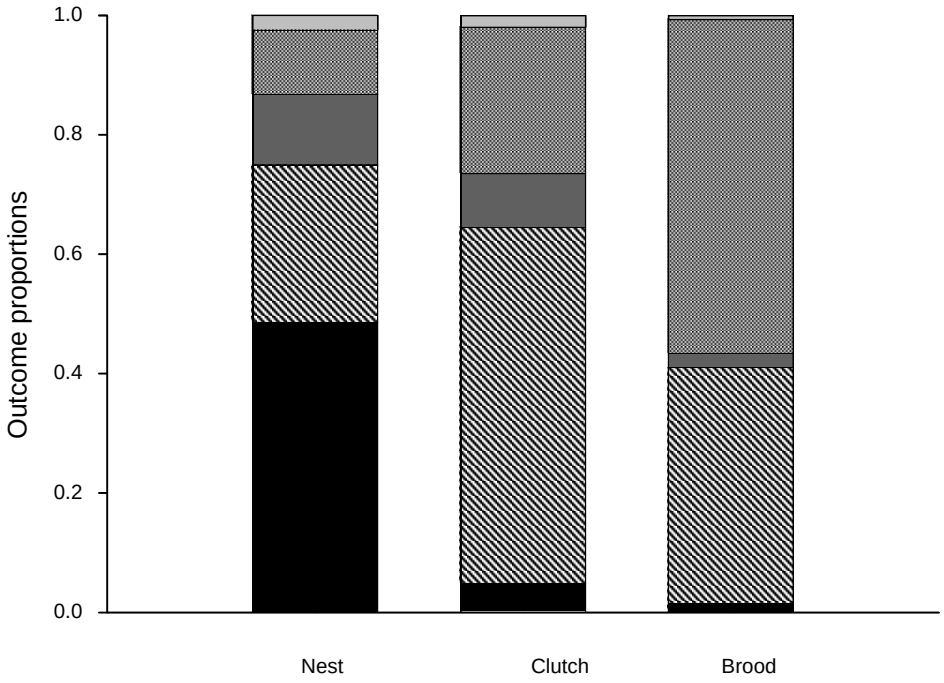


Figure 1.2: Outcomes of Crimson Finch nests, clutches and broods

Appendix

Appendix A: Photos of the study species, Crimson Finch (*Neochmia phaeton*).

Figure A1.1: Adult (a) male and (b) female Crimson Finch (*Neochmia phaeton*). Used with permission of Stuart Cooney and J. Lindley McKay, respectively.

CHAPTER II. VARIATION IN BODY CONDITION INDICES OF CRIMSON FINCHES BY SEX, BREEDING STAGE, AGE, TIME OF DAY, AND YEAR

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This article has been published as: Milenkaya O, Weinstein N, Legge S, Walters, JR. 2013. Variation in body condition indices of crimson finches by sex, breeding stage, age, time of day, and year. *Conservation Physiology* 1: doi: 10.1093/conphys/cot020.

Abstract. Body condition indices are increasingly applied in conservation to assess habitat quality, identify stressed populations before they decline, determine effects of disturbances, and understand mechanisms of declines. To employ condition indices in this manner, we need first to understand their baseline variability and sources of variation. Here, we used crimson finches (*Neochmia phaeton*), a tropical passerine, to describe the variation in seven commonly used condition indices by sex, age, breeding stage, time of day, and year. We found that packed cell volume, haemoglobin, total plasma protein, and scaled mass were all significantly affected by an interaction between sex and breeding stage. Furcular fat varied by sex and breeding stage and also trended by year, scaled mass showed a positive trend with age and varied by time of day, and haemoglobin additionally varied by year. Pectoral muscle scores and H/L ratio varied and trended by year, respectively. Year effects might reflect a response to annual variation in environmental conditions; therefore, those indices showing year effects may be especially worthy of further investigation of their potential for conservation applications. Pectoral muscle

scores and heterophil to lymphocyte ratio may be particularly useful due to the lack of influence of other variables on them. For the other indices, the large variation that can be attributed to individual covariates, such as sex and breeding stage, suggests that one should not interpret the physiological condition of an individual as measured by these indices from their absolute value. Instead, the condition of an individual should be interpreted relative to conspecifics by sex, breeding stage, and possibly age.

Keywords: Body condition; crimson finch; habitat quality; haematocrit; heterophil to lymphocyte ratio; Neochmia phaeton

INTRODUCTION

Body condition is the physiological state of an individual and reflects how successful that individual is in interacting with its environment. Condition is higher when an individual acquires and assimilates more resources (Tomkins *et al.*, 2004), and is usually employed in a relative sense to compare individuals within populations or between places and times. Without a single or direct measure of condition itself, researchers employ body condition indices as tools to measure specific aspects of that physiological state (e.g. nutritional status, stress levels, and immune function), in both basic ecological and applied conservation frameworks.

Conservation physiology is an emerging scientific discipline that applies physiological concepts, tools, and knowledge to conservation in broad ways (Cooke *et al.*, 2013). Body condition and body condition indices are a physiological concept and tool, respectively, with

many applications in conservation (Table 2.1; Stevenson and Woods, 2006). Loss, fragmentation, and degradation of habitat continue on a global scale, and it is critical to biodiversity conservation to assess the effects of changes in habitat on biota. Measuring habitat quality directly is not always feasible, and measuring the condition of individuals offers an alternative method to assess habitat quality (Johnson, 2007; Homyack, 2010; Ellis *et al.*, 2012). Body condition indices have been used to assess habitat quality, inform habitat management and restoration, identify stressed populations before they decline, determine effects of disturbances, and understand mechanisms of declines (Table 2.1). They have been used to identify fine-scale habitat requirements that may otherwise be missed by traditional occupancy modeling (Maron *et al.*, 2012) and to provide insights into the nutritional status of animals in different habitat types (Dyer *et al.*, 2009, 2010). Condition indices have been used to assess the effects of habitat fragmentation on a wide range of vertebrates, including birds (Suorsa *et al.*, 2003), mammals (Henry *et al.*, 2007; Johnstone *et al.*, 2012a), and amphibians Qanin *et al.*, 2011).

Condition indices have also been used to assess impacts of stressors and disturbances other than habitat alteration (Table 2.1). Condition indices were employed, for example, to detect deleterious effects of ecotourism on wildlife (Walker *et al.*, 2005; Ellenberg *et al.*, 2007; Semeniuk *et al.*, 2009), of the presence of logging roads and nearby timber harvesting on northern spotted owls (*Strix occidentalis caurina*; Wasser *et al.*, 1997), and of oiling on sea otters even after they were treated (*Lontra canadensis*; Ben-David *et al.*, 2002). Other applications of condition indices in conservation are in testing hypotheses about the agents of population decline (e.g. Owen *et al.*, 2005) and elucidating the mechanisms of declines (Maute, 2011). Finally, Cooke *et al.* (2013) encourage us to move beyond the identification of problems and towards the constructive use of this knowledge in providing conservation solutions.

Use of condition indices in conservation is hampered by the paucity of data on their baseline variability and sources of variation. Despite their frequent use, condition indices are poorly described for many species in the wild and, in particular, for those from the tropics (Stevenson and Woods, 2006). The covariates that may affect these indices are even less well documented, and understanding of this variability is needed to inform our interpretation of condition indices (Dawson and Bortolotti, 1997; Fair *et al.*, 2007).

Likely sources of variation that may affect condition indices include sex, age, breeding stage, time of day, and annual and seasonal variation in the environment. While the last two parameters represent the sort of interaction between environment and individual that reflects uses of these indices in conservation, the first four parameters represent variables that potentially confound these uses. Condition indices may vary between males and females because of influences of sex hormones (Shallin Busch *et al.*, 2011) and because of differences in sex-specific workload, especially during breeding (Horak *et al.*, 1998b). Age may affect condition indices if individuals experience physiological senescence, have variable exposure to immune challenges with age, or allocate their resources differently with age. Condition indices may vary across the different stages of the breeding cycle because of hormonal changes and different energy requirements associated with these stages (Williams *et al.*, 2004; Fair *et al.*, 200 7). Finally, time of day is known to affect the mass and fat stores of diurnal birds due to overnight fasting (Pravosudov and Grubb, 1997; Sepp *et al.*, 2010).

This study is part of a larger research project, the objectives of which are to assess the consequences of different land-management regimens on wildlife physiology and to test whether

condition indices predict fitness such that they can inform habitat management. The habitats under consideration are northern Australia's tropical savanna and interstitial areas embedded within this matrix, including riparian habitats, all of which are threatened by non-native herbivores (cattle, horses, donkeys, buffalo, and pigs) and inappropriate fire regimens (Franklin *et al.*, 2005; Woinarski *et al.*, 2011). Broadly, we are examining the impacts of differing fire and introduced herbivore management on the persistence and physiology of native species, and more specifically, we are investigating whether condition indices can be used to provide prior warning of impending species declines. To examine this, we are comparing condition indices in relationship to the presence/absence of introduced herbivores, and to whether fire is managed (small-scale and low-intensity fires) or unmanaged (frequent, extensive, and high-intensity fires).

Here, we take the first step towards assessing the impact of land-management regimens on wildlife physiology by reporting baseline condition indices sampled from a native passerine in habitat that has been managed for conservation. We then explore the variability of these indices by sex, breeding stage, age, time of day, and year. Our goal in describing this variation is to inform our interpretation of condition indices as conservation tools when comparing across populations.

METHODS

Species description and general methods

Crimson finches (*Neochmia phaeton*, Family Estrildidae) are restricted to riparian zones throughout the tropical savannas of northern Australia and New Guinea (Higgins *et al.*, 2006). Two subspecies of crimson finches are recognized, *N. p. phaeton* and *N. p. evangelinae* (Higgins *et al.*, 2006); the latter includes populations in southern Papua New Guinea and four populations on the Cape York peninsula, Australia and is listed as vulnerable in the Commonwealth of Australia (Dorricott and Garnett, 2007) and as near threatened internationally (Garnett *et al.*, 2011). The main threats to *N. p. evangelinae* in Australia include fire regimens and invasive plant species that alter the vegetation structure used by the finches (Dorricott and Garnett, 2007). In contrast, *N. p. phaeton* is widely distributed throughout northern Australia and is listed as being of least concern (Garnett *et al.*, 2011). *Neochmia phaeton phaeton* is not as threatened as its conspecific, but it is a riparian habitat specialist and is therefore susceptible to habitat fragmentation caused by land-management practices such as burning and grazing.

Neochmia phaeton phaeton are small (females 9.7 g and males 10.0 g), sedentary passerines that breed during the wet season (roughly December−April in our study area; Milenkaya *et al.*, 2011). They breed as socially monogamous pairs, in which the male builds the nest, the female lays a clutch of an average of five eggs, and both sexes incubate the eggs, and provision and defend the young (Milenkaya *et al.*, 2011). Detailed breeding biology and life-history traits of crimson finches from our study area are described by Milenkaya *et al.* (2011).

We monitored a population of *N. p. phaeton* at the Australian Wildlife Conservancy's Mornington Wildlife Sanctuary in northwest Australia (17° 30'49" S, 126°06'39" E, elevation 200 m). The study area was a 2 km stretch of riparian habitat along Annie Creek that is actively managed for conservation. Here we monitored the crimson finch population for breeding activity

and sampled the individuals for condition indices over four consecutive breeding seasons (from 15 November 2006 to 11 April 2007, from 5 December 2007 to 31 May 2008, from 9 December 2008 to 29 May 2009, and from 10 December 2009 to 10 May 2010).

We captured adult crimson finches in mist-nets during the morning (up to 6 h) to minimize time-of-day effects on condition indices (Norte *et al.*, 2009b; Sepp *et al.*, 2010). We banded the birds with a metal band (Australian Bird and Bat Banding Scheme) and up to three plastic colour bands for individual recognition. We determined the sex of each bird based on their sexually dimorphic plumage (Higgins *et al.*, 2006). To sample for haematological condition indices, we punctured the birds' brachial vein with a needle and collected whole blood (up to 40 µl) into plastic, sodium-heparinized micro-haematocrit capillary tubes. We plugged the tubes and stored them on ice until further processing (within several hours; see subsection Condition indices below).

We sampled 372 individual birds, which we aged based on known hatch dates, juvenal plumage, and molt limits. We were able to assign an accurate age to the individuals that were originally banded as nestlings or juveniles (25 %, $n = 92$). Birds that were in adult plumage upon first capture were aged as being in their first year (23%, $n = 85$) if they had a molt limit between their retained, juvenal primary coverts and adjacent newer feathers (Milenkaya *et al.*, 2011), and in at least their second year if they had newly molted and fresh primary coverts at the beginning of the breeding season (10%, $n = 39$). Together, we refer to these individuals as known-aged birds. In contrast, all other individuals could not be aged because they were first captured as adults, and data on their molt were not collected (42%, $n = 156$).

We monitored the breeding attempts of individual birds closely and could therefore attribute captured birds as being in one of the following stages of the breeding cycle at the time of capture: pre-breeding, nest building, egg laying, incubating, nestling, or post-breeding. Crimson finches in our study area are multi-brooded (Milenkaya *et al.*, 2011), so the nest building, egg laying, incubating, and nestling stages occur throughout the breeding season and do not necessarily represent the first breeding attempt of the season. The pre- and post-breeding stages, however, correspond to the beginning and end of the breeding seasons, respectively. Individuals were considered to be in the post-breeding stage when it was 3 weeks or more after their final breeding attempt ended (either through nest failure or because the last set of young became independent at 3 weeks post-fledging).

Condition indices

Mass corrected for size reflects nutrient stores (Brown, 1996) and is perhaps the most common measure of condition. Along with fat and muscle scores, these data are minimally invasive to collect and are therefore often used in field studies. Fat scores correspond to energy reserves, while muscle scores indicate protein as well as energy reserves. We weighed birds using a 30 g spring scale to 0.1g and measured the distance from the tip of the beak to the back of the head using calipers as a measure of structural size. We did not measure tarsus length because measuring it precisely and consistently is challenging (Pyle, 1997), especially on a small passerine, such as the crimson finch. We used the mass and head-beak measurement to calculate a scaled mass index (scaled mass) as a measure of mass corrected for size, following Peig and Green (2009). We calculated scaled mass separately for males and females because they are

sexually dimorphic in size (Milenkaya *et al.*, 2011). Finally, we scored the amount of pectoral muscle around the keel bone on a 0−3 scale (muscle score) and the amount of fat in the furcular hollow on a 0−4 scale (fat score; Table 2.2).

Other readily available condition indices include haematological parameters that are a result of an individual's nutritional status, stress level, and immune function. Packed red blood cell volume (PCV) is the proportion of red blood cells to the total volume of blood, and is often considered an aggregate indicator of overall health (e.g. Garvin *et al.*, 2007). Low PCV and anaemia (PCV <35% in birds; Campbell and Ellis, 2007) may be caused by blood loss (e.g. parasitism; Szabo *et al.*, 2002), by destruction of erythrocytes (e.g. infectious agents or toxins), or by decreased production of erythrocytes [e.g. disease, nutritional stress (Harrison and Harrison, 1986, but see Fair *et al.*, 2007), or toxin exposure (Campbell and Ellis, 2007)]. High PCV may be due either to dehydration or to an increased energy demand and resultant need for increased oxygen-carrying capacity (Carpenter, 1975; Horak *et al.*, 1998a). The relationship between PCV and the oxygen-carrying capacity of blood is parabolic, such that both very low and very high PCV values result in decreased oxygen transport capability (Birchard, 1997). Packed cell volume is related to haemoglobin concentration (Velguth *et al.*, 2010), which also reflects the oxygen-carrying capacity of the blood (Birchard, 1997) and is lower in clinically sick birds compared with healthy birds (Averbeck, 1992). Before collecting blood with a capillary tube, we collected ~5 µl of it in a Hemacue cuvette and used the portable HemoCue Hb 201+ Analyzer (HemoCue, Inc., Cypress, CA, USA) in the field to estimate haemoglobin concentration (haemoglobin) from whole blood. Within a few hours of collecting blood in capillary tubes, we centrifuged (Hettich Haematokrit 210) the tubes for 15 min at 1433.6*g* and read the proportion of red blood cells to the total volume of blood (packed cell volume).

Total plasma protein is a measure of proteins present in plasma; primarily albumin and globulin. Dehydration causes increases in both albumin and globulin, but an increase in globulin alone suggests inflammation and immune system stimulation (Rosenthal, 2000), and some have found that overall total plasma protein increases with inflammation/infection (de Lope *et al.*, 1998; Ots and Horak, 1998). Decreases in total plasma protein may be caused by parasites (Norte *et al.*, 2009a), and poor nutrition may result in decreased albumin (Rosenthal, 2000), suggesting that albumin levels may reflect diet. Total plasma protein is therefore sometimes interpreted as an indicator of nutritional status (Gavett and Wakeley, 1986; Brown, 1996) and as a measure of body condition (e.g. Schoech and Bowman, 2003). During the 2008−09 and 2009−10 field seasons, we extracted the plasma from the capillary tube after centrifugation and read the total plasma protein value (in grams per decilitre) with a hand-held refractometer (HR-200 ATC refractometer; AFAB Enterprises, Eustis, FL, USA). The total plasma protein values for bird samples obtained with this technique are sometimes consistent with and sometimes higher than values of those obtained from chemical analyses (George, 2001).

Heterophils and lymphocytes are white blood cells primarily involved in the immune response (Campbell and Ellis, 2007). A high heterophil to lymphocyte ratio (H/L ratio) suggests an active inflammation response (Campbell and Ellis, 2007) and can be correlated with elevated corticosterone levels in response to chronic stress (Davis *et al.*, 2008). We sampled for H/L ratio only during the 2008−09 and 2009−10 field seasons. During these years, we prepared blood smears immediately from collected blood and fixed the slides in 100% methanol on the same day. We then stained the smears with Dip Quick Stain Set (Jorgensen Laboratories, Inc., Loveland, CO, USA) at a later date. One of us (O.M.) performed a leucocyte differential count under x1000 magnification by identifying 100 leucocytes as a heterophil, lymphocyte,

eosinophil, basophil, or monocyte. The H/L ratio was calculated as the relative proportion of heterophils to lymphocytes counted in the blood smear.

Statistical analyses

We used all sampled individuals to describe the distribution (mean± SD, range) of each condition index and to test for pairwise correlations between the indices. If an individual was sampled more than once, we used the average value for that individual for each condition index to describe the distribution of the indices. However, we selected at random one sampling occasion of each individual to include in the analyses of pairwise correlations. We tested whether the continuous variables [packed cell volume, haemoglobin, total plasma protein, scaled mass, and log(H/L ratio)] were correlated with one another by using Pearson's correlation (cor function in R version 2.14.1; R Development Core Team, 2012). We tested whether these continuous indices are correlated to muscle and fat scores, and whether muscle and fat scores are correlated to each other, by using polyserial and polychoral correlations, respectively (package polycor in R version 2.14.1; Fox, 2010).

To test the effects of sex, age, year, time of day, and breeding stage, as well as the interaction between sex and breeding stage, on each condition index we used restricted maximum likelihood to fit linear regression models. For these analyses, we included only known-aged individuals in the data set. To determine normality, we used the Shapiro-Wilk test and visual examination of the model residuals. The H/L ratios were base e log transformed to fit the assumptions of normality, whereas other condition indices were normally distributed. We

included individual as a random effect in each of these models because some individuals were sampled more than once. To determine whether this analysis missed any significant effects due to small sample size, we conducted a second analysis in which all individuals were included, regardless of whether they were of known age or not. We calculated the time of day of capture as the length of time (in minutes) since sunrise.

After finding significant effects of year and of the interaction between sex and breeding stage on many condition indices (see Results), we examined the parameter estimates and inferred statistical significance from the 95% confidence intervals for those estimates to better understand the effects of these terms on the condition indices. We set statistical significance at $\alpha = 0.05$. Our figures show least-square means (±SEM) which are consistent with the raw data. We ran all models in JMP 9.0 (SAS Institute Inc., Cary, NC, USA).

RESULTS

We sampled 372 individual birds for some or all of the condition indices during the 4 year study, of which 40% were sampled once ($n = 149$), while the rest were sampled more than once, as follows: twice, 25% ($n = 94$); three times, 13% ($n = 49$); four times, 10% ($n = 37$); five times, 5% (n = 20); six times, 4% (n = 15); and seven times or more, 2% ($n = 7$). The distributions of observed values (means± SD, minimum, maximum) for each condition index are summarized in Table 2.3. Of the pairwise correlations among condition indices, only one correlation was strong and significant, that of packed cell volume to haemoglobin ($r = 0.71$, $P < 0.0001$; Table 2.4).

Here we present the results of the regression analysis in which only known-aged individuals were included because these results are consistent with the analysis in which all individuals, whether they were of known age or not, were included. With the exception of H/L ratio, all condition indices varied by an interaction between sex and breeding stage (although muscle and fat score trends were not significant after Bonferroni correction; Table 2.5). Packed cell volume did not vary among males by breeding stage, but was lower among females than among males during the laying and incubating stages, and was comparable during the other stages of the breeding cycle (Figure 2.1A). Packed cell volume was lowest for egg-laying females and highest in the incubating (males only) and the nestling stages (both sexes; Figure 2.1A). Haemoglobin followed similar patterns to PCV between the sexes and across the breeding stages (Figure 2.1B). Total plasma protein was elevated among egg-laying females and was lower in the nestling stage than in the pre-breeding stage for each sex (Figure 2.1C). Females were heavier for their size than males during the egg-laying stage due to egg mass, and were comparable to males during the other breeding stages. Both sexes trended towards a gain in scaled mass during the post-breeding stage (Figure 2.1D). Male muscle did not vary significantly between the breeding stages, but females had high muscle during the nest-building stage, the lowest during the nestling stage, and then high again during the post-breeding stage (Figure 2.1E). Males and females had similar fat reserves during the pre-breeding stage, and while females maintained high fat until the nestling stage, males decreased in fat during the nest-building stage (Figure 2.1F). Fat scores remained low in the post-breeding stage for both sexes (Figure 2.1F). Heterophil to lymphocyte ratios did not significantly vary by sex, breeding stage, or the interaction between sex and breeding stage (Figure 2.1G and Table 2.5).

Scaled mass was positively correlated with age, and this trend appears to be linear (Figure 2.2); however, scaled mass no longer varied significantly by age after Bonferroni correction (Table 2.5). No other condition indices varied by age (Table 2.5).

We found annual variation among haemoglobin, muscle, H/L ratio, and fat, although the trend for the latter two indices (both *P*-values = 0.002) was no longer significant after Bonferroni correction (Table 2.5 and Figure 2.3). Haemoglobin was lowest during the 2007−08 breeding season (Figure 2.3A), muscle was significantly lower in 2008−09 and 2009−10 than during the other two breeding seasons (Figure 2.3B), H/L ratios trended lower in 2008−09 compared with the 2009−10 breeding season (Figure 2.3C), and fat scores trended lower in the 2006−07 and 2008−09 breeding seasons compared with the other two seasons (Figure 2.3D). Scaled mass was the only condition index to vary with time of day (Table 2.5).

DISCUSSION

We describe condition indices for a small tropical granivore, the crimson finch, and demonstrate that these indices vary by sex, breeding stage, and to a lesser extent age, year and time of day. Our results demonstrate that researchers should control for these sources of variation (statistically or via sampling design) to interpret differences in condition correctly between individuals and populations.

Effects of egg laying by females

We found that most of the condition indices varied significantly by an interaction between sex and breeding stage. For females, much of this effect is most parsimoniously explained as a consequence of egg laying. Packed cell volume and haemoglobin decrease while total plasma protein and scaled mass increase in egg-laying females. This pattern has been reported previously (packed cell volume, Fair *et al.*, 2007; and total plasma protein, Horak *et al.*, 1998a; Saino *et al.*, 2001; Wagner *et al.*, 2008). The nadir for packed cell volume among egg-laying females is probably caused by changes in hormone levels (Wagner *et al.*, 2008), and this decrease in the proportion of red blood cells, and subsequently of haemoglobin, is not sufficiently low to be considered anaemia (Campbell and Ellis, 2007). The high total plasma protein levels among egg-laying females may reflect female investment in their offspring's immunity by their transfer of immunoglobulins to the eggs (Saino *et al.*, 2001), but this hypothesis should be tested. Finally, the increased scaled mass among egg-laying females is an artifact of the developing egg mass and clearly does not reflect improved body condition. Generally, the changes in condition indices during egg laying for a given female cannot be interpreted as changes in her condition reflective of her interaction with the environment; however, a comparison of the magnitude of change between females in different environments may be informative in some cases.

Packed cell volume and haemoglobin

Consistent with the result that packed cell volume and haemoglobin are positively and strongly correlated in crimson finches (Table 2.4) and in birds generally (Velguth *et al.*, 2010), we found that the interaction between sex and breeding stage was very similar between these two

indices. Males did not vary in either index with breeding stage, while females did. Their egg-laying decrease persisted through the incubating stage, when females still had lower values than males; however, female values increased thereafter and were again comparable to males during the nestling and post-breeding stages. A similar pattern was found among mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*; Morton, 1994).

The interaction between sex and breeding stage may explain the inconsistent results of studies that considered only sex, but did not consider both sex and breeding stage. Some studies found males to have higher PCV values than females (Saino *et al.*, 1997; Owen *et al.*, 2005), while another found females to have higher values (Kilgas *et al.*, 2006a), and still others found no sex difference (Dawson and Bortolotti, 1997; Kasprzak *et al.*, 2006; Hatch *et al.*, 2010). In a meta-analysis of previously published articles, Fair *et al.* (2007) concluded that PCV was not different between the sexes. We suggest that the sexes may vary in their packed cell volume and haemoglobin values, but that this difference is stage dependent. We would not have found a sex effect had we not tested for the interaction term between sex and breeding stage, because the main effect of sex was not significant in our models.

Total plasma protein

Significant decreases in protein concentration from the pre- breeding to the nestling stage occurred in both sexes, consistent with the findings of Horak *et al.* (1998a) (but see Saino *et al.*, 2001). The low total plasma protein levels in females during the nestling stage may be due to depleted protein levels following egg production, but this does not explain why males also have

their lowest total plasma protein levels during this stage, suggesting that a different mechanism is involved. Breeding birds may be suppressing their immune function (Greenman *et al.*, 2005) and thereby causing a decrease in total plasma protein levels during the nestling stage (Ardia, 2005). However, this condition index is also influenced by other factors. Total plasma protein levels increase with the nutritional value of food (Gavett and Wakeley, 1986; Brown, 1996), so the variability in total plasma protein among crimson finches may reflect the variability of food resources across the breeding season (e.g. Horak *et al.*, 1998a). Total plasma protein levels also increase with disease through an increase in circulating globulins (Ots and Horak, 1998), as well as with dehydration. Dehydration is unlikely to be a factor among crimson finches, because they inhabit riparian areas where they have ready access to water. The changes between the pre-breeding and nestling stages we documented may therefore be interpreted as reflecting either changes in diet or changes in immune challenges, response, and/or function. The interpretation of total plasma protein levels in ecological studies is complicated by the fact that several factors can impact this index, and disentangling the mechanism behind a given trend is challenging. For example, high total plasma protein levels may be attributed to an individual being in good condition due to good nutrition, to an individual being in poor condition due to disease, or to dehydration. The lack of a clear and consistent interpretation of total plasma protein suggests that it should be interpreted with caution.

Scaled mass, fat, and muscle

Body mass is known to increase with time of day in diurnal birds due to overnight fasting (Pravosudov and Grubb, 1997; Sepp *et al.*, 2010), and we found the same among crimson finches, although fat and muscle scores did not change with time of day.

Both sexes had lower fat scores while breeding compared with the pre-breeding stage, but the timing of fat loss differed between the sexes, with males losing their fat during the nest-building stage, whereas females maintained high fat levels until the nestling stage. Crimson finch males, and not females, build the nests (Milenkaya *et al.*, 2011). This activity may explain the loss of fat among males during this stage, either because it is energetically costly or because it is adaptive to maintain lower fat stores during a period of high mobility. Crimson finch females not only had less fat but also had their lowest muscle scores during the nestling stage, suggesting that this is the most challenging time of the breeding season for them. Similar results were found among chick-rearing black-legged kittiwakes (*Rissa tridactyla*; Kitaysky *et al.*, 1999), American kestrels (*Falco sparverius*; Dawson and Bortolotti, 1997), and Savi's warblers (*Locustella luscinioides*; Neto and Gosler, 2009). However, male and female crimson finches provision the young to an approximately equal extent (personal observation by Olga Milenkaya, Virginia Tech), and males did not lose any muscle, fat, or scaled mass during the nestling stage, suggesting that more than simply the cost of provisioning young is involved in the changes we observed in females at this stage.

The optimal body mass of a bird is influenced by physiological and ecological trade-offs between essential activities. The trade-off between starvation and predation (McNamara and Houston, 1990) is an example; fat reserves decrease starvation risk but may increase predation risk, while pectoral muscle reserves lower predation risk through increased flight performance

(reviewed by Rogers, 2005). Food availability and predictability, in conjunction with predatory pressure and physiological demands such as thermoregulation, migration, and molt, may all impact optimal mass and the optimal allocation of resources between fat and muscle reserves. All of these variables may change throughout the breeding season of crimson finches, which may in turn affect optimal levels of scaled mass, fat, and muscle. Unfortunately, most of what we know about adaptive mass and its associated trade-offs, and the role of fat and muscle, comes from the study of migrants and northern-hemisphere temperate species, with little being known about sedentary birds in the tropics, such as crimson finches. We suggest that if fat and muscle scores are to be used as indicators of condition among sedentary and tropical birds, then we need to understand the costs and benefits of these reserves better for species that do not face the challenge of migration and that live in climates that are less variable or thermally challenging.

Sex, age, and year effects

Most of the condition indices we measured also varied significantly by sex. The mechanism behind the variation due to sex is important for interpreting condition because if, for example, this variation is solely due to hormones during the breeding season then sex may be a less important covariate if birds are sampled during the non-breeding season. Moreover, given that sex also interacts with breeding stage, condition indices should not be collected during the breeding season without detailed knowledge of the reproductive state of the individuals, a suggestion also made by others (Saino *et al.*, 2001).

Scaled mass was the only condition index to vary with age in crimson finches (Table 2.5). Lack of pervasive effects of age on condition indices is consistent with some studies (Sheridan *et al.*, 2004), but inconsistent with others, which found that age correlates with total plasma protein (Dyer *et al.*, 2010), PCV (through an interaction with sex), haemoglobin and H/L ratios (Norte *et al.*, 2009b). Ultimately, age effects are best tested longitudinally, which we were unable to do because we sampled few individuals across years and within the same breeding stage.

Two condition indices varied significantly between years in crimson finches, including haemoglobin and muscle scores; H/L ratio and fat scores also varied by year, but these trends were not significant after Bonferroni correction. Others have also found that these and additional condition indices vary by year or season, suggesting an environmental effect on condition (Norte *et al.*, 2009b; Vinkler *et al.*, 2010). However, the annual variation we found was not consistent between condition indices. For example, muscle was lowest during the 2009−10 breeding season, but this was an average year for haemoglobin. Haemoglobin, muscle scores, H/L ratio, and fat scores reflect different aspects of the physiological state of the individual, which may explain the inconsistent trends between these condition indices across years.

Use of condition indices in conservation

We suspect that the year effects we observed are likely to have resulted from differences in environmental conditions between years, for example variation in food supply mediated by weather. It is this type of relationship between individual condition and environmental conditions

that is useful in conservation. If the year effect indeed reflects the environment, then the condition indices that show these year effects, i.e. haemoglobin, pectoral muscle scores, and to a lesser extent, H/L ratio and fat scores, may be the most appropriate ones for conservation applications. We documented considerable variability in condition indices attributable to sex, breeding stage, and the interaction between sex and breeding stage, and to a lesser extent age and time of day. This variation must be accounted for, either statistically or via sampling design, in order to interpret condition indices as indicators of environmental conditions. For example, in interpreting differences between two habitats using haemoglobin as an index, one would need to control for the confounding effects of breeding stage and a sex by stage interaction. In such cases, one should not view an absolute value of a given index as a measure of the physiological condition of an individual, but rather the condition of an individual is relative to conspecifics of the same sex, breeding stage, and possibly age. This has previously been suggested for at least some condition indices (e.g. PCV, Fair *et al.*, 2007).

If we assume for the moment that the year effects in our analyses do represent responses to annual variation in environmental conditions, then the two condition indices that exhibited no confounding effects such as sex and stage but did exhibit a year effect, i.e. pectoral muscle score and to a lesser extent H/L ratio, represent better choices for conservation applications. Those condition indices that exhibit several confounding effects but no year effect are the poorest choices because the link between the environment and the condition index is not as direct and is confounded by other variables. However, our assumption about the source of year effects could be incorrect. Although others have demonstrated that condition indices do vary with habitat or environmental quality (Owen *et al.*, 2005; Johnson, 2007; Homyack, 2010), we cannot exclude the possibility that some or all of the year effects we observed in our study were a function of

something other than environmental variation, such as a cohort effect. Understanding the mechanism of how pectoral muscle scores and H/L ratio are affected by environmental conditions, and what the consequences of that are for individuals and populations, are topics for further research.

Underlying the use of condition indices in conservation is the often implicit assumption that condition and fitness are positively correlated; that is, even if a condition index exhibits a relationship to habitat or environmental conditions, if this relationship has no consequences for survival or reproduction then it does not inform conservation. Indeed, some condition indices have been found to correlate with primary components of fitness, such as reproductive success (mean corpuscular volume, Bearhop *et al.*, 1999; total plasma protein, Gregg *et al.*, 2006) and survival (haemoglobin, Ben-David *et al.*, 2002; and H/L ratio, globulin concentration, and albumin to globulin ratio, Kilgas *et al.*, 2006b). Of the four condition indices that we suggest may be useful in conservation, both haemoglobin and H/L ratio have been found to predict survival (Ben-David *et al.*, 2002; Kilgas *et al.*, 2006b), indicating that they may be particularly useful indices, and we are not aware of any studies that tested whether muscle or fat score relate to fitness. However, the hypothesis that condition indices are meaningful indicators of fitness has been questioned (Dawson and Bortolotti, 1997; Lailvaux and Kasumovic, 2011) and needs to be validated (Stevenson and Woods, 2006; Wikelski and Cooke, 2006; Johnson, 2007; Johnstone *et al.*, 2012b) if condition indices are to be useful tools for conservation.

ACKNOWLEDGMENTS

We are especially grateful to our field assistants Roy Churchwell, Evan Rehm, and Jennifer Bruce for helping to collect these data. Thanks to Michelle Hall, Kim Maute, and Butch Maher for their invaluable help during the field seasons, and to J. Lindley McKay for his unwavering moral support. We thank two anonymous reviewers for helping to improve this manuscript. We thank the personnel at Mornington Wildlife Sanctuary and members of the Avian Ecology Laboratory at Virginia Tech. This study was based out of the WildlifeLink Centre for Research and Conservation at Mornington Wildlife Sanctuary. This work was supported by the Australian Wildlife Conservancy.

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Tables

Table 2.1: Examples of body condition indices being applied in conservation. These indices include those that reflect resource (e.g. food) acquisition and allocation, such as body mass and measures of fat reserves, as well as haematological, biochemical, and endocrine indices that assess other aspects of physiological condition

Conservation application	Condition index	Species	References
Assessing habitat quality	Fat score, mass, stored fat, haematocrit, H/L ratio, WBC counts, non-estrified fatty acids, glucose, glycerol, uric acid, β-hydroxybutyrate, and triglycerides	Southwestern willow flycatcher (*Empidonax traillii extimus*)	Owen *et al.* (2005)
Assessing habitat requirements	H/L ratio	Eastern yellow robin (*Eopsaltria australis*)	Maron *et al.* (2012)
Assessing nutritional requirements	Mass, WBC counts, packed cell volume, total plasma protein, serum calcium, albumin, serum phosphorus, uric acid, creatine kinase, and aspartate aminotrasferase	Greater sage grouse (*Centrocercus urophasianus*)	Dyer *et al.* (2009, 2010)

Assessing effects of habitat fragmentation	Corticosterone and mass adjusted for structural body size	Eurasian treecreeper (*Certhia familiaris*)	Suorsa *et al.* (2003)
	Haematocrit	Bats: *Artibeus jamaicensis* and *Artibeus obscurus*	Henry *et al.* (2007)
	Haemoglobin, haematocrit, N/L ratio, WBC counts, mean red blood cell volume, mean cell haemoglobin content, mean cell hemoglobin concentration, and red blood cell distribution width	Agile antechinus (*Antechinus agilis*)	Johnstone *et al.* (2012a)
	Corticosterone and mass adjusted for structural body size	Common toad (*Bufo bufo*)	Janin *et al.* (2011)
Assessing effects of ecotourism	Haematocrit, leucocrit, total serum protein, WBC differentials, and total antioxidant capacity to total oxidative status ratio	Southern stingray (*Dasyatis americana*)	Semeniuk *et al.* (2009)

	Corticosterone	Magellanic penguin (*Spheniscus magellanicus*)	Walker *et al.* (2005)
	Corticosterone and mass adjusted for structural body size	Yellow-eyed penguin (*Megadyptes antipodes*)	Ellenberg *et al.* (2007)
Assessing stress due to logging activity	Corticosterone	Northern spotted owl (*Strix occidentalis caurina*)	Wasser *et al.* (1997)
Assessing effects of oiling on wildlife	Haemoglobin	River otter (*Lontra canadensis*)	Ben-David *et al.* (2002)

For a review of body condition indices used in conservation broadly, see Stevenson and Woods (2006), and for reviews of the use of body condition indices to assess habitat quality in particular, see Johnson (2007), Ellis *et al.* (2012), and Homyack (2010).

Abbreviations: H/L ratio, heterophil to lymphocyte ratio; N/L ratio, neutrophil to lymphocyte ratio; and WBC, white blood cell.

Table 2.2: Scoring criteria for furcular fat and pectoral muscle

Score	Furcular fat	Muscle
0	No fat observed	No pectoralis observed
1	Fills <33% of fuculum	Keel is very prominent, with minimal pectoralis
2	Fills 34−66% of furculum	Pectoralis is clear, but does not exceed the keel
3	Fills 67−99% of furculum	Pectoralis exceeds keel
4	Fat is flush with furculum	−

Table 2.3: The distribution of observed values for each condition index among crimson finches, including the mean, standard deviation, minimum, maximum, and sample size (*n*)

Condition index	Mean	SD	Minimum	Maximum	*n*
Packed cell volume (%)	48.5	2.92	40	58	322
Haemoglobin (g/L)	174.4	12.81	142	224	335
Total plasma protein (g/dl)	4.93	0.62	3.25	7.2	186
Heterophil to lymphocyte ratio	0.835	0.96	0.10	8.9	149
Scaled mass (g)	9.96	0.72	7.67	12.16	362
Muscle score	2.09	0.54	0.5	3	362
Fat score	2.06	0.93	0	4	362

Table 2.4: Pairwise correlations between condition indices. Included here are the correlation coefficient, the sample size in parentheses, and asterisks indicating significance after Bonferroni correction for the Pearson's correlations (**P < 0.001 and ***P < 0.0001)

	Packed cell volume	Haemoglobin	Total plasma protein	Scaled mass	Log(H/L ratio)	Muscle score	Fat score
Packed cell volume	1	0.71 (215)***	-0.22 (115)	-0.13 (223)	-0.06 (92)	0.07 (225)	-0.06 (223)
Haemoglobin		1	-0.18 (105)	-0.15 (238)	0.00 (90)	-0.09 (251)	-0.14 (249)
Total plasma protein			1	0.40 (113)**	-0.05 (93)	0.07 (115)	0.41 (114)
Scaled mass				1	-0.22 (94)	0.17 (264)	0.29 (262)
Log(H/L ratio)					1	-0.10 (97)	-0.04 (96)
Muscle score						1	0.17 (279)
Fat score							1

Correlations between a continuous variable [packed cell volume, haemoglobin, total plasma protein, scaled mass, and log(H/L ratio)] and either muscle score or fat score are polyserial correlations, the correlation between muscle score and fat score is a polychoral correlation, and neither are tested for significance.

Table 2.5: The variation of each condition index by sex, year, age, breeding stage, sex by breeding stage interaction, and time of day. Included here are the sample size (*n*) and r^2 for each model, and the degrees of freedom (d.f.), F-ratio (*F*) and *P*-value, with an asterisk denoting significance after Bonferroni correction for each covariate in the model

Condition index covariates	*n*	r^2	d.f.	*F*	*P*-value
Packed cell volume (%)	268	0.70			
Sex			1	4.06	0.05
Year			3	1.88	0.13
Age			4	1.37	0.25
Stage			5	7.63	<0.0001*
Sex × stage			5	4.98	0.0002*
Time of day			1	0.96	0.33
Haemoglobin (g/l)	273	0.70			
Sex			1	2.84	0.09
Year			3	7.13	0.0001*
Age			4	0.94	0.44
Stage			5	4.91	0.0003*
Sex × stage			5	5.39	0.0001*
Time of day			1	1.23	0.27
Total plasma protein (g/dl)	187	0.71			
Sex			1	18.35	<0.0001*
Year			1	0.93	0.34
Age			4	1.70	0.15

Stage			5	12.40	<0.0001*
Sex × stage			5	9.75	<0.0001*
Time of day			1	0.22	0.64
Log(H/L ratio)	146	0.61			
Sex			1	1.71	0.19
Year			1	9.86	0.002
Age			4	0.95	0.44
Stage			5	1.50	0.20
Sex × stage			5	0.58	0.72
Time of day			1	1.03	0.31
Scaled mass (g)	310	0.67			
Sex			1	0.76	0.38
Year			3	1.56	0.20
Age			4	2.49	0.04
Stage			5	13.14	<0.0001*
Sex × stage			5	14.38	<0.0001*
Time of day			1	12.16	0.0006*
Muscle score	320	0.55			
Sex			1	4.58	0.03
Year			3	26.93	<0.0001*
Age			4	0.58	0.68
Stage			5	3.06	0.01
Sex × stage			5	2.75	0.02
Time of day			1	0.88	0.35
Fat score	318	0.29			
Sex			1	29.10	<0.0001*

Year			3	4.96	0.002
Age			4	0.58	0.68
Stage			5	9.35	<0.0001*
Sex × stage			5	2.78	0.02
Time of day			1	2.87	0.09

Figure legends

Figure 2.1: The variation in condition indices among crimson finches by sex and breeding stage. Least-squares means (±SEM) of each condition index by sex and breeding stage, including packed cell volume (A), haemoglobin (B), total plasma protein (C), scaled mass (D), muscle score (E), fat score (F), and heterophil to lymphocyte ratio (H/L ratio; G). Sample sizes are given within each bar.

Figure 2.2: The variation in scaled mass among crimson finches by age. Least-squares means (±SEM) of scaled mass (in grams) by age. Scaled mass trended positively with age, but the variable age was no longer significant in the model after Bonferroni correction. Sample sizes are given within each bar. Other condition indices did not vary significantly by age and are not illustrated here.

Figure 2.3: Annual variation in haemoglobin, muscle, H/L ratio, and fat score among crimson finches. Least-squares means (±SEM) of haemoglobin (A), muscle score (B), H/L ratio (C), and fat score (D) by year. We include the H/L ratio and fat score here because they trended with year (both *P*-values = 0.002) even though these trends were not significant after Bonferroni correction. The H/L ratio values (C) were back transformed from a base e log to a linear scale. Sample sizes are given within each bar. Other condition indices did not significantly vary by year and are not illustrated here.

Figures

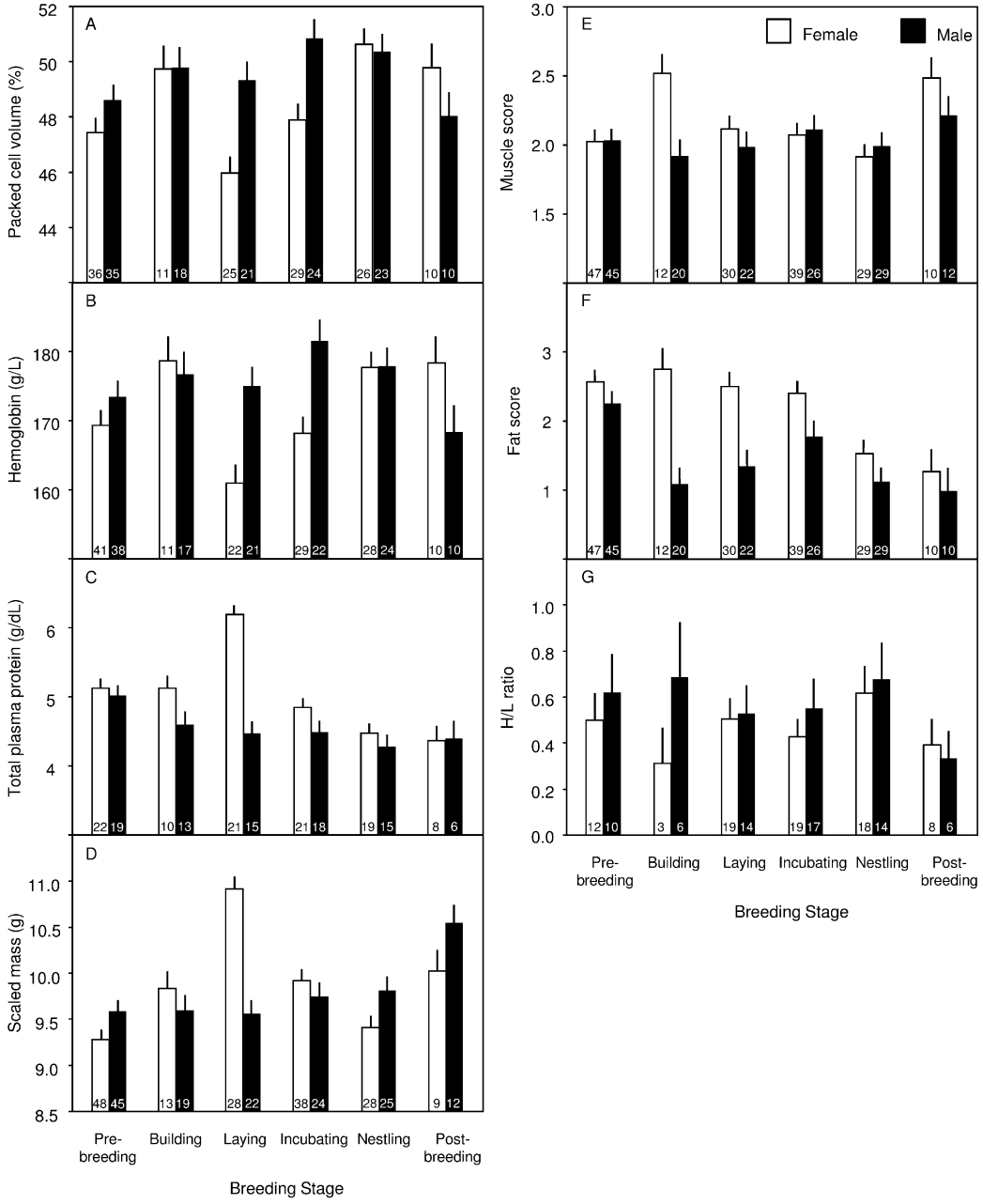

Figure 2.1: Variation in condition indices among crimson finches by sex and breeding stage

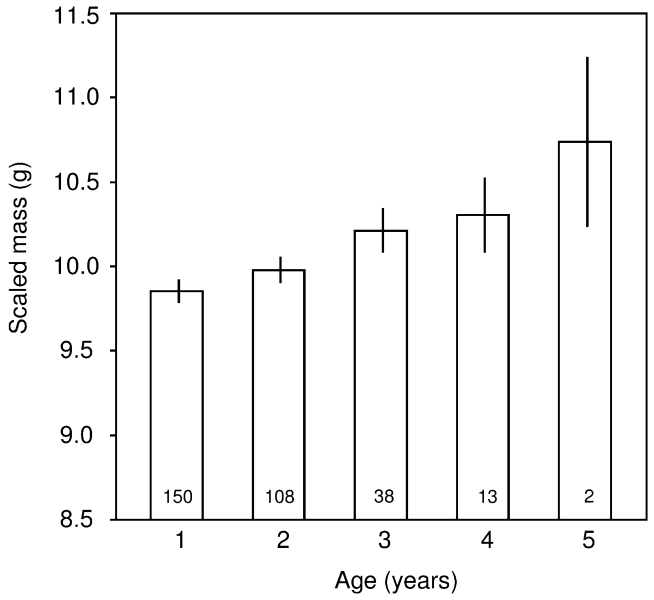

Figure 2.2: Variation in scaled mass among crimson finches by age

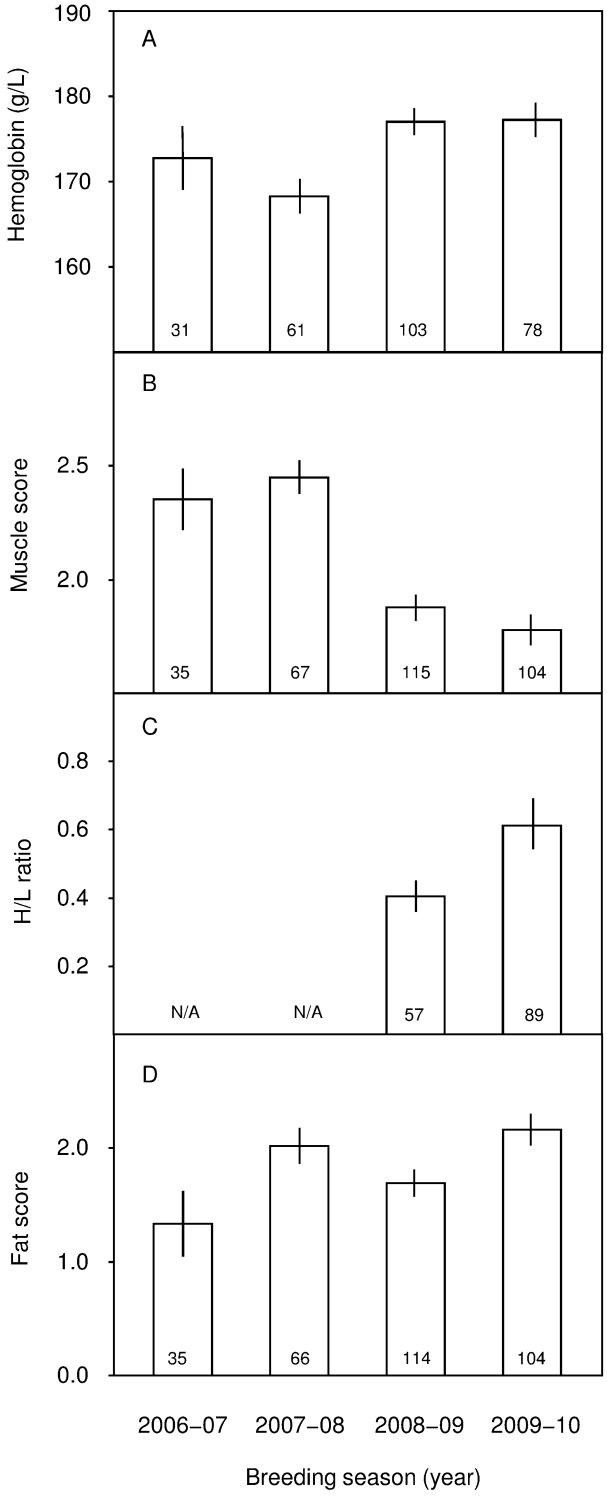

Figure 2.3: Annual variation in haemoglobin, muscle, H/L ratio, and fat score among crimson finches

CHAPTER III. BODY CONDITION INDICES ARE REPEATABLE ACROSS SHORT, BUT NOT LONG, TIME PERIODS IN A TROPICAL BIRD SPECIES

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Submitted for publication.

Abstract. It is common in evolutionary ecology to interpret body condition indices as indicators of individual quality, but this hypothesized relationship has been questioned and remains poorly validated. Here, we test one of the fundamental predictions of this condition-quality hypothesis, that condition indices are repeatable within individuals. We sampled crimson finches (*Neochmia phaeton*) for seven commonly used condition indices and tested whether individual condition relative to conspecifics in the same context (e.g., breeding stage) was repeatable. We calculated the indices' repeatability across several temporal scales, from short (within breeding season) to long (over two years) time periods, as well as without consideration of time scale. Most condition indices were repeatable when sampled without consideration of time scale, all were repeatable within a short time period, and none were repeatable over the longest time period. This provides only partial support for the condition-quality hypothesis, because although condition indices were generally repeatable, this was primarily attributed to short term, instead of long term, repeatability. Condition indices may be meaningful indicators of short-term survival

or fitness potential, but our findings are inconsistent with the idea that condition indices are indicators of inherent individual quality.

Keywords: body condition; condition indices; crimson finch; individual quality; intraclass correlation coefficient; Neochmia phaeton*; phenotypic plasticity; repeatability*

INTRODUCTION

The concepts of individual quality and condition are widely employed in organismal ecology and evolution. Individual quality can be defined as the genotypic and phenotypic heterogeneity among conspecifics that is positively correlated with fitness (Wilson and Nussey 2010). By definition, individuals vary in quality. Those of higher quality are expected to be more successful at interacting with their environment, thereby improving their condition. Condition is usually defined as the physiological state of an individual and is higher when one acquires and assimilates more resources (Hunt et al. 2004; Tomkins et al. 2004; Peig and Green 2009; but see Hill 2011 for a different definition). Condition is a term often employed in a relative sense to compare individuals within populations or between places and times. Researchers interpret condition as a reflection of individual quality (Rowe and Houle 1996; Cotton et al. 2004; Peig and Green 2009) because those of superior quality are relatively more successful in acquiring resources vital for improving their realized fitness.

In light of the challenges inherent to measuring fitness, and without a direct measure of either individual quality or condition, researchers have turned to the use of condition indices.

These tools measure specific aspects of an individual's physiological state (e.g., nutritional status, stress levels, and immune function) and therefore reflect condition and by extension, are expected to reflect individual quality (Peig and Green 2009). Indeed, some condition indices have been found to correlate with primary components of fitness such as reproductive success (Bearhop et al. 1999; Gregg et al. 2006) and survival (Ben-David et al. 2002; Kilgas et al. 2006). Thus condition indices are thought to be indicators of individual quality, and either explicitly or implicitly, researchers often interpret them in this way (Moyes et al. 2009; Peig and Green 2009; Wilson and Nussey 2010; Lailvaux and Kasumovic 2011). Some even use the terms condition and quality interchangeably (e.g., Hõrak et al. 1998; Hanssen et al. 2009; Edler and Friedl 2010).

We term this common interpretation of condition indices the condition-quality hypothesis (analogous to the CORT-fitness hypothesis; Bonier et al. 2009). This hypothesis states that condition indices are meaningful indicators of individual quality and therefore predict fitness. The assumptions of this hypothesis are that condition indices measure condition, and that the relative condition among individuals reflects their quality. Although it is commonly used in interpreting condition indices, this hypothesis has been questioned (Dawson and Bortolotti 1997b; Lailvaux and Kasumovic 2011) and its assumptions and predictions remain mostly untested.

Because individual quality involves inherent components that do not change in adulthood such as one's genetics and certain parental effects, a prediction of the condition-quality hypothesis is that relative condition as measured by condition indices should be repeatable within individuals, and over long time periods. That is, while one's condition indices are expected to vary across contexts (e.g., breeding stage), one's condition relative to others in the

same context should not. For example, an individual identified as high quality by virtue of being in better condition at a given time is expected to remain above average at a later time compared to others in the same context. Here, we test this prediction of the condition-quality hypothesis by accounting for the natural variation in condition indices across contexts and then examining whether the remaining variation in condition indices are repeatable within individuals and across time.

Repeatability, or the intraclass correlation coefficient (ICC), is the proportion of total variation (among and within individuals) that is attributed to the variance among individuals (Eq.1; Becker 1984; Lessells and Boag 1987; Nakagawa and Schielzeth 2010; Wolak et al. 2012):

$$\mathrm{ICC} = \frac{\sigma_{\alpha}^2}{\sigma_{\alpha}^2 + \sigma_{\varepsilon}^2} \qquad \text{Eq. 1}$$

where σ_{α}^2 is the among-individual variance and σ_{ε}^2 is the within-individual variance, including error. The ICC has several applications in the life sciences depending on the context. Variation within multiple samples from the same subject, taken at the same time, is a quantification of measurement error or consistency (e.g., Saino et al. 1997), variation among individuals of a family is regarded as the upper limit to heritability as used in evolutionary biology (Boake 1989; Falconer and Mackay 1996), and variation within individuals over time is a quantification of where a phenotype is on a continuum between being static and being plastic (Westneat et al. 2011). In our application we control for the contexts that are known to impact condition indices such as sex, breeding stage, time of day, and annual variation such that we assess condition indices relative to others in the same circumstances. Thus our application of the ICC measures the extent to which differences in relative condition among individuals are consistent over time.

We sampled crimson finches (*Neochmia phaeton*; Family Estrildidae; Hombron and Jacquinot 1841) for seven commonly used condition indices: packed cell volume, hemoglobin concentration, total plasma protein, heterophil to lymphocyte ratio, mass corrected for structural body size, and pectoral muscle and furcular fat scores. Here, we test if these condition indices are repeatable, on a large dataset of wild animals across several temporal scales, from short (within breeding season) to long (over two years) time periods. If repeatable then these indices may be useful measures of individual quality.

METHODS

Study species and site

We studied a wild population of crimson finches, a species restricted to riparian zones throughout tropical savannas in northern Australia and New Guinea (Higgins et al. 2006). They are small (mass ~ 10.0 g) and sedentary passerines that breed during the wet season (roughly December through April in our study area; Milenkaya et al. 2011). Detailed breeding biology and life history traits of our study population are described by Milenkaya et al. (2011). Crimson finches do not hold territories and forage in communal areas, making them particularly well suited for this study because their relative body condition is not mediated by territory quality and we are therefore able to compare individuals within the same environmental context. This allows us to isolate intrinsic quality effects from extrinsic (habitat) effects (Harrison et al. 2011) while examining animals in their natural context.

Our study site was in the Australian Wildlife Conservancy's Mornington Wildlife Sanctuary in northwest Australia (17°30'49″ S, 126°06'39″ E, elevation 200 m), and consisted of riparian habitat along a two-kilometer stretch of Annie Creek. That our study population occupies such a small area further supports our premise that habitat quality is not likely to significantly vary between individuals. We monitored this crimson finch population for breeding activity, and sampled the individuals for condition indices during four consecutive breeding seasons (15 November 2006 – 11 April 2007, 5 December 2007 – 31 May 2008, 9 December 2008 – 29 May 2009, and 10 December 2009 – 10 May 2010).

General field methods

We captured adult crimson finches in mist-nets during the morning (up to six hours after sunrise) to minimize time-of-day effects on condition indices (Norte et al. 2009; Sepp et al. 2010). We banded the birds with a metal band (Australian Bird and Bat Banding Scheme) and up to three plastic color bands for individual recognition. We determined the sex of each bird based on its sexually-dimorphic plumage (Higgins et al. 2006).

We monitored the breeding attempts of birds at our study site and identified them as being in one of the following stages of the breeding cycle during capture: pre-breeding, nest building, egg laying, incubating, nestling, or post-breeding. Individuals were considered to be in the post-breeding stage three or more weeks after their final breeding attempt failed. If their final breeding attempt was successful, then they were considered to be in the post-breeding stage three

or more weeks after their young fledged because juveniles usually become independent at this time (Milenkaya et al. 2011).

Condition indices

Packed cell volume (PCV), or hematocrit, is the proportion of red blood cells compared to the total volume of blood and is often considered an aggregate indicator of overall health (e.g., Garvin et al. 2007). Low packed cell volume may be caused by parasitism (Szabó et al. 2002), exposure to some toxins (Campbell and Ellis 2007), or micronutrient deficiencies (Sturkie and Griminger 1986), all of which may lead to anemia (packed cell volume < 35% in birds; Campbell and Ellis 2007). High packed cell volume may be caused by dehydration which reduces plasma volume (Campbell and Ellis 2007) or is sometimes interpreted as reflecting a state of higher energy demand and work load (Carpenter 1975; Hõrak et al. 1998). Hemoglobin concentration reflects the blood's oxygen carrying capacity (Birchard 1997) and is lower in clinically sick birds compared to their healthy counterparts (Averbeck 1992). Furthermore, hemoglobin has antioxidant properties (Dafre et al. 2007), and higher hemoglobin concentrations are interpreted as reflecting higher condition (Averbeck 1992; Słomczyński et al. 2006). Heterophils and lymphocytes are white blood cells primarily involved in the immune response (Campbell and Ellis 2007). A high heterophil to lymphocyte ratio (H/L ratio) indicates an active inflammation response (Campbell and Ellis 2007) and can be correlated with elevated corticosterone levels in response to chronic stress, such that higher H/L ratios are most often interpreted as indicating poor condition (Davis et al. 2008). Total plasma protein is a measure of protein concentration in plasma and is generally thought to reflect nutritional status because it

varies with diet quality (Gavett and Wakeley 1986; Brown 1996). Total plasma protein may also be affected by inflammation/infection (de Lope et al. 1998; Ots and Hõrak 1998), and some have interpreted it as a positive measure of body condition (Dawson and Bortolotti 1997a; Ots et al. 1998; Schoech and Bowman 2003). Mass corrected for size indicates nutrient stores (Brown 1996) and is perhaps the most common measure of condition along with fat and muscle scores which correspond to energy and protein reserves, respectively.

Upon capturing the birds, we punctured their brachial vein with a needle and collected ~5 uL of blood in a Hemacue cuvette for measurement of hemoglobin concentration. We used the portable HemoCue Hb 201^{+} Analyzer (HemoCue, Inc., Cypress, CA, USA) in the field to estimate hemoglobin concentration from whole blood. We then collected whole blood (up to 40 uL) in plastic, sodium-heparinized micro-hematocrit capillary tubes, plugged the tubes, and stored them on ice until further processing.

During the 2008–2009 and 2009–2010 field seasons only, prior to plugging and storing the capillary tubes, we smeared a small amount (~1 – 5 uL) of blood from the capillary tube onto a glass slide in order to calculate the H/L ratio. On the same day, we fixed the slides in 100% methanol and later stained them using Dip Quick Stain Set (Jorgensen Laboratories, Inc., Loveland, Colorado, USA). One of us (O.M.) counted 100 white blood cells under 1000× magnification with oil immersion, and conducted white blood cell differentials in which each of the white blood cells was identified as either a heterophil, lymphocyte, eosinophil, basophil, or monocyte. The H/L ratio was calculated as the relative proportion of heterophils to lymphocytes counted in the blood smear.

To calculate packed cell volume, we centrifuged the capillary tubes for fifteen minutes at 1433.6 *g* within a few hours of collecting the blood and read the proportion of red blood cells to the total volume of blood, a direct measure of packed cell volume. During the 2008–2009 and 2009–2010 field seasons only, we extracted the plasma from the capillary tube after centrifuging and read the total plasma protein value with a hand-held refractometer (HR-200 ATC refractometer, AFAB Enterprises, Eustis, Florida, USA).

To calculate each bird's mass relative to body size, we first weighed birds using a 30 g spring scale to 0.1 g and measured the distance from the tip of the beak to the back of the head using calipers as a measure of structural body size. We did not use tarsus length as our measure of structural body size because measuring it precisely and consistently is challenging and often inconsistent (Pyle 1997), especially on small birds such as crimson finches. We then used the mass and head-beak measurement to calculate a scaled mass index (scaled mass) as a measure of mass corrected for structural body size following Peig and Green (2009). We calculated scaled mass separately for males and females because crimson finches are sexually dimorphic in size (Milenkaya et al. 2011). Finally, we scored the amount of pectoral muscle around the keel bone on a 0 – 3 scale and the amount of fat in the furcular hollow on a 0 – 4 scale (Table 3.1). One person (O.M.) assigned 90% of the scores (n = 402 out of 449 sampling occasions).

Temporal scales

To understand how repeatability of condition indices varies across different temporal scales, we calculated repeatability for each index at four different time intervals. First, we

analyzed all of the repeated measures that we collected, regardless of time scale to determine if condition indices are generally repeatable. Second, we asked if condition indices are repeatable within a relatively short time period: within a breeding season, including the immediate pre and post-breeding stages, which is roughly December through April for our study population. Next, we tested if condition indices are repeatable after one year by using repeated samples taken one year ± 10 days of the original sampling date (1 year ± 10 days analysis). Finally, we asked if condition indices are repeatable across a long time period by using all repeated measures sampled more than two years after the original sampling date (2 years analysis). This analysis could not be done for total plasma protein and H/L ratio because we only sampled for these indices during the final two years of the study.

Because some individual birds were never recaptured and therefore were not resampled for condition indices, they could not be included in our repeatability analyses. If the condition-quality hypothesis is true one might expect our repeatability analyses to be biased toward high quality individuals because birds in poorer condition would have lower survival and therefore be less likely to be available for resampling. Therefore we tested whether condition indices of individuals that were never recaptured differed from those of individuals included in our repeatability analyses.

Repeatability analyses

Although repeatability has been assessed with methods other than the ICC (Mansour et al. 1981; Nussey et al. 2007; Romero and Reed 2008; Pierotti et al. 2009; Dingemanse et al.

2010), the ICC calculated from the variance components of a one-way analysis of variance (ANOVA method; Becker 1984; Lessells and Boag 1987) remains the most common method in ecology, behavioral ecology, and evolutionary ecology (Wolak et al. 2012). Recently, newer approaches for calculating the ICC have been recommended over the ANOVA method including the use of linear mixed models (LMM method for approximately normal data) and generalized linear mixed models (GLMM method for non-Gaussian data; Nakagawa and Schielzeth 2010) because of several benefits. The LMM and GLMM methods allow one to control for covariates that affect the measures, resulting in "adjusted repeatability" (R_M) as the point estimate of repeatability (Nakagawa and Schielzeth 2010). This is precisely what is required for our application as it results in an estimate of differences between individuals in relative condition. These methods also readily calculate a confidence interval around the point estimate, which is rarely reported for the ANOVA method (Wolak et al. 2012). Additionally, unlike the ANOVA method, the LMM and GLMM methods constrain the repeatability point estimate and its confidence interval to be positive, which is more relevant than negative repeatability estimates (Nakagawa and Schielzeth 2010; but see Schielzeth and Bolund 2010 for an exception).

We used both the ANOVA and the LMM method to calculate each condition indices' repeatability estimate from individuals that were sampled at least twice for some or all of the condition indices. To avoid pseudoreplication, we excluded some repeated measures. For the within-season analysis, if an individual was sampled multiple times within a season for multiple seasons, then we used the season in which the individual was sampled the most number of times. For the 1 year ± 10 days and 2 years analyses, if an individual could be included multiple times in the analyses, then we randomly chose just one set of samples to analyze. All condition indices

were normally or approximately normally distributed, except for H/L ratios, which were base-10 log transformed to fit the assumptions of normality.

To calculate repeatability with the ANOVA method, we used the variance components from an ANOVA where the individual bird identity was the independent variable and condition indices were the dependent variables (Becker 1984; Lessells and Boag 1987; Hatch and Smith 2010). Standard error was calculated following Becker (1984), and the repeatability estimate was interpreted as being significant if the ANOVA was significant at $\alpha = 0.05$. We ran ANOVAs in JMP Pro 10 (SAS Institute Inc., Cary, North Carolina, USA).

To calculate adjusted repeatability (R_M) with the LMM method, we used the rpt package developed by Nakagawa and Schielzeth (2010) in R version 2.14.1 (R Development Core Team 2013). We calculated R_M by fitting linear mixed models using restricted maximum-likelihood and included covariates as fixed effects and the individual bird identity as the grouping random effect (Nakagawa and Schielzeth 2010). This method allowed us to control for covariates that are known to affect these condition indices in our study population, which included sex, breeding stage, an interaction between sex and breeding stage, time of day, and year (Table 3.2; Milenkaya et al. 2013). Previously we found that bird age had no significant effects on condition indices in our study population (Milenkaya et al. 2013) and therefore age was not included in our analyses of R_M. Standard error and confidence intervals were calculated with parametric bootstrapping (1000 iterations), and significance testing was inferred from the 95% CI with $\alpha = 0.05$ (Nakagawa and Cuthill 2007).

RESULTS

Over four years, we sampled 311 individual adult crimson finches for some or all of the condition indices, of which 156 were only sampled once and 155 were sampled more than once and were used in these repeatability analyses. The number of days between samples for each repeatability analysis is summarized in Table 3.3. Four condition indices did not differ between individuals that were not recaptured and those that were included in our repeatability analyses, including total plasma protein (two sample t-test = 1.36, df = 113, $P = 0.18$, medians = 4.7 and 5.0 g/dl, respectively), H/L ratio (two sample t-test = 1.69, df = 138, $P = 0.09$, medians = 0.48 and 0.60, respectively), muscle (two sample t-test = 0.53, df = 248, $P = 0.60$, both medians = 2.0), and fat (two sample t-test = 1.64, df = 261, $P = 0.10$, both medians = 2.0). Packed cell volume and hemoglobin were lower (two sample t-test = 3.95, df = 196, $P = 0.0001$, medians = 0.480 and 0.495, and two sample t-test = 3.06, df = 213, $P = 0.003$, medians = 172 and 175 g/l, respectively) and scaled mass was higher (two sample t-test = 3.84, df = 259, $P = 0.0002$, medians = 10.0 and 9.8 g) in the samples that were included in the repeatability analyses compared to those from individuals that were not recaptured.

Estimates of adjusted repeatability (R_M) calculated with the LMM method are enumerated in Table A3.1 and are illustrated in Figure 1. Most condition indices were repeatable when analyzed across all repeated measures regardless of timescale, with the exception of muscle and fat scores. All indices were repeatable at the shortest time scale, within a breeding season, but fewer condition indices were repeatable across the longer time periods. Only packed cell volume and total plasma protein were repeatable in the 1 year ± 10 days analysis. At this time scale, these estimates of adjusted repeatability, although significant, have very large confidence intervals (CI width = 0.71 and 0.89, respectively), indicating that these point

estimates have low precision. Furthermore, the lower bound of the total plasma protein CI is very close to zero (0.03), suggesting that it is close to statistical insignificance. None of the condition indices were significantly repeatable at the longest time scale of two or more years.

Estimates of repeatability using the ANOVA method were largely consistent with the LMM results but were inconsistent on five occasions (Table A3.1). Repeatability was significant when using the ANOVA method but not significant when using the LMM method for hemoglobin after 1 year ± 10 days, and muscle and fat scores for all repeated samples (Table A3.1). Repeatability was significant when using the LMM method but not the ANOVA method on two occasions: total plasma protein within a breeding season and after one year (Table A3.1).

DISCUSSION

The condition-quality hypothesis states that condition indices are meaningful indicators of individual quality and therefore predict fitness. We tested a key prediction of this hypothesis, that condition indices are repeatable, by using the LMM method (Nakagawa and Schielzeth 2010) to isolate and test the consistency of differences between individuals in their condition relative to one another. We did this on a large dataset of wild animals across several temporal scales, from short (within breeding season) to long (over two years) time periods. We found only partial support for the prediction that condition indices are repeatable because although most indices were generally repeatable, and all were repeatable over a short time period (within a breeding season when the average time between samples was two months), they were less, or not at all, repeatable at longer time periods. This suggests that a single snapshot of an individuals' relative condition may indicate how successful they currently are at acquiring resources relative

to their conspecifics, as well as their likely physiological state for the next few months, but may not predict how well they will fare well into the future. It would thus be difficult to claim that these indices reliably reflect inherent individual quality.

We confirmed that the individuals included in our repeatability analyses did not constitute a biased sample with respect to condition for four of the seven condition indices. In the other three cases the individuals included in our analyses were in "worse" condition than the individuals that were never recaptured in two instances (packed cell volume, hemoglobin) and in "better" condition in one instance (scaled mass). The differences in the median scores for the individuals that were resampled and those that were not, although statistically significant, were small. These results raise the interesting question of whether such small differences in median PCV (0.015), hemoglobin (3 g/l) and scaled mass (0.2 g) between individuals are biologically relevant. It is noteworthy that H/L ratio and muscle score did not significantly differ between individuals that were resampled and those that were not because we have previously suggested that these two indices may be the more useful indices since they are not confounded by covariates such as sex and breeding stage (Milenkaya et al. 2013). Whether the small differences in PCV, hemoglobin and scaled mass have biological significance should be more directly tested. These results do not compromise our test of repeatability of condition indices because even if our sample is biased toward individuals in "better" condition, relative condition within that sample still should be repeatable.

Methodology

Previous studies in which repeatability of condition indices was assessed have produced inconsistent results and hence our findings are consistent with some studies and contradict others. We suggest that much of the inconsistency of previous work is due to use of the ANOVA method for calculating repeatability, which does not account for the variation exhibited by these indices across different contexts. Many condition indices are known to vary predictably with factors such as sex and breeding stage and it is important to use a method for calculating repeatability that can account for this variation. Because of this we consider the LMM method more accurate than the ANOVA method and the results of the two did sometimes differ. For example, use of the LMM method for total plasma protein within a breeding season allowed us to control for sex, breeding stage and a sex by breeding stage interaction, and in doing so we found that total plasma protein is significantly repeatable at this temporal scale. Had we used only the ANOVA method, which cannot account for such covariates, we would have concluded that total plasma protein was not repeatable at this time scale.

By controlling for individual covariates and thereby evaluating relative condition we obtained results not previously reported and we elaborate on them here, namely (a) that packed cell volume and hemoglobin are indeed repeatable within short time periods, and (b) that there is a consistent pattern among condition indices generally; that they are repeatable within short, but not long, time periods. We therefore conclude that individuals have a "physiological phenotype" that is consistent within a period of about two months, but that this phenotype may not indicate individual quality because it is no longer consistent across longer time periods.

Results of previous studies of packed cell volume and hemoglobin are contrary to ours, including one on gray catbirds (*Dumetella carolinensis*) where packed cell volume was not

repeatable after just one month (Hatch and Smith 2010) and another on great tits (*Parus major*), where packed cell volume was not repeatable within an autumn/winter season or within a 45 day period; although, interestingly, it was repeatable within the spring season in the same study (Norte et al. 2008). Few others have reported the repeatability of hemoglobin in wild populations but Norte et al. (2008) found that it was not repeatable over any of the time periods measured including 45 days, within a season, within a year, or over four years of study.

In previous studies of other condition indices, total plasma protein was found to be repeatable within a season (but only within spring, and not within autumn/winter) among great tits (Norte et al. 2008) but was not repeatable after four months in greenfinches (*Carduelis chloris*; Hõrak et al. 2002). While it was found to be repeatable among great tits after a period of four years (Norte et al. 2008), it was not repeatable after just one year in upland geese (*Chloephaga picta*; Gladbach et al. 2010). Some previous studies of H/L ratio have found that it is repeatable over long periods (Norte et al. 2008), while others have found that it is only repeatable among females (Gladbach et al. 2010), and still others have found that it was not repeatable at all (Ochs and Dawson 2008).

We recommend that other investigators test for the effects of covariates in their study species and that they incorporate that information into their analysis of repeatability to describe the repeatability of condition indices more accurately. This will then allow us to determine whether the lack of consistency across studies is an artifact of different methodologies or if it reflects true variation in the repeatability of condition indices.

Muscle and fat scores

Two condition indices deviate from the general pattern of our results: muscle and fat scores are not repeatable in general and are only weakly repeatable within a short time period. Since we found that muscle and fat scores had the lowest repeatability estimates in our study, we conclude that these indices are poor candidates for indicating individual quality, at least in our study population of a tropical, sedentary bird. We are not aware of any other studies in which the repeatability of pectoral muscle and furcular fat scores was tested. Since muscle and fat scores may be more informative for migratory birds and those facing a more variable or challenging environment (Danner 2012), then the repeatability of fat and muscle scores should be tested in these species if fat and muscle scores are to be employed as indicators of individual quality. Further complicating the interpretation of fat in any species is that it is regulated on shorter time scales than other condition indices and in response to immediate environmental conditions. Fat reserves in birds vary considerably throughout the day and respond to changes in the environment (e.g., temperature) on a daily basis (Gosler 1996). We controlled for time of day, but cannot exclude the possibility that these indices are indeed repeatable in our population but that this was masked by environmental effects such as temperature for which we did not control in our study.

Condition and phenotypic plasticity

Our primary finding is that condition indices may not be meaningful indicators of individual quality because they are only repeatable within short, but not long, time periods. Lack

of repeatability in a phenotype occurs when much of the total variation is attributed to within-individual variation. One reason for this variability within individuals may be that the trait of interest exhibits phenotypic plasticity (Ouyang et al. 2011; Westneat et al. 2011), the expression of different phenotypes from a given genotype in response to different environments (Pigliucci 2001; Nussey et al. 2007). Condition (and condition indices) reflects regulated physiological processes, and is likely regulated to different optima under different circumstances. Nussey et al. (2007) suggested that condition itself is a labile trait and is therefore likely to show phenotypic plasticity. For example, high packed cell volume may be adaptive under some circumstances such as during the provisioning of nestlings which is aerobically demanding, but it may be maladaptive under other circumstances, such as during the non-breeding season because of the increased circulatory costs (Clemens 1990). In this case a high quality individual would have relatively high packed cell volume during nestling provisioning and relatively low packed cell volume during the non-breeding season, such that repeatability of packed cell volume across seasons would be low.

If condition exhibits phenotypic plasticity, then it is best examined as a reaction norm in which optimal condition varies with the environmental context (Nussey et al. 2007). In the case of a single population-wide reaction norm, individual quality may be manifested in the relative ability of individuals to make appropriate changes in their condition in response to different environmental contexts. If this is the case, assessing whether particular individuals are consistently more successful in regulating condition would require understanding regulatory strategies (Williams 2008; Williams 2012) and measuring relative condition appropriately. This is a difficult but conceivable proposition. More insidious is the possibility of variation among individuals in their reaction norms, such that individuals vary in how they respond to the same

environmental gradient because their individual optima differ (Nussey et al. 2007). This could result in individuals of potentially similar individual quality expressing different physiological phenotypes under the same environmental conditions. Attempting to use any condition index for which this is the case as a proxy for individual quality is pointless. Where this is not the case an index may prove to be a reliable proxy, but a thorough understanding of regulation of that aspect of condition and the resulting variation therein will be required to assess this possibility. Certainly our results indicate that a single snapshot of an individual's relative condition, although informative of an individual's state under the current environmental scenario, should not be interpreted as reflecting individual quality.

ACKNOWLEDGMENTS

We are especially grateful to our field assistants Roy Churchwell, Evan Rehm, and Jennifer Bruce for helping to collect these data. Thanks to Michelle Hall, Kim Maute, and Butch Maher for their invaluable help during the field seasons and to J. Lindley McKay for his unwavering moral support. We greatly appreciate Sara Zeigler for her assistance with R, Shinichi Nakagawa for the helpful discussion on repeatability, and Tony D. Williams for the discussion on condition and individual quality. William Hopkins, Ignacio T. Moore, Dana Hawley, Sara Zeigler, Victoria Garcia, and Michelle Jusino provided comments on earlier versions of this manuscript. This work was conducted under the ethics permits CAEC/6/2005 and DEC AEC 43/2007. This study was funded by the Australian Wildlife Conservancy and was based out of the WildlifeLink Centre for Research and Conservation at Mornington Wildlife Sanctuary.

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Tables

Table 3.1: Scoring criteria for furcular fat and pectoral muscle.

Score	Furcular fat	Pectoral muscle
0	No fat observed	No pectoralis observed
1	Fills <33% of furculum	Keel is very prominent, with minimal pectoralis
2	Fills 34−66% of furculum	Pectoralis is clear, but does not exceed the keel
3	Fills 67−99% of furculum	Pectoralis exceeds keel
4	Fat is flush with furculum	

Table 3.2: Individual covariates that were included in our models for calculating R_M. These were included if the condition indices were previously found to vary significantly by the covariate in our study population (●; Milenkaya et al. 2013).

	Individual covariates included in the models				
Condition index	Sex	Stage	Sex × Stage	Year	Time of day
Hemoglobin	●	●	●	●	
Packed cell volume	●	●	●		
Total plasma protein	●	●	●		
Scaled mass	●	●	●		●
Fat score	●	●		●	
H/L ratio				●	
Muscle score				●	

Note: Time of day is the number of minutes since sunrise that the bird was captured. The interaction term between sex and breeding stage was excluded from the total plasma protein analyses for the 1 year ± 10 days analysis in order for the model to converge.

Table 3.3: Number of days between repeated samples for each condition index. Included here are the mean, standard deviation (SD) and range of the number of days between samples for each of the seven condition indices at each of the temporal scales for which repeatability was analyzed.

	All repeated samples			Within a breeding season		
Condition index	Mean	SD	Range	Mean	SD	Range
Packed cell volume	212	188	9 − 873	60	36	9 − 163
Hemoglobin	208	188	9 − 873	62	35	9 − 163
Total plasma protein	143	130	20 − 417	59	34	20 − 151
H/L ratio	148	130	21 − 376	56	32	21 − 146
Scaled mass	190	182	1 − 873	52	35	1 − 163
Muscle score	180	180	1 − 873	49	35	1 − 163
Fat score	182	183	1 − 873	51	37	1 − 163

	1 year ± 10 days			2 years		
Condition index	Mean	SD	Range	Mean	SD	Range
Packed cell volume	363	5	354 − 372	912	167	747 − 1254
Hemoglobin	364	6	355 − 377	910	171	732 − 1254
Total plasma protein	360	4	355 − 367	N/A	N/A	N/A
H/L ratio	360	4	355 − 367	N/A	N/A	N/A
Scaled mass	366	6	355 − 377	902	172	732 − 1254

Muscle score	366	6	355 − 379	920	177	732 − 1254
Fat score	365	6	354 − 379	915	175	732 − 1254

Note: N/A = not applicable.

Figure legends

Figure 3.1: Adjusted repeatability (R_M) and 95% confidence interval for crimson finch condition indices at four temporal scales including (1) for all repeated measures of the index regardless of time scale (All), (2) within a breeding season including its immediate pre-breeding and post-breeding stages (Within season), (3) one year later and within ten days of the original sample date (1 year), and (4) for all samples over two years after the original sampling date (2 years). The number of samples in each analysis and the number of individuals that were sampled can be found in Table A3.1. An asterisk (*) denotes significance at the $\alpha = 0.05$ level.

Figures

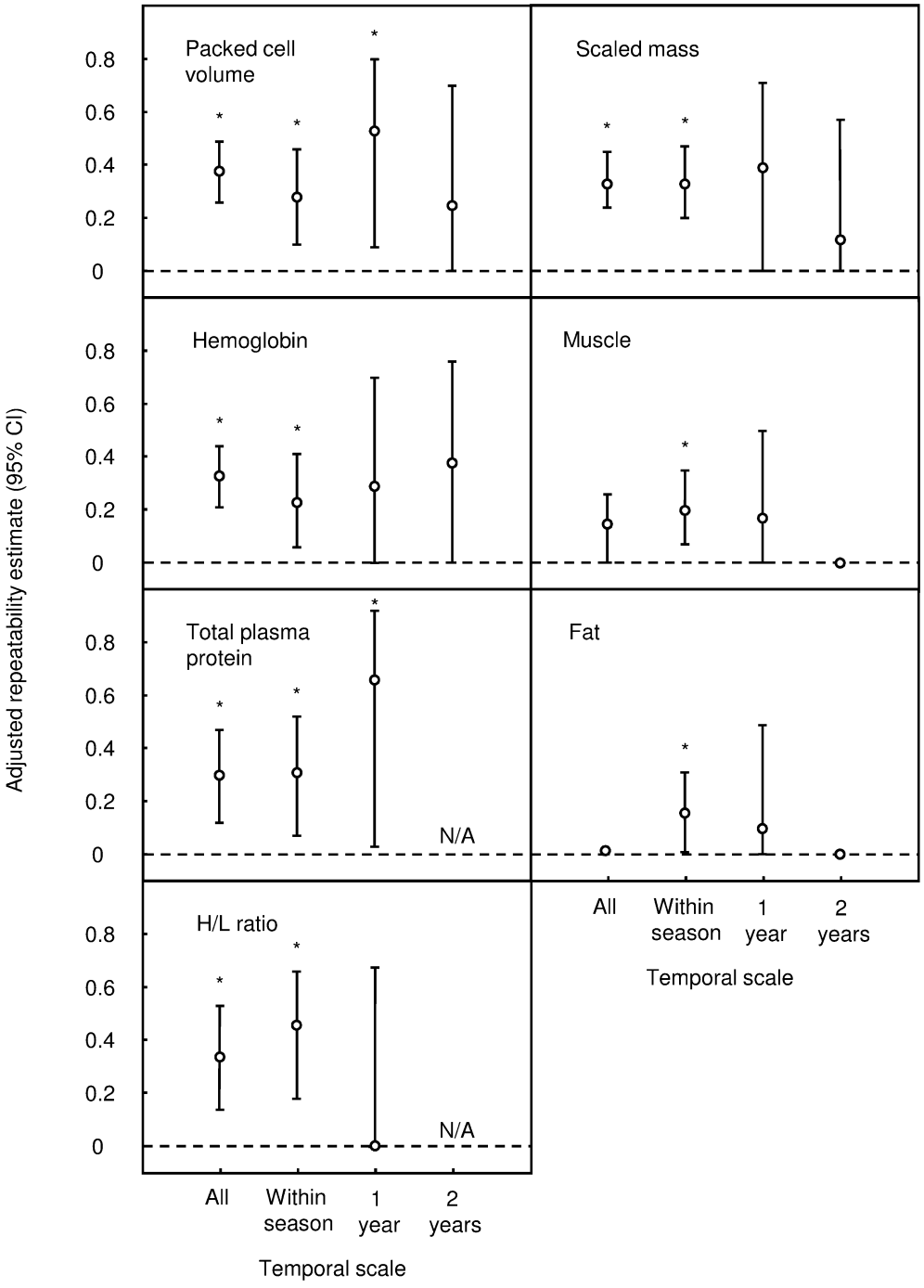

Figure 3.1: Adjusted repeatability (R_M) and 95% confidence interval for crimson finch condition indices

Appendix

Appendix A: Table of repeatability estimates calculated by the LMM and ANOVA methods.

Table A3.1: Repeatability estimates for each condition index across four temporal scales. The temporal scales included here are (1) for all repeated measures of the index regardless of time scale, (2) within a breeding season including its immediate pre-breeding and post-breeding stages, (3) one year later and within ten days of the original sample date (1 year ± 10 days), and (4) for all samples over two years after the original sampling date (2 years).

				LMM method			ANOVA method		
Condition index	Temporal scale	*n*	*k*	R_M	SE	95% CI	R	SE	P-value
PCV	All repeated samples	349	123	0.39	0.06	0.26 − 0.49*	0.74	0.03	<0.0001
	Within a breeding season	193	84	0.29	0.09	0.10 − 0.46*	0.69	0.05	<0.0001
	1 year ± 10 days	44	22	0.54	0.18	0.09 − 0.80*	0.83	0.07	0.0003
	2 years	44	22	0.26	0.22	0 − 0.70	0.44	0.18	0.71

Hemoglobin	All repeated samples	375	133	0.34	0.06	0.21 − 0.44*	0.70	0.04	<0.0001
	Within a breeding season	208	92	0.24	0.09	0.06 − 0.41*	0.65	0.06	0.001
	1 year ± 10 days	46	23	0.30	0.21	0 − 0.70	0.69	0.11	0.03
	2 years	46	23	0.39	0.22	0 − 0.76	0.46	0.17	0.65
TPP	All repeated samples	182	69	0.31	0.09	0.12 − 0.47*	0.66	0.06	0.001
	Within a breeding season	123	54	0.32	0.12	0.07 − 0.52*	0.59	0.08	0.07
	1 year ± 10 days	26	13	0.67	0.21	0.03 − 0.92*	0.58	0.19	0.29
	2 years	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
H/L ratio	All repeated samples	124	49	0.35	0.10	0.14 − 0.47*	0.64	0.07	0.02
	Within a breeding season	81	36	0.47	0.12	0.18 − 0.66*	0.77	0.06	<0.0001
	1 year ± 10 days	18	9	0	0.02	0 − 0.67	0.43	0.29	0.66
	2 years	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Scaled mass	All repeated samples	431	146	0.34	0.06	0.24 − 0.45*	0.68	0.04	<0.0001

	Within a breeding season	249	105	0.34	0.07	0.20 − 0.47*	0.67	0.05	<0.0001
	1 year ± 10 days	56	28	0.40	0.18	0 − 0.71	0.56	0.13	0.26
	2 years	50	25	0.13	0.18	0 − 0.57	0.45	0.16	0.69
Muscle score	All repeated samples	449	151	0.16	0.08	0 − 0.26	0.65	0.04	<0.0001
	Within a breeding season	278	118	0.21	0.07	0.07 − 0.35*	0.73	0.04	<0.0001
	1 year ± 10 days	58	29	0.18	0.15	0 − 0.50	0.51	0.14	0.46
	2 years	48	24	0.00	−	−	0.27	0.19	0.99
Fat score	All repeated samples	445	151	0.00	0.01	0 − 0	0.57	0.04	0.03
	Within a breeding season	274	117	0.17	0.08	0.01 − 0.31*	0.62	0.05	0.003
	1 year ± 10 days	58	29	0.10	0.15	0 − 0.50	0.60	0.12	0.13
	2 years	50	25	0.00	−	−	0.40	0.17	0.85

Note: PCV = packed cell volume; TPP = total plasma protein; N/A = not applicable; *n* = number of samples in the analysis; *k* = number of individuals that were sampled. Repeatability was estimated by using the LMM (Nakagawa and Schielzeth 2010) and

ANOVA (Becker 1984; Lessells and Boag 1987) methods. For the LMM method, we present the adjusted repeatability (R_M), standard error (SE) and 95% confidence interval (CI). An asterisks (*) at the CI denotes significance at $\alpha = 0.05$ because the CI does not cross zero (Nakagawa and Cuthill 2007). A dash (−) in the SE and CI column indicates that these values could not be calculated because some R_M estimates were exactly zero. For the ANOVA method, we present the repeatability estimate (R), its standard error (SE; Becker 1984) and *P*-value for the ANOVA. The repeatability estimate is significant if the ANOVA is significant at $\alpha = 0.05$.

CHAPTER IV. BODY CONDITION INDICES PREDICT REPRODUCTIVE SUCCESS BUT NOT SURVIVAL IN A SEDENTARY, TROPICAL BIRD

Olga Milenkaya, Daniel Catlin, Sarah Legge, and Jeffrey R. Walters

Abstract. Body condition is expected to predict individual fitness because those in better condition have more resources to allocate towards improving their fitness. However, the hypothesis that condition indices are meaningful proxies for fitness has been questioned. Here, we ask if intraspecific variation in condition indices predicts key components of realized fitness including annual reproductive success and survival. We monitored a population of crimson finches (*Neochmia phaeton*), a sedentary, tropical passerine, for reproductive success and survival over four breeding seasons. Additionally, we sampled them for seven commonly used condition indices including mass adjusted for body size, muscle and fat scores, packed cell volume, hemoglobin concentration, total plasma protein, and heterophil to lymphocyte ratio. Our study population is well suited for this research because they forage in common areas and do not hold territories such that variation in condition between individuals is not confounded by differences in habitat quality. Furthermore, we controlled for factors that are known to impact condition indices in our study population (e.g., breeding stage) such that we assessed condition among individuals relative to others in the same context. Condition indices that reflect energy reserves predicted both the probability of an individual fledging young and the number of fledged young that survived to independence, although only during some years. Those that were relatively heavy for their body size produced about three times more independent young

compared to relatively light individuals. That energy reserves are a meaningful predictor of reproductive success up to five months later in a sedentary passerine is noteworthy and supports the idea that energy reserves are at least sometimes predictors of fitness. However, hematological indices failed to predict any measure of reproductive success and none of the indices predicted survival. Therefore, some but not all condition indices may be informative proxies for fitness. However, because we also found that most indices did not predict any component of fitness, we therefore question the ubiquitous interpretation of condition indices as surrogates for individual quality and fitness.

Keywords: crimson finch; ecological physiology; fitness; hematology; individual quality; Neochmia phaeton*; scaled mass index*

INTRODUCTION

Predicting individual fitness of wild organisms is important because intraspecific variation in fitness has broad implications for evolution and higher ecological processes within populations and communities. Researchers are therefore interested in measures that may be meaningful proxies for fitness and predict individual differences in reproductive success and survival. One such proxy is body condition (hereafter "condition"). Condition is most often defined as the pool of resources that an individual has acquired (and presumably assimilated) that can be allocated toward improving fitness (Rowe and Houle 1996; Hunt et al. 2004; Tomkins et al. 2004; but see Hill 2011 for a different definition). Condition is most informative when it is

employed in a relative sense to compare individuals within populations or between places and times. Many life history trade-offs are mediated by condition because allocating resources for one trait means that fewer resources are available for other traits (Stearns 1992). Therefore, the pool of available resources (condition) has traditionally been expected to predict fitness since those with more resources can allocate more toward improving their realized fitness. This condition-fitness relationship may be mediated by individual quality because those of superior quality are expected to be better at acquiring and using resources, thereby improving their fitness. Whether related to individual quality or not, those in better condition are expected to have higher fitness.

However, there is no direct way to test wither condition predicts fitness because condition is not directly quantifiable and researchers instead use condition indices as its surrogate. These indices reflect different aspects of an animal's physiology including resource acquisition and allocation, nutritional status, immunocompetence and stress. We emphasis that condition indices are not the same as condition (Green 2001), but are instead tools for understanding aspects of condition.

Because condition indices measure condition and condition is expected to predict fitness, condition indices are often interpreted as indicators of individual quality and fitness. And indeed, some condition indices have been demonstrated to predict reproductive traits (Bearhop et al. 1999; Gregg et al. 2006) and survival (Ben-David et al. 2002; Verhulst et al. 2004; Kilgas et al. 2006b). But the common interpretation of condition indices as proxies for fitness has been questioned (Lailvaux and Kasumovic 2011; Milenkaya et al. submitted 2013) and condition indices remain poorly validated. Here, we test whether condition indices are meaningful proxies

for fitness by asking if seven commonly-used condition indices predict annual reproductive success and survival.

There are two common challenges to testing whether condition indices are meaningful proxies for fitness: first, condition indices vary by context (e.g. breeding stage) such that differences in condition indices may reflect the context rather than individual condition *per se*. Because we have previously determined how condition indices in our study population vary by sex, breeding stage, age, year, and time of day (Milenkaya et al. 2013b), we can control for this variance and assess individual condition relative to others in the same context. Second, while condition is expected to be related to fitness, it is also subject to extrinsic factors such as the quality of the environment (Andersson 1982; Johnson 2007; Ellis et al. 2012). This makes it difficult to infer fitness from condition where animals have access to habitats of varying quality such as in species that hold territories. However, in our study system we are able to evaluate variation in condition largely independent of habitat quality. Individuals in our study population do not hold territories (Milenkaya et al. 2011) and forage in common areas within a small study area (O. Milenkaya personal observation) such that variation among individuals in condition is mostly not confounded by variation in habitat quality. We acknowledge that other confounding factors such as social structure may influence condition in our study population but we expect these effects to be weaker than those caused by differences in habitat quality in territorial species. By assessing condition indices relative to others in the same context and environment, we were able to largely avoid confounding factors found in previous field studies of relationships between condition indices and fitness components.

METHODS

Study species and study area

Crimson finches (*Neochmia phaeton*, Family Estrildidae) are small (~10 g) passerines that occupy riparian areas in northern Australia and southern New Guinea (Higgins et al. 2006). They breed as socially monogamous pairs in which the male builds the nest, the female lays a clutch of one to seven eggs (average = five), and both sexes incubate the eggs, and provision and defend the young (Milenkaya et al. 2011). We studied a population of wild crimson finches at the Australian Wildlife Conservancy's Mornington Wildlife Sanctuary in northwest Australia (17°30'49″ S, 126°06'39″ E, elevation 200 m) where our study area consisted of riparian habitat along a two kilometer stretch of creek. We monitored individual birds for reproductive success and survival, and sampled them for condition indices over four consecutive breeding seasons (15 November 2006 – 11 April 2007, 5 December 2007 – 31 May 2008, 9 December 2008 – 29 May 2009, and 10 December 2009 – 10 May 2010).

Our study population is well suited for this research because individuals vary in both reproductive success (Milenkaya et al. 2011) and condition (Milenkaya et al. 2013b). Furthermore, nests and fledglings are easy to detect which allowed us to document reproductive success with relative accuracy. Because the birds are sedentary, fairly conspicuous and restricted to a narrow habitat zone, recapture probabilities are high (89−93%; Milenkaya et al. 2011) and therefore estimates of survival are robust. Finally, intraspecific variation in condition among individuals of our study population is mostly not confounded by differences in habitat quality.

General field methods

We captured adult crimson finches in mist-nets and banded them with a metal band (Australian Bird and Bat Banding Scheme) and up to three plastic color bands for individual recognition. We determined the sex of each bird based on their sexually dimorphic plumage (Higgins et al. 2006).

We monitored the breeding attempts of individual birds and identified captured birds as being in one of the following stages of the breeding cycle at the time of capture: pre-breeding, nest building, egg laying, incubating, nestling, or post-breeding. Crimson finches in our study area are multi-brooded (Milenkaya et al. 2011), so the nest building, egg laying, incubating, and nestling stages occur throughout the breeding season and do not necessarily represent the first breeding attempt of the season. The pre and post-breeding stages, however, correspond to the beginning and end of the breeding seasons, respectively.

Some birds were of known age because they were banded as nestlings, juveniles or sub-adults. Of those that were first banded when they were already in adult plumage, they were identified as being in their first breeding season if they had retained juvenal greater primary covert(s) (Milenkaya et al. 2011). The remaining birds first captured as adults were categorized as either 1) in at least their second breeding season (if they had newly molted greater primary coverts at the beginning of the breeding season) or 2) of unknown age (if data on the coverts were not collected or if presence of a molt-limit was ambiguous).

Condition indices

We sampled birds for both traditional condition indices that reflect energy reserves (mass adjusted for body size, and muscle and fat scores) as well as hematological parameters that reflect other aspects of condition. Although hematological indices do not measure energy reserves they measure aspects of physiology that may be related to fitness and are broadly considered as condition indices. We previously described the indices that we measured in Milenkaya et al. (2013b), but we briefly summarize them here. We weighed birds, measured the distance from the tip of the beak to the back of the head as a measure of structural size, and used these morphological measures to calculate a scaled mass index (scaled mass (g)) as a measure of mass corrected for size following Peig and Green (2009). We scored the amount of pectoral muscle around the keel bone (muscle score) and the amount of fat in the furcular (fat score) as in Milenkaya et al. (2013b).

Packed cell volume (PCV) is the proportion of red blood cells to the total volume of blood, and may be considered an aggregate indicator of overall health (e.g., Garvin et al. 2007) because it reflects oxygen carrying capacity (Carpenter 1975; Hõrak et al. 1998) and is negatively affected by parasitism (Szabó et al. 2002), disease, nutritional stress (Harrison and Harrison 1986, but see Fair et al., 2007), and toxin exposure (Campbell and Ellis 2007)). PCV is positively correlated with hemoglobin concentration (Velguth et al. 2010), which also reflects the bloods oxygen carrying capacity (Birchard 1997) and is lower in clinically sick, compared to healthy, birds (Averbeck 1992). To sample for hematological condition indices, we punctured the birds' brachial vein with a needle, collected ~5 uL of blood in a Hemacue cuvette and used the portable HemoCue Hb 201+ Analyzer (HemoCue, Inc., Cypress, CA, USA) in the field to estimate hemoglobin concentration from whole blood (hemoglobin (g/l)). We collected additional whole blood (up to 40 μL) into plastic, sodium-heparinized micro-hematocrit capillary

tubes, plugged the tubes and stored them on ice. Within a few hours, we centrifuged (Hettich Haematokrit 210) the capillary tubes for fifteen minutes at 1433.6 × g and read the proportion of red blood cells to the total volume of blood (packed cell volume (%)).

Total plasma protein is a measure of proteins, primarily albumin and globulin, present in plasma. Low values may be caused by parasites (Norte et al. 2009) and poor nutrition may result in decreased albumin (Rosenthal 2000). Total plasma protein is therefore sometimes interpreted as an indicator of nutritional status (Gavett and Wakeley 1986; Brown 1996) and as a positive measure of condition (e.g., Schoech and Bowman 2003). However, total plasma protein also increases with inflammation/infection (de Lope et al. 1998; Ots and Hõrak 1998). During the 2008−2009 and 2009−2010 field seasons, we extracted plasma from capillary tubes after centrifuging, and read the total plasma protein value (g/dL) with a hand-held refractometer (HR-200 ATC refractometer, AFAB Enterprises, Eustis, Florida, USA).

Heterophils and lymphocytes are white blood cells primarily involved in the immune response (Campbell and Ellis 2007) and the ratio of heterophils to lymphocytes (H/L ratio) can be correlated with elevated corticosterone levels in response to chronic stress (Davis et al. 2008). We sampled for H/L ratio during the 2008−2009 and 2009−2010 field seasons by preparing blood smears in the field and fixing the slides in 100% methanol on the same day. We later stained the smears with Dip Quick Stain Set (Jorgensen Laboratories, Inc., Loveland, Colorado, USA) and one of us (O.M.) performed a leukocyte differential under 1000× magnification by identifying 100 leukocytes as a heterophil, lymphocyte, eosinophil, basophil, or monocyte. The H/L ratio was calculated as the relative proportion of heterophils to lymphocytes counted in the blood smear.

Statistical analyses

We conducted the following analyses to determine if condition indices predict reproductive success and survival using (a) data from all four years of the study (4-year dataset), and (b) data from the latter two years of the study (2008−2009 and 2009−2010 breeding seasons; 2-year dataset). We conducted the 2-year analyses separate from the 4-year analyses because some of the condition indices (H/L ratio and total plasma protein) were only sampled in the latter two years of our study and therefore could not be included in the 4-year dataset. Within each dataset the individual birds we used for analyses of survival and reproductive success are not identical because we did not have reproductive success data on all individuals that were monitored for survival.

Our analyses of whether condition indices predict survival and reproductive success include several covariates that affect either the dependent variable or the condition indices of crimson finches in our study area (Milenkaya et al. 2013b). These covariates include the birds' sex (Sex), their breeding stage at the time of condition sampling (Stage), their age category (Age), and the breeding season (Year). All condition indices were approximately normally distributed except for H/L ratio which we therefore Log base-10 transformed. The condition indices were centered with a mean of zero before being analyzed.

Principal components analysis

Indicators of individual quality may be less informative singularly than within a multivariate approach (Wilson and Nussey 2010). We therefore performed a principal components analysis (PCA) using the correlation matrix for all of the condition indices within the 4-year and 2-year datasets for both the survival and reproductive success analyses. The 4-year datasets include packed cell volume, hemoglobin, scaled mass, muscle score and fat score, and the 2-year datasets additionally include H/L ratio and total plasma protein. We extracted the principal components with an eigenvalue > 1 to use as additional condition indices and included them as explanatory variables in our models of survival and reproductive success. We conducted the PCAs in R version 3.0.0 (R Development Core Team 2013).

Survival and reproductive success analyses

We broadly approached our analysis of how condition indices may influence survival or reproductive success in a similar way. To reduce the number of models under consideration, we first identified the most relevant baseline model with a multiple step procedure (see below; Lebreton et al. 1992). We then built our models of condition indices upon the structure of these baseline models. While it is reasonable to predict that a combination of condition indices may be more informative than a condition index alone, we did not include combinations of condition indices in the interest of limiting the number of models under consideration. Instead, we included separate models for the principal components (see above) which incorporate information from all of the indices. We created a model for the additive effect of each condition index (including the PCs) upon the baseline model. Because condition indices may have non-linear effects on survival and reproductive success, we also considered additional models in which quadratic terms of the

condition indices were included. We controlled for covariates known to affect condition indices in our study population (Milenkaya et al. 2013b) by including additional models where these individual covariates were included as additive effects with the condition indices that they impact. In summary, the candidate model sets included six types of models: (1) baseline, (2) baseline + condition, (3) baseline + condition + condition^2, (4) baseline + condition + covariate(s), (5) baseline + condition + condition^2 + covariate(s), and (6) the set of models that were included in the baseline model selection process (see below; Tables A4.1, B4.1 and B4.2).

We used (Q)AICc, evidence ratios and model weights to evaluate the evidence for relationships of individual covariates and condition indices to survival and reproductive success. Where we found such evidence, we further assessed the impact of that condition index by calculating model-averaged predictions and presenting them with unconditional standard error. We also calculated model-averaged predictions for the covariates included in the baseline models to assess their effect on survival and reproductive success. We used model-averaging because we had high model uncertainty, and we did so across the entire candidate model set. In the interest of brevity and clarity we do not show model-averaged predictions across all categories of covariates, i.e., Sex × Age × Stage × Year, but instead just show those for which we have the highest sample sizes and that are representative of the overall patterns.

Survival analyses

To test the effects of condition indices on apparent survival (φ) of adult crimson finches, we fit Cormack-Jolly-Seber models in Program MARK (White and Burnham 1999). We used

both recapture and resighting events within our study area to build the encounter histories, but we excluded birds that were opportunistically resighted outside of the study site because these birds were known to have dispersed and were not systematically monitored for survival after dispersal (n = 10 individuals). We only included individuals for whom we had data on condition indices and their breeding stage at the time of sampling, and we tested for apparent monthly survival following the occasion in which the individual was sampled for condition (rather than the occasion during which the individual was first banded). The datasets and analyses are summarized in Table 4.1.

We tested for goodness of fit by using the median ĉ test to estimate the variance-inflation factor (ĉ) for the fully time dependent model where both the apparent survival rate (φ) and the recapture probability (ρ) varied with time (φ(t) ρ(t)). Where appropriate, we adjusted for the median ĉ value and used quasi Akaike's information criterion corrected for small sample sizes (QAICc) thereafter in evaluating the evidence for our models.

In the multiple step procedure to determine the most relevant baseline model, we first evaluated the evidence for structural parameters (t and Year, where applicable) in both φ and ρ (Lebreton et al. 1992). In the first step, we structured φ to be saturated with the structural parameters (φ(t +Year+(t × Year)) and compared alternate versions of ρ, testing all combinations of t and Year as well as a constant ('.') model. Having selected the best structure for ρ, we then compared alternate versions of φ in the same manner as for ρ, and selected the best structure for φ.

After developing a baseline model with structural components, we added the following nuisance covariates to test for potential effects on both φ and ρ: Sex, Age, Sex × Age, and

additionally for ρ also Stage, Sex × Stage, and Age × Stage. We did not consider Stage as a covariate for φ because we do not expect breeding stage to impact apparent survival. We compared models where combinations of these nuisance variables were added to the best structural model for ρ (with φ held constant at the best structural model), and, after selecting the best model for ρ, we repeated the process for φ (with ρ held constant at the best model including nuisance covariates). We excluded some of the covariates from our 4-year baseline model selection process because we lacked sufficient data to model them: Sex × Age for φ and Sex × Stage for ρ. At each step, if more than one model was competitive, we selected the most parameterized model to proceed to the next step in an effort to explain the maximum amount of underlying variation at each step. This process allowed us to narrow our candidate model set and to select the best baseline model (Table 4.1) to use as the foundation with which our hypotheses of interest were tested. Although this process allowed some variables to be included that are overall poorly supported and did not significantly improve overall fit (*sensu* Arnold 2010), our goal was to create a baseline model that explained the maximum amount of underlying variation, but was not over-fit.

We evaluated the evidence for our models using an information theoretic approach as previously described and we model-averaged to estimate φ and ρ (95% CI). In this way, we analyzed survival for the 4 and 2-year datasets as well as survival within each of the four breeding seasons because condition indices may predict survival within, if not across, years. However, since we failed to find any patterns in the within-season analyses that were not evident from the 4 and 2-year analyses, we do not elaborate on the within-season analyses or show their results here.

Reproductive success analyses

Approximately half of the breeding pairs in our study area fail to fledge young during a given breeding season with predation being the primary cause of nest failure (Milenkaya et al. 2011). Because so many individuals have an annual reproductive success of zero, we asked two separate questions regarding condition and reproductive success: (1) do condition indices predict whether or not an individual will fledge young; and (2) for those that do fledge at least one young, do their condition indices predict the number of young that they fledge? Because crimson finch fledglings have only a 55% survival rate from fledging to independence (Milenkaya et al. 2011), the number of young produced that survive to independence is a better measure of annual reproductive success than the number of young fledged. We therefore also asked (3) whether condition indices of those adults that are successful at fledging at least one young predict the number of those young produced that survive to independence. In summary, we asked three separate questions of both the 4 and 2-year datasets for a total of six analyses.

To address the first question, we built generalized linear mixed models with a binomial distribution and the logit link function where the response variable was whether (1) or not (0) the individual had fledged young in a given breeding season. To address the second and third questions, we ran the models with a poisson distribution and the log link function where the response variable was the number of young fledged and the number of young produced that survived to independence, respectively. In all of these analyses, the individual bird's identity was used as a random factor because some individuals were sampled across breeding seasons. If an individual was sampled more than once for condition within a breeding season, then we

randomly selected which sampling occasion to include for that year. The explanatory variables of interest in the models were the condition indices and principal components.

We determined the best baseline models by evaluating how Stage, Age, Year and, where feasible, their pairwise interactions affected reproductive success within each dataset. We did not include Sex as a covariate because we do not expect reproductive success to vary by sex. Age was included in the baseline model for two of the analyses within the 4-year dataset, but the identified effect, unknown-aged adults having lower reproductive success than known-aged birds, has no biological interpretation, suggesting that it reflects data structure instead of biological reality. We therefore concluded that we lack the resolution to understand how age affects reproductive success within the 4-year dataset and excluded Age from further consideration. This problem did not exist in the 2 year dataset because in these latter two years of the study, only one individual was of unknown age.

We built our models of condition indices upon the structure of the baseline model and evaluated the evidence for them as previously described. We used R packages lme4 (Bates et al. 2013) and AICcmodavg (Mazerolle 2013).

RESULTS

Principal components analysis

We extracted two and three principal components (PCs) from the 4 and 2-year datasets, respectively. In all cases, the first PC was primarily explained by a positive correlation between

packed cell volume and hemoglobin concentration (Table 4.2). The highest loading for the second PC in the 4-year dataset for both survival and reproductive success was muscle score. The second and third PCs varied between analyses of the 2-year dataset, but were consistent in involving those indices that most closely reflect energy reserves, namely fat, muscle and scaled mass (Table 4.2). Together, the two PCs of the 4-year datasets explained >63% of the total variance, and the three PCs of the 2-year datasets explained >65% of the total variance.

Survival

Complete QAICc results are provided in Table A4.1. The baseline models for the 4 and 2-year datasets include time dependence for the recapture rate, but not the survival rate (Table 4.1). The model-averaged apparent monthly survival rate was 0.95 (0.94−0.96) from the 4-year dataset, and 0.96 (0.91−0.98) from the 2-year dataset. The model-averaged recapture rate varied monthly from 0.50 (0.32−0.68) to 1 (1−1) and from 0.82 (0.63−0.92) to 1 (1−1) for the 4 and 2-year datasets, respectively.

The baseline model for φ from the 4-year dataset includes Sex (evidence ratio = 1.3) and Age (evidence ratio = 1.3). The model-averaged predictions indicate that females have higher survival than males, and birds in their first breeding season have higher survival than older birds or those of unknown age, but the confidence intervals overlap between the sex and age categories (Table 4.3). The baseline model for φ from the 2-year dataset included Year (evidence ratio < 1) and Sex (evidence ratio = 4.9) with the model-averaged predictions indicating that males have higher survival than females and that survival was higher in the 2009−2010 compared to the

2008−2009 breeding season (Table 4.3). Again, the confidence intervals overlap between the sex and year categories (Table 4.3).

We found high model uncertainty in all of our analyses with the top models only having 10−16% of the weight (Table A4.1). In both analyses, the baseline model was competitive with the top model because it was within two QAICc units of the top model and the condition indices were uninformative variables; that is, they did not improve model fit over the baseline model (Arnold 2010; Table A4.1).

Reproductive success

Complete AICc results are provided in Tables B4.1 and B4.2. In the analysis of whether or not an individual fledged young, birds sampled during the latter stages of the reproductive cycle had a higher probability of fledging young than did birds sampled at earlier breeding stages (4-year dataset: nestling stage> incubation > egg-laying > pre-breeding stage; 2-year dataset: nestling stage > all other stages; Table 4.4). The model of Stage has evidence ratios of 26300.0 and 44.2 against the null model for the 4 and 2-year datasets, respectively. The baseline model for the number of young fledged did not include any covariates (null model) for the 4-year dataset and included Year, Age and a Year by Age interaction term in the 2-year data set (evidence ratio for Year = 5.6, Age <1, Year × Age = 2.9; Table 4.5). Birds in their first breeding season fledged fewer young than older birds, but only during the 2008−2009 breeding season (Table 4.5). The baseline model for the number of young produced that survived to independence included Year for the 4-year dataset (evidence ratio = 42485.4) and Year, Age and a Year by

Age interaction term in the 2-year dataset (evidence ratio for Year = 123.7, Age < 1, Year × Age = 60.7; Table 4.6). The number of young fledged that survived to independence for the population was average during the 2007−2008 and 2009−2010 breeding seasons, comparatively low during the 2006−2007 season and highest during the 2008−2009 season. Birds in their first breeding season produced fewer young that survived to independence, but only during the 2008−2009 breeding season (Table 4.6).

In our analysis of whether condition indices predict if an individual will fledge young in the 2-year dataset, there is substantial model-uncertainty with the top model having only 11% of the weight. The baseline model is within two delta AICc units of the top model. However there is less model uncertainty in the larger 4-year dataset with the top model having 66% of the weight. This model includes a quadratic effect of PC2 and its evidence ratio is 13.2 against the baseline model, and 33.0 against the linear model of PC2. The effect of PC2 on the probability of fledging young is approximately parabolic around the mean, such that having an average PC2 score minimizes the probability of fledging young compared to above or below average PC2 scores that maximize the probability of successfully fledging at least one young (Figure 4.1).

In the analysis of whether condition indices predict the number of young fledged by successful breeders, there is substantial model-uncertainty and the baseline models are among the top models in both the 4 and 2-year datasets with 17% and 9% of the weight, respectively.

In the analysis of whether condition indices predict the number of young produced that survive to independence, the top two models in both the 4 and 2-year datasets are a model with a quadratic term for scaled mass and a model with a linear effect of scaled mass. Combined, these two models have 41% and 70% of the weight in the 4 and 2-year datasets, respectively. The

evidence ratios for the top model (scaled mass + scaled mass^2) are 7.0 and 22.0 against the baseline model, and of 2.2 and 1.7 against the linear model of scaled mass for the 4 and 2-year datasets, respectively. In the 4-year dataset, the third best model (PC2 + PC2^2) is within two AICc units of the top model and has an evidence ratio of 2.8 against the baseline model, and 2.2 against the linear model of PC2.

Scaled mass has a positive effect on the number of young that survive to independence from low to above average mass, but this effect then plateaus at the highest values of scaled mass (Figure 4.2). The effect of scaled mass on reproductive success from the 4-year analysis (Figure 4.2a) is qualitatively similar to that from the 2-year analysis (Figure 4.2b), but is weaker, is more muted, exhibits less variation and is not evident in all years. From the 2-year analysis, birds with optimal scaled mass are predicted to have an approximately three-fold increase in reproductive success over birds with low scaled mass: during an average year for reproductive success (2009−2010), an individual in at least their second-breeding season and at an optimal scaled mass is predicted to produce 1.5 ± 0.7 young that survive to independence compared to 0.5 ± 0.4 young for an individual with a low scaled mass (Figure 4.2b). During the year with high population-wide reproductive success (2008−2009), individuals of optimal scaled mass are predicted to produce 3.4 ± 1.2 young compared to 1.2 ± 1.1 young for individuals with low scaled mass (Figure 4.2b).

DISCUSSION

We tested the common interpretation of condition indices as proxies for fitness by asking if condition indices predict reproductive success and survival. We found partial support for this

hypothesis because although two condition indices predicted annual reproductive success, most condition indices failed to do so and none predicted survival. We conclude that condition indices are sometimes, but not always predictors of fitness components, and that a more nuanced interpretation of condition is needed.

Effects of Sex, Age, Stage and Year on survival and reproductive success

Although Sex, Year and Age are included in some of the baseline models affecting apparent survival, only the effect of Sex in the 2-year analysis is well supported (Table 4.3), indicating that males had higher survival than females during some years (2008−2009 and 2009−2010 breeding seasons). In contrast to these findings, we had previously found that the effect of Sex on survival was poorly supported in our study population during 2004−2007 (Milenkaya et al. 2011). These previous findings and our current evidence that males and females differ in apparent survival only in the 2-year and not in the 4-year dataset suggests that apparent survival may vary between the sexes only during some years. We did not find strong evidence for annual variation in survival during 2006−2010 in this study, but did document annual variation during 2004−2007 in a previous study (Milenkaya et al. 2011). In considering both studies, there are both annual and sex differences in crimson finch apparent survival but they are not strong because they were not evident in all years. Our findings from the two shorter studies, if considered independent of each other, would have led to different conclusions: that there is annual variation but no sex differences in apparent survival based on Milenkaya et al. (2011), and the opposite based on the current study, demonstrating the need for long-term datasets to reveal true patterns in survival.

The baseline models for reproductive success included the effects of Stage, Year, Age, and a Stage by Age interaction (Tables 4.4, 4.5, 4.6). The Stage effect applied to the probability of fledging young and simply accounted for the fact that the farther along its nest was when a bird was sampled, the more likely it was to succeed in fledging young. The only variable that was strongly supported in analyses of the number of young fledged and the number of young produced that survive to independence was Year, indicating annual variation in reproductive success. Age was poorly supported overall, indicating no strong effects of age on reproductive success in our data set. However, we were not able to fully evaluate age effects as our sample of known-aged birds was limited.

Condition indices and reproductive success

The strongest support for a condition index influencing fitness is that the probability of an adult successfully fledging young varies by PC2. Because nearly half of all breeding crimson finches fail to fledge any young in a given breeding season (Milenkaya et al. 2011), the probability of fledging young is an important component of fitness. PC2 is positively weighted by all of the condition indices from the 4-year dataset (packed cell volume, hemoglobin, scaled mass, muscle and fat scores) such that one end of the axis represents individuals with high energy reserves and high oxygen-carrying capacity, while the other end of the spectrum represents low energy reserves and low oxygen-carrying capacity (generally interpreted as good and poor condition, respectively). Although the axis is a combination of all of the indices, it is influenced most by muscle score (loading 0.61) and to a lesser extent by fat score (loading 0.48, Table 4.2). However, adding muscle or fat score alone did not improve model fit over the

baseline model (Table B4.1), indicating that the multivariate approach manifested in the principal components analysis provides meaningful information beyond that resulting from examining condition indices individually. For example, having a lot of muscle does not incur fitness benefits, but having a lot of muscle in conjunction with high values for the other indices does. Concurrently maintaining various physiological systems appears to be important for fitness and therefore assessing condition across these systems in a multivariate framework is a useful approach.

Birds with both high and low PC2 values have higher fledging probability over birds with average PC2 values and this effect is strongest in the pre-breeding stage, becoming progressively weaker the closer the individual is to fledging young (Figure 4.1). Therefore, condition immediately before the onset of breeding is an important predictor of the probability that an individual will successfully fledge young up to five months later.

Our finding that the average value of PC2 is least adaptive and that the extremes are most optimal was unexpected and the reason for this pattern is not immediately obvious. To explore possible explanations for this pattern, we conducted post-hoc tests comparing individuals in the upper and lower quartiles of PC2 scores. We asked if these individuals differed in age, reproductive effort during the current breeding season (number of nesting attempts, clutches laid, and broods hatched), reproductive effort and success the previous breeding season, and survival to the following breeding season (through band re-sighting). We found no difference in these variables between the low and high PC2 groups leaving unexplained the pattern that those with low energy reserves and oxygen-carrying capacity are equally successful at fledging young as those with high energy reserves and oxygen-carrying capacity. However, this pattern suggests

that there may be two separate physiological strategies for maximizing the probability of fledging young. Others have also concluded that intraspecific variation in measures of individual quality may be due to a diversity of life-history tactics, which complicates the interpretation of these measures (Moyes et al. 2009; Lailvaux and Kasumovic 2011). Individuals with high energy reserves but low oxygen-carrying capacity, or vice versa, occupy the mid-range of the PC2 axis and were least likely to fledge young, perhaps indicating a maladaptive mismatch across physiological systems.

Scaled mass immediately prior to and during the breeding season positively predicts the number of independent young that a bird produces. Individuals that are heavier for their body size are more successful breeders than those with average or below average mass for their body size. That an individual may increase their annual reproductive success three-fold by optimizing their mass is striking. This pattern suggests that individuals that are able to maintain energy reserves are most likely to be able to carry reproduction to completion. Thus, even though individuals with low energy reserves (i.e., low PC2 scores) may fledge young as well as heavier birds, they are less likely to have them survive to independence indicating that that this is a less effective strategy for maximizing fitness than that represented by high PC2 scores.

Others have also found that energy reserves are positively related to fecundity. For example, female lesser snow geese (*Chen caerulescens*) rely almost entirely on their body reserves during breeding and individuals deplete their reserves to a minimum threshold below which they either die or abandon their clutch (Ankney and MacInnes 1978). The consequence of this behavior is that heavier birds have more resources to allocate toward their clutch and therefore lay more eggs (Ankney and MacInnes 1978). Among common eiders (*Somateria*

mollissima), heavier females are more likely to hatch at least one young and to tend their young rather than abandoning them to be cared by others (Hanssen et al. 2003a) which increases their survival (Bustnes and Erikstad 1991). Although clear examples of pre-breeding body mass positively affecting key components of reproductive success, these are extreme examples that are not universal even among precocial birds (reviewed by Winkler and Walters 1983). Here we provide an example of this from a small passerine whose breeding biology clearly differs from that of snow geese, common eiders and other capital breeders. Passerines are generally income breeders (Meijer and Drent 1999) and our findings that heavier individuals have higher reproductive success supports the broad premise of condition indices as proxies for fitness: that individuals with more energy reserves allocate these additional resources toward improving their fitness and that mass adjusted for size accurately reflects this fitness potential.

However, others have documented that additional energy reserves may not always improve reproductive success. For example, mass adjusted for size failed to explain hatching failure among Florida scrub-jays (*Aphelocoma coerulescens*) where environmental conditions and parental experience were more important factors (Wilcoxen et al. 2011). In green-rumped parrotlets (*Forpus passerinus*), mass adjusted for size failed to explain the variation in the number of eggs laid and the number of young fledged (Sheridan et al. 2004), and among great tits (*Parus major*), the probability of double-brooding (Kilgas et al. 2006a). Although no explanation was provided as to why energy reserves in parrotlets and great tits failed to explain reproductive parameters, presumably these traits were limited by something other than energy reserves, as was found with the Florida scrub-jays (Wilcoxen et al. 2011). Thus, while macronutrients are limiting reproductive success in some species such as capital breeders and crimson finches, reproduction in others may be constrained by other factors such that energy

reserves are less influential. This highlights a major concern in using condition indices as indicators of fitness: something other than condition may be the more important factor affecting fitness, and where condition is important, one cannot assume that a given index is measuring that aspect of condition that is most relevant to fitness. It is therefore challenging to predict under which circumstances condition indices will be meaningful.

Unlike the traditional condition indices that reflect energy reserves, hematological indices did not predict reproductive success among crimson finches. Others have also found that hematological condition indices do not predict fecundity parameters such as the probability of double-brooding (packed cell volume, protein concentrations, H/L ratio; Kilgas et al. 2006a), the number of eggs laid or young fledged (packed cell volume, hemoglobin, protein concentrations, white-blood cell counts; Sheridan et al. 2004), and laying date or clutch size (lymphocytes, heterophils, H/L ratio; Hanssen et al. 2003b). Furthermore, Dawson and Bortolotti (1997) questioned the use of packed cell volume as a condition index. However, our result that hematological indices are uninformative of reproductive success is not universal: re-nesting greater sage-grouse (*Centrocercus urophasianus*) had higher total plasma protein values than those that did not re-nest (Gregg et al. 2006), the proportion of glycosylated hemoglobin and plasma protein of collared flycatchers (*Ficedula albicollis*) was positively correlated with both clutch size and the number of young fledged (Gustafsson et al. 1994), and mean corpuscular volume (but not packed cell volume) among great skua (*Catharacta skua*) predicted the number of young fledged (Bearhop et al. 1999). Therefore both the traditional and hematological indices may sometimes, but not always, be meaningful indicators of reproductive success. Our concern is that there is no clear way to predict which condition indices may be informative, and for which species and under which circumstances.

Condition indices and survival

Condition indices had no relationship to the survival of crimson finches either within a breeding season or across years. Others have found that condition indices only predict survival during particularly challenging times. For example, mass adjusted for structural body size predicted the survival of Florida scrub-jays through a disease epidemic (Wilcoxen et al. 2010) but not otherwise (T. Wilcoxen unpublished data) and fat scores predicted the survival of wintering great tits when they were food limited but not otherwise, and only among subordinate but not dominant classes (Gosler 1996). Furthermore, stress physiology predicted the survival of marine iguanas during a starvation event (Romero and Wikelski 2001; Romero and Wikelski 2010), and although corticosterone is not strictly a condition index it is relevant here because it is involved in the metabolism of energy reserves. During our study, we did not observe such dramatic selective events suggesting that perhaps the environment was simply not challenging enough for condition to be meaningful for survival. However, our study area has a variable environment with wet season (December – March) rainfall varying from 339 mm in the last year of our study to 870 mm the previous year (Australian Wildlife Conservancy unpublished data). Thus crimson finches face environmental stochasticity and we found that annual variation in reproductive success exists, suggesting that environmental conditions are not always ideal and that some years may indeed be challenging. Yet condition indices failed to predict survival even during these years. It remains to be seen, however, if condition indices would predict survival through a rare, particularly strong selective event, if these occur.

One reason that condition indices failed to predict survival in our study may be that the indices we measured are not relevant to the survival of our study species. For example, hemoglobin concentration predicted the survival of sea otters while fat reserves did not, and Ben-David et al. (2002) suggested that the natural history and physiology of their study species explains this difference: fat is quickly utilized by otters due to their high metabolic rate, and as diving foragers, it is oxygen-carrying capacity that determines their ability to acquire food. Therefore, it is hemoglobin concentration and not fat that is the more meaningful condition index for this species (Ben-David et al. 2002). It is not uncommon that some condition indices predict survival while others in the same study do not (Svensson et al. 2001; Ben-David et al. 2002; Kilgas et al. 2006b; Wilcoxen et al. 2010). Therefore, condition indices are not broadly applicable and may need to be selected for use in research based on their relevance to the study organism. It is possible that none of the seven indices that we measured reflect the relevant physiological state that affects survival among crimson finches. For example, fat reserves can generally be interpreted as being beneficial for survival among migrating birds and species that face unpredictable thermal challenges (such as those in the arctic or at high latitudes). However, it is less clear how to interpret fat scores among a tropical and sedentary passerine, such as crimson finches, for which the costs and benefits of fat reserves and their associated trade-offs are poorly understood. Identifying the condition indices that are relevant to survival requires a deep knowledge of the species life history, its primary stressors and sources of mortality. This is why predicting which condition indices are most relevant may be easiest for species that have more extreme physiological demands. These might include species that are thermally challenged or food-limited (energy reserves), aerial insectivores (PCV, hemoglobin), and migrating birds

(energy reserves). Identifying the relevant condition indices for species without such extreme demands is more challenging.

Alternatively, condition indices in our study may have failed to indicate survival, not because they are irrelevant to crimson finches, but because they were sampled at the wrong time of year. To predict survival condition indices likely need to be sampled prior to, or during, the challenge that contributes most to mortality. We do not know the primary sources of mortality in our study population. However, crimson finches occupy a highly seasonal, tropical environment with distinct dry and wet seasons, and we suspect that the most food-limiting time of their year is likely during the end of the dry season when grass seeds are most depleted (Lewis 2007). If we had measured condition at this time of the year, then condition indices may have predicted survival (but perhaps not subsequent reproductive success) with the most relevant indices likely to be those that reflect energy reserves and perhaps stress indices. Condition indices that reflect oxygen carrying capacity, however, may be more meaningful among those that fly longer distances to locate food, such as zebra finches (*Taeniopygia guttata*). We measured condition during breeding which corresponds to the wet season when crimson finches are less food-stressed. Perhaps this timing explains why some condition indices predicted reproductive success, but none predicted survival. We encourage researchers to consider the relevance of both the condition indices and the timing of sampling in employing these indices as predictors of fitness.

Conclusions

Although traditional condition indices predicted reproductive success among crimson finches, most of the indices that we measured failed to do so and none predicted survival. These results only partially support the interpretation of condition indices as proxies for fitness because they are only sometimes, but not always potentially meaningful. This conclusion is supported by the literature in that condition indices are inconsistent in their relation to fitness, and we therefore question the ubiquitous interpretation of condition indices as proxies for fitness. How then, should condition indices be interpreted?

First, that the two indices for which we found support are scaled mass and PC2, which is primarily explained by muscle and fat scores, supports the use of traditional condition indices that reflect energy reserves over hematological parameters that reflect other aspects of condition. While hematological indices are attractive for their specificity and because they integrate various physiological systems, the traditional indices of mass, muscle and fat scores more directly measure available resources that can be allocated toward improving fitness. They are also easier and less costly to sample, are less intrusive and risky to the individual being sampled, and may be easier to interpret than hematological indices. However, the best supported condition index was PC2, which is an axis of variation among both traditional and hematological parameters, suggesting that the two types of indices are more informative when integrated via a multivariate approach than when assessed individually.

Second, where we found that condition indices predict a component of fitness, its quadratic effect was always better supported than a linear effect of that index. We therefore echo the suggestion of others that more is not necessarily better and that the relationship between a

condition index and fitness is not necessarily linear (as in sexual selection theory; reviewed by Cotton et al. 2004; Hill 2011; Lailvaux and Kasumovic 2011).

The wide discrepancy in whether condition indices predict fitness, and if so, which indices in particular are meaningful, suggests that not all indices are relevant to all species or contexts (Cotton et al. 2004). Researchers should consider which physiological aspects of condition would be most informative in their study system and select condition indices based on this justification. They should then validate their choice of indices. This complicates the use of condition indices because one of their great benefits is that they are easier to sample in many species than is fitness and for this reason are used as its surrogate. However, the evidence thus far suggests that careful validation of condition indices is needed before they can be interpreted as indicators of individual quality or fitness. Furthermore, as we saw with scaled mass in our study, if a condition index is found to predict a component of fitness, it may only do so during some years and not others, demonstrating that the condition-fitness relationship is not broadly applicable across all contexts. This point was articulated by Lailvaux and Kasumovic (2011) who argued that measuring individual quality is context-dependent because a given resource allocation strategy may be adaptive under some contexts but maladaptive under others, and there may be more than one strategy that maximizes fitness over a lifetime. This suggests (a) that condition indices are not always meaningful indicators of fitness because this relationship is context-dependent, and (b) that understanding lifetime resource allocation decisions, their associated trade-offs and relationships to fitness will offer more insights and may indeed contradict what one finds from snapshots of resource allocation (e.g., condition indices).

We conclude by suggesting that the interpretation of condition indices as proxies for individual quality and fitness must be revamped and refined. We previously found that condition indices are only repeatable within individuals across short, but not long time periods (Milenkaya et al. 2013a) suggesting that condition indices do not indicate inherent individual quality. And in this study, we found that condition indices are not reliable proxies for fitness. Together, these two studies demonstrate that condition indices should be interpreted more narrowly. Rather than being interpreted as indicators of individual quality or of having long-term consequences for fitness, condition indices instead should be considered as possible indicators of current and short-term success. Condition indices at a single point in time indicate how well an individual is currently acquiring and assimilating resources and, because we previously found condition indices to be repeatable over several months, how well they will likely be faring several months into the future (Milenkaya et al. 2013a). High values among traditional condition indices indicate that the individual has relatively more resources. However, those additional resources may not necessarily result in fitness benefits and we need to better understand how this relationship differs across contexts. The other indices, such as hematological parameters, provide information about specific systems such as the oxygen carrying capacity of blood or the immunoglobulin profiles important for immune function. Although these condition indices are insights into one's current physiological state, they are not proxies for individual quality or fitness. A single snapshot of condition may not be as meaningful as the more complex and long-term physiological processes that influence fitness. For example, individual quality may be better understood through the resource allocation decisions made over a lifetime (Lailvaux and Kasumovic 2011), the individual's mechanism for regulating their condition (Williams 2008;

Williams 2012) or the individual's capacity to maintain optimal functionality of essential cellular processes (Hill 2011).

ACKNOWLEDGMENTS

We are especially grateful to our field assistants Roy Churchwell, Evan Rehm and Jennifer Bruce for helping to collect these data. Thanks to Michelle Hall, Kim Maute and Butch Maher for their invaluable support during the field seasons and to Victoria Garcia for statistical assistance. We thank Dana Hawley, Ignacio T. Moore and William Hopkins for helpful discussions on condition. O.M. particularly thanks J. Lindley McKay for his moral support. This study was funded by the Australian Wildlife Conservancy and was based out of the WildlifeLink Centre for Research and Conservation at Mornington Wildlife Sanctuary.

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Tables

Table 4.1: Summary of survival analyses of the 4 and 2-year datasets. Included here are the sample size of individuals (*n*), time period covered by the dataset, number of monthly re-sighting occasions analyzed, number of models in the candidate model set, estimated variance-inflation factor ($\hat{c} \pm SE$), baseline model, and the condition indices included in the analysis (● = included, N/A = not applicable; H/L ratio = heterophil to lymphocyte ratio, TPP = total plasma protein, PCs = principal components).

	4-year analysis	2-year analysis
n	232	109
Time period	Nov 2006 − Apr 2010	Feb 2009 − Apr 2010
Number of re-sighting occasions	21	8
Number of candidate models	52	64
$\hat{c} \pm SE$	1.21 ± 0.004	1.1 ± 0.006
Baseline model	φ(Sex+Age) ρ(*t*+Year+Sex+Stage)	φ(Year+Sex) ρ(*t*+Sex)
Packed cell volume	●	●
Hemoglobin	●	●
Scaled mass index	●	●
Muscle score	●	●
Fat score	●	●
TPP	N/A	●

H/L ratio	N/A	●
PC1	●	●
PC2	●	●
PC3	N/A	●

Table 4.2: Results of the principal components analysis (PCA) for the reproductive success and survival analyses of both the 4 and 2-year datasets. Included are the eigenvalue, percent of variation in the data explained by the component (percent), cumulative percent of variation explained by the components (cumulative percent), and loadings on each component by the condition indices with the highest loadings in bold (H/L ratio = heterophil to lymphocyte ratio; TPP = total plasma protein).

	4-year survival		4-year reproductive success		2-year survival			2-year reproductive success		
	PC1	PC2	PC1	PC2	PC1	PC2	PC3	PC1	PC2	PC3
Eigenvalue	1.85	1.30	1.91	1.28	2.14	1.40	1.09	2.26	1.21	1.12
Percent	37.05	26.43	38.10	25.57	30.60	20.00	15.56	32.24	17.23	16.05
Cumulative percent	37.05	63.48	38.10	63.68	30.60	50.60	66.17	32.24	49.47	65.52
Packed cell volume	**-0.60**	0.37	**-0.60**	0.38	**0.57**	-0.13	0.30	**0.55**	-0.16	0.35
Hemoglobin	**-0.61**	0.31	**-0.60**	0.32	**0.55**	-0.21	0.36	**0.53**	-0.21	0.41
Scaled mass	0.37	0.46	0.36	0.39	-0.36	-0.50	0.06	-0.35	**-0.53**	0.08

Muscle score	0.16	**0.60**	0.19	**0.61**	0.09	**-0.63**	-0.10	0.19	-0.47	-0.25
Fat score	0.33	0.44	0.34	0.48	-0.26	-0.16	**0.66**	-0.28	-0.05	**0.67**
H/L ratio	N/A	N/A	N/A	N/A	-0.08	0.49	0.49	0.01	**0.62**	0.28
TPP	N/A	N/A	N/A	N/A	-0.40	-0.15	0.31	-0.42	-0.20	0.34

Table 4.3: Model-averaged predictions of the monthly apparent survival rate (φ) of adult crimson finches from the covariates in the baseline models. Included here are the estimates' standard error (SE) and 95% confidence interval (95% CI). M = male, F = female. The 4-year dataset estimates are based on birds during the 2006−2007 breeding season in the pre-breeding stage. The 2-year dataset estimates are based on after-1st breeding season aged birds during the nestling stage.

Dataset	Baseline model	Age or Year category	Sex	φ	SE	95% CI
4-year	φ(Sex+Age) ρ(*t*+Year+Sex+Stage)	1st breeding season	M	0.98	0.02	0.85 − 1
			F	0.98	0.02	0.86 − 1
		After-1st breeding season	M	0.93	0.02	0.89 − 0.96
			F	0.95	0.01	0.91 − 0.97
		Unknown age	M	0.94	0.01	0.91 − 0.96
			F	0.95	0.01	0.93 − 0.97
2-year	φ(Year+Sex) ρ(*t*+Sex)	2008−2009	M	0.97	0.01	0.93 − 0.99
			F	0.93	0.02	0.88 − 0.96
		2009−2010	M	0.98	0.02	0.91 − 1
			F	0.95	0.03	0.85 − 0.99

Table 4.4: Model-averaged predictions of the probability that an individual crimson finch will fledge young from the covariates in the baseline model. We include the prediction and its unconditional standard error (SE). In the interest of brevity and clarity, we do not present predictions for all Age × Sex × Stage × Year categories, but only for those for which we have the largest sample sizes. We present the category upon which the prediction was based and its corresponding sample size (*n*). M = male, F = female.

Dataset	Baseline variable	Level of variable	Prediction	SE	Prediction based on	*n*
4-year	Stage	Pre-breeding	0.44	0.06	F, 2008−2009	13
		Egg-laying	0.51	0.07	F, 2008−2009	13
		Incubating	0.64	0.07	F, 2008−2009	8
		Nestling	0.81	0.06	F, 2008−2009	9
2-year	Stage	Pre-breeding	0.63	0.12	M, 2009−2010, after-1st breeding season	8
		Egg-laying	0.57	0.10	F, 2008−2009, after-1st breeding season	9
		Incubating	0.54	0.10	M, 2009−2010, after-1st breeding season	8
		Nestling	0.84	0.07	M, 2009−2010, after-1st breeding season	8

Table 4.5: Model-averaged predictions of the number of young fledged among crimson finches from the covariates in the baseline model. We include the prediction and its unconditional standard error (SE). In the interest of brevity and clarity, we do not present predictions for all Age × Sex × Stage × Year categories, but only for those for which we have the largest sample sizes. We present the category upon which the prediction was based and its corresponding sample size (*n*). M = male, F = female.

Dataset	Baseline variable	Level of variable	Prediction	SE	Prediction based on	*n*
4-year	Null	N/A	N/A	N/A	N/A	N/A
2-year	Year + Age + (Year × Age)	2008−2009, 1st-breeding season	3.84	0.55	F, nestling stage	6
		2008−2009, after 1st-breeding season	4.67	0.50	M, incubating stage	5
		2009−2010, 1st breeding season	3.47	0.58	F, nestling stage	4
		2009−2010, after 1st-breeding season	3.43	0.34	M, nestling stage	6

Table 4.6: Model-averaged predictions of the number of young produced annually that survive to independence among crimson finches from the covariates in the baseline model. We include the prediction and its unconditional standard error (SE). In the interest of brevity and clarity, we do not present predictions for all Age × Sex × Stage × Year categories, but only for those for which we have the largest sample sizes. We present the category upon which the prediction was based and its corresponding sample size (*n*). M = male, F = female.

Dataset	Baseline variable	Level of variable	Prediction	SE	Prediction based on	*n*
4-year	Year	2006−2007	0.31	0.11	M, pre-breeding stage	10
		2007−2008	1.06	0.23	F, nestling stage	10
		2008−2009	1.38	0.21	M, nestling stage	8
		2009−2010	1.00	0.19	M, nestling stage	8
2-year	Year + Age + (Year × Age)	2008−2009, 1st-breeding season	1.36	0.35	F, nestling stage	6
		2008−2009, after 1st-breeding season	3.26	0.85	F, egg-laying stage	5
		2009−2010, 1st breeding season	1.03	0.37	F, nestling stage	4
		2009−2010, after 1st-breeding season	1.01	0.20	M, nestling stage	6

Figure legends

Figure 4.1: The effect of PC2 on the probability of a crimson finch fledging at least one young by the breeding stage during which the individual was sampled for condition indices (pre-breeding, egg-laying, incubating, and nestling stages). PC2 is an axis of variation in individual condition indices with those having high energy reserves and high oxygen carrying capacity on the positive end of the axis, and those having low energy reserves and low oxygen carrying capacity on the negative end of the axis.

Figure 4.2: Model-averaged predictions by scaled mass of the number of young fledged over a breeding season that survived to independence. Scaled mass was centered to have a mean of zero such that the scale of the x-axis is the difference in grams from the mean. Predictions are presented for the 4-year analysis (A) which corresponds to the 2006−2007, 2007−2008, 2008−2009 and 2009−2010 breeding seasons, and for the 2-year analysis (B) which corresponds to the 2008−2009 and 2009−2010 breeding seasons. Birds of any age are shown with unfilled circles; after-first year breeders in black; and birds in their first breeding season in grey. Note that the scale of the y-axis differs between the 4-year (A) and 2-year (B) panels.

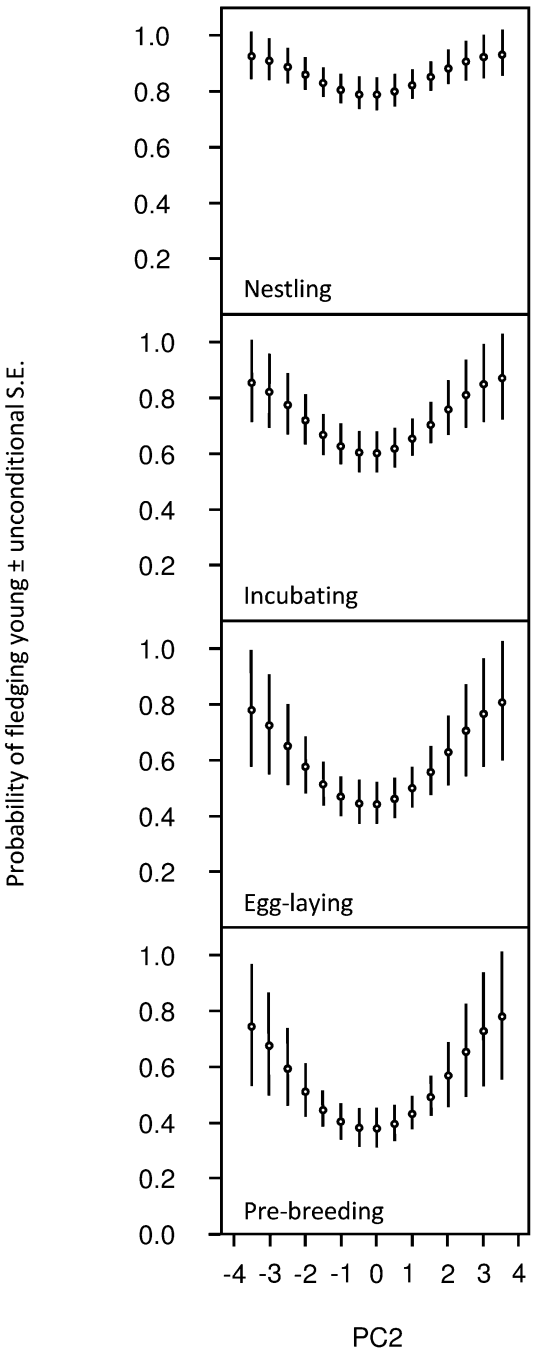

Figure 4.1: The effect of PC2 on the probability of a crimson finch fledging at least one young

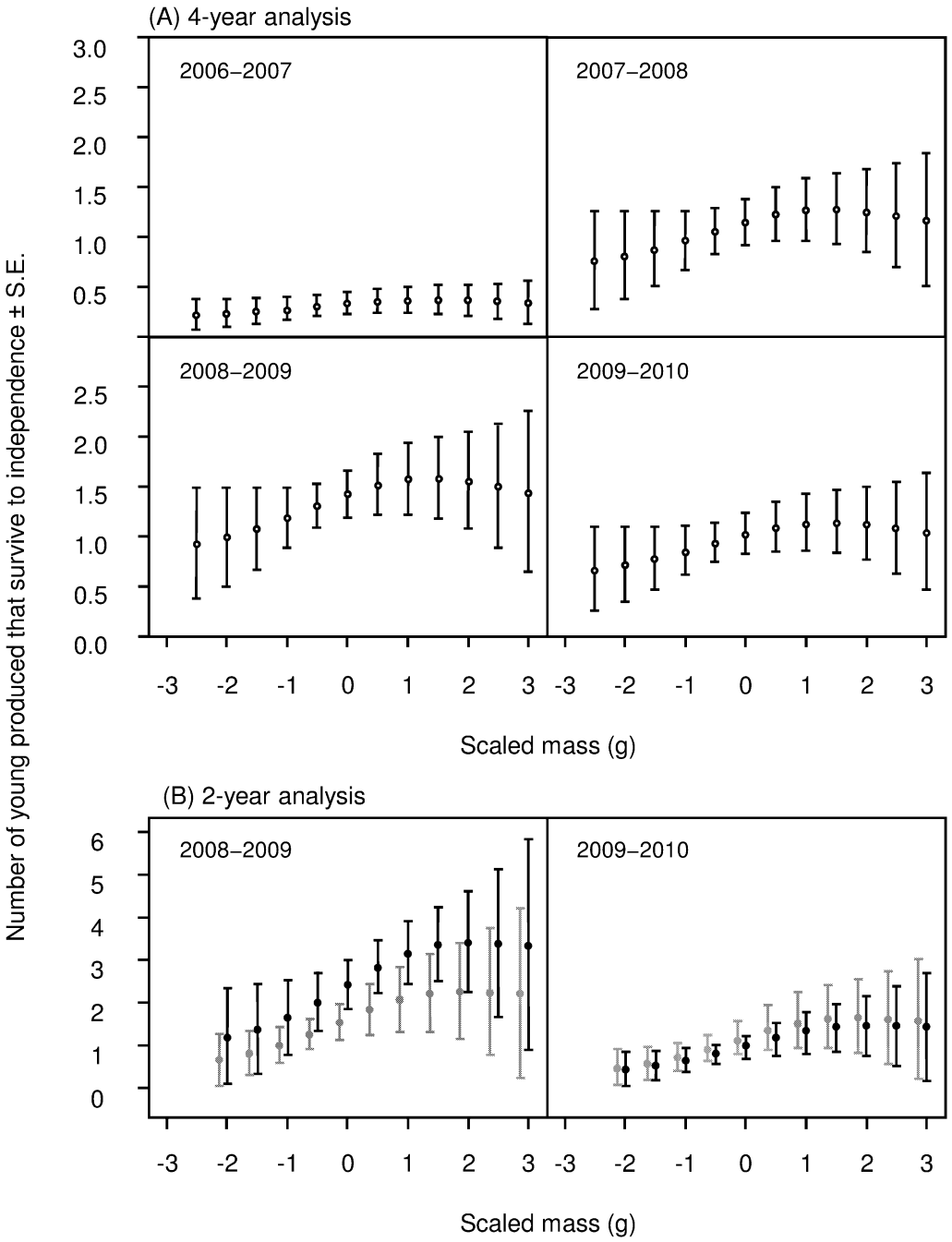

Figure 4.2: Model-averaged predictions by scaled mass of the number of young fledged over a breeding season that survived to independence

Appendix A: Tables of ranked models that describe intraspecific variation in survival.

Table A4.1: QAICc table of results for the survival analyses of the 4 and 2-year datasets among crimson finches. Included are all of the models from the candidate model set where φ = apparent monthly adult survival, ρ = recapture probability, *t* = time dependence, PCV = packed cell volume, Hb = hemoglobin concentration, SMI = scaled mass index, Muscle = muscle score, Fat = fat score, HL = heterophil to lymphocyte ratio, TPP = total plasma protein, Time = time of day, and PCs = principal components. See Methods for an explanation of the covariates including Sex, Stage, Age, Time of Day, and Year. The baseline model is in bold. Also included are the number of parameters in the model (k), the quasi-Akiake's Information Criterion corrected for small sample size (QAICc), the difference in QAICc of a model from that of the top model (ΔQAICc), the model weight (W), and its deviance (Qdev).

Dataset	Model	k	QAICc	ΔQAICc	W	Qdev
4-year	φ(.) ρ(*t*+Year+Sex)	25	1446.30	0.00	0.10	1395.30
	φ(Sex+Age) ρ(*t*+Year+Sex+Stage)	33	1446.52	0.22	0.09	1378.78
	φ(Age) ρ(*t*+Year+Sex+Stage)	32	1446.69	0.38	0.08	1381.05
	φ(Sex+Age+PCV) ρ(*t*+Year+Sex+Stage)	34	1446.75	0.44	0.08	1376.90

φ(Sex) ρ(*t*+Year+Sex+Stage)	31	1446.78	0.48	0.08	1383.24
φ(.) ρ(*t*+Year+Sex+Stage)	30	1447.26	0.95	0.06	1385.81
φ(Sex+Age+PCV+PCV^2) ρ(*t*+Year+Sex+Stage)	35	1447.53	1.23	0.05	1375.57
φ(Sex+Age+Hb+Hb^2) ρ(*t*+Year+Sex+Stage)	35	1448.18	1.88	0.04	1376.22
φ(Sex+Age+PC2) ρ(*t*+Year+Sex+Stage)	34	1448.29	1.99	0.04	1378.44
φ(Sex+Age+Hb) ρ(*t*+Year+Sex+Stage)	34	1448.41	2.11	0.03	1378.56
φ(Sex+Age+Fat) ρ(*t*+Year+Sex+Stage)	34	1448.51	2.20	0.03	1378.66
φ(Sex+Age+SMI) ρ(*t*+Year+Sex+Stage)	34	1448.55	2.24	0.03	1378.70
φ(Sex+Age+PC1) ρ(*t*+Year+Sex+Stage)	34	1448.58	2.28	0.03	1378.73
φ(Sex+Age+Muscle) ρ(*t*+Year+Sex+Stage)	34	1448.58	2.28	0.03	1378.73
φ(Sex+Age+Muscle+Year) ρ(*t*+Year+Sex+Stage)	37	1448.85	2.55	0.03	1372.66
φ(Sex+Age+PC1+PC1^2) ρ(*t*+Year+Sex+Stage)	35	1449.10	2.80	0.02	1377.14
φ(Sex+Age+PC2+Year) ρ(*t*+Year+Sex+Stage)	37	1449.15	2.85	0.02	1372.96
φ(Sex+Age+Muscle+Muscle^2) ρ(*t*+Year+Sex+Stage)	35	1449.18	2.87	0.02	1377.22
φ(.) ρ(*t*+Year+Sex+Age)	27	1449.37	3.07	0.02	1394.20
φ(.) ρ(*t*+Year+Sex+Stage+Age)	32	1449.70	3.40	0.02	1384.06
φ(Sex+Age+PC2+PC2^2) ρ(*t*+Year+Sex+Stage)	35	1449.97	3.67	0.02	1378.01

φ(Sex+Age+Fat+Fat^2) ρ(*t*+Year+Sex+Stage)	35	1450.39	4.08	0.01	1378.43
φ(Sex+Age+PC2+PC2^2+Year) ρ(*t*+Year+Sex+Stage)	38	1450.41	4.11	0.01	1372.10
φ(Sex+Age+SMI+SMI^2) ρ(*t*+Year+Sex+Stage)	35	1450.57	4.27	0.01	1378.61
φ(Sex+Age+Muscle+Muscle^2+Year) ρ(*t*+Year+Sex+Stage)	38	1450.68	4.38	0.01	1372.37
φ(.) ρ(t+Year+Sex+Age+(Sex × Age))	29	1451.68	5.37	0.01	1392.33
φ(.) ρ(t+Year+Sex+Age+(Sex × Age)+Stage)	34	1451.87	5.57	0.01	1382.03
φ(Sex+Age+Fat+Stage+Year) ρ(*t*+Year+Sex+Stage)	42	1452.97	6.67	0.00	1366.15
φ(Sex+Age+Fat+Fat^2+Stage+Year) ρ(*t*+Year+Sex+Stage)	43	1454.04	7.73	0.00	1365.07
φ(Sex+Age+PCV+Stage+(Sex × Stage)) ρ(t+Year+Sex+Stage)	44	1459.11	12.80	0.00	1368.00
φ(Sex+Age+PCV+PCV^2+Stage+(Sex × Stage)) ρ(t+Year+Sex+Stage)	45	1461.14	14.84	0.00	1367.90
φ(Sex+Age+SMI+Stage+(Sex × Stage)+Time) ρ(t+Year+Sex+Stage)	45	1461.35	15.05	0.00	1368.11
φ(Sex+Age+Hb+Stage+(Sex × Stage)+Year) ρ(t+Year+Sex+Stage)	47	1461.51	15.21	0.00	1363.97
φ(Sex+Age+PC1+Stage+(Sex × Stage)+Year) ρ(t+Year+Sex+Stage)	47	1461.53	15.23	0.00	1363.99
φ(Sex+Age+SMI+SMI^2+Stage+(Sex × Stage)+Time) ρ(t+Year+Sex+Stage)	46	1463.17	16.87	0.00	1367.78
φ(Sex+Age+Hb+Hb^2+Stage+(Sex × Stage)+Year) ρ(t+Year+Sex+Stage)	48	1463.64	17.34	0.00	1363.94
φ(Sex+Age+PC1+PC1^2+Stage+(Sex × Stage)+Year) ρ(t+Year+Sex+Stage)	48	1463.66	17.36	0.00	1363.97
φ(.) ρ(t+Year+Sex+Stage+Age+(Stage × Age)+Sex)	42	1465.59	19.29	0.00	1378.77

	φ(.) ρ(t+Year+Sex+Stage+Age+(Stage × Age)+Sex+(Sex × Age))	44	1468.62	22.32	0.00	1377.52
	φ(.) ρ(*t*+Year+Stage)	29	1468.67	22.37	0.00	1409.32
	φ(.) ρ(*t*+Year+Stage+Age)	31	1470.70	24.40	0.00	1407.17
	φ(.) ρ(*t*+Year)	24	1476.42	30.12	0.00	1427.50
	φ(.) ρ(*t*+Year+Age)	26	1479.01	32.70	0.00	1425.92
	φ(Year) ρ(*t*+Year)	27	1479.24	32.94	0.00	1424.08
	φ(t) ρ(*t*+Year)	42	1484.46	38.16	0.00	1397.64
	φ(.) ρ(*t*+Year+Sex+Stage+Age+(Stage × Age))	41	1485.85	39.55	0.00	1401.16
	φ(*t*+Year) ρ(*t*+Year)	45	1490.07	43.77	0.00	1396.82
	φ(*t*+Year+(*t* × Year)) ρ(*t*+Year)	102	1575.94	129.63	0.00	1354.70
	φ(*t*+Year+(*t* × Year)) ρ(*t*)	99	1588.99	142.69	0.00	1374.79
	φ(*t*+Year+(*t* × Year)) ρ(Year)	84	1615.02	168.72	0.00	1435.48
	φ(*t*+Year+(*t* × Year)) ρ(.)	81	1649.92	203.62	0.00	1477.21
	φ(*t*+Year+(*t* × Year)) ρ(*t*+Year+(*t* × Year))	159	1655.79	209.49	0.00	1294.01
2-year	φ(Year+Sex+Fat+Fat^2) ρ(*t*+Sex)	13	291.74	0.00	0.16	264.63
	φ(Year+Sex+PC2+$PC2^2$) ρ(*t*+Sex)	13	292.83	1.09	0.09	265.72

φ(Year+Sex) ρ(*t*+Sex)	11	293.18	1.44	0.08	270.38
φ(Year+Sex+Muscle) ρ(*t*+Sex)	12	293.41	1.67	0.07	268.46
φ(Year+Sex+SMI) ρ(*t*+Sex)	12	293.81	2.07	0.06	268.86
φ(Year+Sex+PC3) ρ(*t*+Sex)	12	293.99	2.25	0.05	269.04
φ(Year+Sex+PC2) ρ(*t*+Sex)	12	294.01	2.27	0.05	269.05
φ(Year+Sex+SMI+SMI^2) ρ(*t*+Sex)	13	294.13	2.39	0.05	267.02
φ(Year+Sex+HL) ρ(*t*+Sex)	12	294.41	2.67	0.04	269.46
φ(Year+Sex+Hb) ρ(*t*+Sex)	12	294.59	2.85	0.04	269.64
φ(Year+Sex+Muscle+Muscle^2) ρ(*t*+Sex)	13	294.84	3.10	0.03	267.73
φ(Year+Sex+Fat) ρ(*t*+Sex)	12	295.00	3.26	0.03	270.05
φ(Year+Sex+TPP) ρ(*t*+Sex)	12	295.23	3.49	0.03	270.28
φ(Year+Sex+PC1) ρ(*t*+Sex)	12	295.32	3.58	0.03	270.37
φ(Year+Sex+PCV) ρ(*t*+Sex)	12	295.33	3.59	0.03	270.38
φ(Year+Sex+Age) ρ(*t*+Sex)	13	295.42	3.69	0.03	268.31
φ(Year+Sex+PC3+PC3^2) ρ(*t*+Sex)	13	295.83	4.09	0.02	268.72
φ(Year+Sex+HL+HL^2) ρ(*t*+Sex)	13	296.00	4.26	0.02	268.88
φ(Year) ρ(*t*+Sex)	10	296.34	4.60	0.02	275.67

φ(Year+Sex+Hb+Hb^2) ρ(t+Sex)	13	296.75	5.01	0.01	269.64
φ(Year+Sex+PC1+PC1^2) ρ(t+Sex)	13	296.92	5.18	0.01	269.80
φ(Year+Sex+PCV+PCV^2) ρ(t+Sex)	13	297.31	5.57	0.01	270.19
φ(Year+Sex+TPP+TPP^2) ρ(t+Sex)	13	297.38	5.64	0.01	270.26
φ(Year+Age) ρ(t+Sex)	12	298.05	6.31	0.01	273.10
φ(Year+Sex+PC3+Stage) ρ(t+Sex)	17	298.62	6.89	0.01	262.73
φ(.) ρ(t)	8	298.86	7.12	0.00	282.43
φ(Year+Sex+Fat+Fat^2+Stage) ρ(t+Sex)	18	299.01	7.27	0.00	260.88
φ(Year+Sex+Age+(Sex × Age)) ρ(t+Sex)	15	299.59	7.85	0.00	268.11
φ(Year) ρ(t+Sex+Age)	12	299.65	7.91	0.00	274.70
φ(Year) ρ(t+Sex+Age+(Sex × Age))	14	300.14	8.40	0.00	270.85
φ(Year) ρ(t+Age)	11	300.37	8.64	0.00	277.57
φ(Year) ρ(t)	9	300.44	8.70	0.00	281.90
φ(Year+Sex+PC3+PC3^2+Stage) ρ(t+Sex)	18	300.83	9.09	0.00	262.71
φ(Year+Sex+Fat+Stage) ρ(t+Sex)	17	300.85	9.11	0.00	264.95
φ(t) ρ(t)	13	305.17	13.44	0.00	278.06
φ(t+Year) ρ(t)	14	305.46	13.72	0.00	276.17

φ(Year) ρ(*t*+Sex+Stage)	15	305.77	14.03	0.00	274.29
φ(Year) ρ(*t*+Stage)	14	308.67	16.93	0.00	279.38
φ(Year+Sex+SMI+SMI^2+Stage+(Sex × Stage)+Time) ρ(*t*+Sex)	23	309.32	17.58	0.00	259.84
φ(Year) ρ(*t*+Sex+Stage+Age)	17	309.45	17.71	0.00	273.56
φ(Year+Sex+SMI+Stage+(Sex × Stage)+Time) ρ(*t*+Sex)	22	309.65	17.92	0.00	262.47
φ(Year) ρ(*t*+Stage+Age)	16	309.67	17.93	0.00	275.99
φ(Year+Sex+Hb+Stage+(Sex × Stage)) ρ(*t*+Sex)	22	310.05	18.31	0.00	262.87
φ(Year) ρ(*t*+Sex+Age+(Sex × Age)+Stage)	19	310.43	18.69	0.00	270.06
φ(Year+Sex+PC1+Stage+(Sex × Stage)) ρ(*t*+Sex)	22	311.06	19.32	0.00	263.87
φ(Year+Sex+PCV+Stage+(Sex × Stage)) ρ(*t*+Sex)	22	311.06	19.32	0.00	263.88
φ(Year+Sex+TPP+Stage+(Sex × Stage)) ρ(*t*+Sex)	22	311.06	19.32	0.00	263.88
φ(Year) ρ(*t*+Sex+Stage+(Sex × Stage))	20	311.07	19.33	0.00	268.44
φ(Year+Sex+Hb+Hb^2+Stage+(Sex × Stage)) ρ(*t*+Sex)	23	312.01	20.27	0.00	262.53
φ(Year+Sex+PCV+PCV^2+Stage+(Sex × Stage)) ρ(*t*+Sex)	23	312.12	20.38	0.00	262.64
φ(Year+Sex+PC1+PC1^2+Stage+(Sex × Stage)) ρ(*t*+Sex)	23	313.22	21.48	0.00	263.73
φ(Year+Sex+TPP+TPP^2+Stage+(Sex × Stage)) ρ(*t*+Sex)	23	313.25	21.52	0.00	263.77
φ(Year) ρ(*t*+Sex+Stage+(Sex × Stage)+Age)	22	315.56	23.82	0.00	268.38

φ(*t*+Year+(*t* × Year)) ρ(*t*)	20	316.04	24.30	0.00	273.41
φ(Year) ρ(*t*+Sex+Stage+(Sex × Stage)+Age+(Sex × Age))	24	316.20	24.46	0.00	264.40
φ(*t*+Year+(*t* × Year)) ρ(*t*+Year)	21	318.10	26.36	0.00	273.20
φ(Year) ρ(*t*+Stage+Age+(Stage × Age)+Sex)	27	321.39	29.65	0.00	262.56
φ(Year) ρ(*t*+Stage+Age+(Stage × Age)+Sex+(Sex × Age))	29	322.11	30.37	0.00	258.51
φ(Year) ρ(*t*+Stage+Age+(Stage × Age))	26	322.15	30.41	0.00	265.67
φ(Year) ρ(*t*+Sex+Stage+(Sex × Stage)+Age+(Sex × Age)+(Stage × Age))	34	323.77	32.03	0.00	248.00
φ(*t*+Year+(*t* × Year)) ρ(Year)	16	327.67	35.93	0.00	293.99
φ(*t*+Year+(*t* × Year)) ρ(.)	15	328.41	36.67	0.00	296.94
φ(Year) ρ(*t*+Sex+Stage+(Sex × Stage)+Age+(Stage × Age))	32	328.73	36.99	0.00	257.87
φ(*t*+Year+(*t* × Year)) ρ(*t*+Year+(*t* × Year))	27	329.06	37.32	0.00	270.23

Appendix B: Tables of ranked models that describe intraspecific variation in reproductive success.

Table B4.1: AICc table of results for the annual reproductive success analyses of the 4-year datasets among crimson finches. We asked three questions of each dataset for a total of six analyses. Included are all of the models from the candidate model set. PCV = packed cell volume, Hb = hemoglobin concentration, SMI = scaled mass index, Muscle = muscle score, Fat = fat score, HL = heterophil to lymphocyte ratio, TPP = total plasma protein, Time = time of day, and PCs = principal components. See Methods for an explanation of the covariates including Sex, Stage, Age, Time, and Year. The baseline model is in bold. Also included are the number of parameters in the model (k), the Akiake's Information Criterion corrected for small sample size (AICc), the difference in AICc of a model from that of the top model (ΔAICc), the model weight (W), and the log-likelihood of each model (LL). An asterisk (*) indicates that the model failed to converge.

Response variable	Model	k	AICc	ΔAICc	W	LL
Fledge or not fledge	Stage+PC2+$PC2^2$	9	435.53	0.00	0.66	-208.48
	Stage+PC2+$PC2^2$+Year	12	440.77	5.24	0.05	-207.89
	Stage	7	440.81	5.28	0.05	-213.23
	Stage+Muscle	8	441.55	6.03	0.03	-212.55
	Stage+SMI	8	441.98	6.45	0.03	-212.76

Stage+PCV	8	442.15	6.63	0.02	-212.85
Stage+Muscle+Muscle^2	9	442.30	6.78	0.02	-211.87
Stage+Fat	8	442.40	6.87	0.02	-212.98
Stage+Hb	8	442.41	6.89	0.02	-212.98
Stage+PC2	8	442.71	7.18	0.02	-213.13
Stage+PC1	8	442.72	7.20	0.02	-213.14
Stage+Fat+Fat^2	9	443.12	7.59	0.01	-212.28
Stage+SMI+SMI^2	9	443.80	8.27	0.01	-212.62
Stage+PCV+PCV^2	9	444.26	8.73	0.01	-212.85
Stage+Hb+Hb^2	9	444.52	8.99	0.01	-212.98
Stage+PC1+PC1^2	9	444.84	9.31	0.01	-213.14
Stage+Year	10	445.25	9.73	0.01	-212.28
Stage+Muscle+Year	11	445.61	10.09	0.00	-211.39
Stage+SMI+Sex+(Sex × Stage)	15	446.63	11.10	0.00	-207.55
Stage+Muscle+Muscle^2+Year	12	446.90	11.37	0.00	-210.96
Stage+PC2+Year	11	447.15	11.62	0.00	-212.16
Stage+PCV+Sex+(Sex × Stage)	14	447.53	12.00	0.00	-209.10

	Stage+SMI+SMI^2+Sex(Sex × Stage)	16	448.25	12.73	0.00	-207.26
	Stage+Fat+Sex	12	448.76	13.23	0.00	-211.89
	Stage+PCV+PCV^2+Sex(Sex × Stage)	15	449.60	14.07	0.00	-209.04
	Stage+Fat+Fat^2+Sex	13	450.04	14.51	0.00	-211.45
	Stage+Hb+Sex+(Sex × Stage)+Year	17	452.25	16.72	0.00	-208.15
	Stage+PC1+Sex+(Sex × Stage)	17	452.63	17.10	0.00	-208.34
	Stage+Hb+Hb^2+Sex+(Sex × Stage)+Year	18	454.48	18.95	0.00	-208.15
	Stage+PC1+PC1^2+Sex(Sex × Stage)	18	454.82	19.29	0.00	-208.32
	Null	2	461.17	25.64	0.00	-228.56
	Year	5	462.37	26.84	0.00	-226.09
Number fledged	**Null**	2	170.15	0.00	0.17	-83.04
	PC2+PC2^2	4	171.60	1.45	0.08	-81.69
	Hb+Hb^2	4	171.90	1.74	0.07	-81.84
	PCV	3	172.12	1.97	0.06	-82.99
	SMI	3	172.19	2.03	0.06	-83.03
	Hb	3	172.19	2.03	0.06	-83.03

PC2*	3	172.19	2.04	0.06	-83.03
Muscle*	3	172.20	2.05	0.06	-83.03
Fat	3	172.22	2.07	0.06	-83.04
PC1	3	172.22	2.07	0.06	-83.04
$PC1+PC1^2$*	4	172.77	2.61	0.05	-82.27
Year	5	173.06	2.91	0.04	-81.36
$Muscle+Muscle^2$	4	173.80	3.64	0.03	-82.79
$Fat+Fat^2$	4	174.03	3.87	0.02	-82.90
$PCV+PCV^2$	4	174.04	3.88	0.02	-82.91
$PC2+PC2^2$+Year	7	174.11	3.96	0.02	-79.73
$SMI+SMI^2$	4	174.28	4.12	0.02	-83.03
Muscle+Year	6	175.19	5.04	0.01	-81.36
PC2+Year	6	175.20	5.04	0.01	-81.36
$Muscle+Muscle^2$+Year	7	176.71	6.55	0.01	-81.03
Stage	7	177.66	7.51	0.00	-81.51
Year+Stage	10	180.43	10.27	0.00	-79.57
Fat+Sex+Stage+Year	12	184.56	14.41	0.00	-79.36

	Fat+Fat^2+Sex+Stage+Year	13	185.77	15.62	0.00	-78.80
	PCV+Sex+Stage+(Sex × Stage)	14	187.25	17.09	0.00	-78.37
	SMI+Sex+Stage+(Sex × Stage)+Time	15	189.25	19.10	0.00	-78.18
	PCV+PCV^2+Sex+Stage+(Sex × Stage)	15	189.61	19.46	0.00	-78.36
	PC1+Sex+Stage+(Sex × Stage)+Year*	17	190.70	20.55	0.00	-76.48
	Hb+Sex+Stage+(Sex × Stage)+Year	17	190.82	20.67	0.00	-76.54
	SMI+SMI^2+Sex+Stage+(Sex × Stage)+Time	16	191.62	21.47	0.00	-78.16
	Hb+Hb^2+Sex+Stage+(Sex × Stage)+Year	18	191.99	21.84	0.00	-75.90
	PC1+PC1^2+Sex+Stage+(Sex × Stage)	18	192.34	22.19	0.00	-76.07
Number independent	Year+SMI+SMI^2	7	336.49	0.00	0.28	-160.92
	Year+SMI	6	337.95	1.47	0.13	-162.74
	Year+PC2+PC2^2	7	338.40	1.92	0.11	-161.88
	Year+PC1	6	339.15	2.66	0.07	-163.33
	Year+PC1+PC1^2	7	339.82	3.33	0.05	-162.59
	Year+Muscle	6	340.10	3.61	0.05	-163.81
	Year+PC2	6	340.12	3.63	0.05	-163.82

Year+Fat+Fat^2	7	340.28	3.80	0.04	-162.82
Year	5	340.47	3.99	0.04	-165.07
Year+Hb+Hb^2	7	340.64	4.16	0.03	-163.00
Year+Fat	6	340.93	4.44	0.03	-164.22
Year+Muscle+Muscle^2	7	341.05	4.57	0.03	-163.21
Year+SMI+SMI^2+Sex+Stage+(Sex × Stage)+Time	19	341.17	4.68	0.03	-149.24
Year+PCV	6	341.30	4.81	0.03	-164.41
Year+Hb	6	342.39	5.90	0.01	-164.95
Year+PCV+PCV^2	7	342.60	6.12	0.01	-163.98
Year+SMI+Sex+Stage+(Sex × Stage)+Time	18	343.64	7.15	0.01	-151.72
Year+Stage	10	346.05	9.56	0.00	-162.38
Year+Fat+Sex+Stage	12	349.73	13.25	0.00	-161.94
Year+Fat+Fat^2+Sex+Stage	13	350.35	13.87	0.00	-161.09
Year+PC1+Sex+Stage+(Sex × Stage)	17	351.88	15.39	0.00	-157.07
Year+PCV+Sex+Stage+(Sex × Stage)	17	353.48	16.99	0.00	-157.87
Year+PC1+PC1^2+Sex+Stage+(Sex × Stage)	18	353.80	17.32	0.00	-156.80
Year+Hb+Sex+Stage+(Sex × Stage)	17	354.64	18.15	0.00	-158.45

Year+Hb+Hb^2+Sex+Stage+(Sex × Stage)	18	355.12	18.63	0.00	-157.46
Year+PCV+PCV^2+Sex+Stage+(Sex × Stage)	18	355.58	19.10	0.00	-157.69
Null	2	361.79	25.30	0.00	-178.86
Stage	7	363.04	26.55	0.00	-174.20

Table B4.2: AICc table of results for the annual reproductive success analyses of the 2-year dataset among crimson finches. We asked three questions of each dataset for a total of six analyses. Included are all of the models from the candidate model set. PCV = packed cell volume, Hb = hemoglobin concentration, SMI = scaled mass index, Muscle = muscle score, Fat = fat score, HL = heterophil to lymphocyte ratio, TPP = total plasma protein, Time = time of day, and PCs = principal components. See Methods for an explanation of the covariates including Sex, Stage, Age, Time, and Year. The baseline model is in bold. Also included are the number of parameters in the model (k), the Akiake's Information Criterion corrected for small sample size (AICc), the difference in AICc of a model from that of the top model (ΔAICc), the model weight (W), and the log-likelihood of each model (LL).

Response variable	Model	k	AICc	ΔAICc	W	LL
Fledge or not fledge	Stage+TPP	8	183.44	0.00	0.11	-83.17
	Stage+TPP+TPP2	9	183.59	0.16	0.11	-82.10
	Stage+Muscle+Muscle^2	9	183.91	0.47	0.09	-82.26
	Stage	7	184.07	0.63	0.08	-84.61
	Stage+Muscle	8	184.54	1.10	0.07	-83.72
	Stage+PCV	8	185.07	1.63	0.05	-83.99

Stage+PC1	8	185.79	2.35	0.04	-84.35
Stage+HL	8	185.90	2.47	0.03	-84.40
Stage+Hb	8	186.08	2.64	0.03	-84.49
Stage+PC3	8	186.13	2.70	0.03	-84.52
Stage+SMI	8	186.14	2.71	0.03	-84.52
Stage+Fat	8	186.15	2.72	0.03	-84.53
Year+Stage	8	186.20	2.77	0.03	-84.55
Stage+Muscle+Muscle^2+Year	10	186.22	2.78	0.03	-82.26
Age+Stage	9	186.30	2.87	0.03	-83.46
Stage+PC2	8	186.32	2.88	0.03	-84.61
Stage+PC1+PC1^2	9	186.64	3.20	0.02	-83.63
Stage+PC3+PC3^2	9	186.68	3.24	0.02	-83.65
Stage+PCV+PCV^2	9	186.77	3.33	0.02	-83.69
Stage+Muscle+Year	9	186.80	3.36	0.02	-83.71
Stage+PC2+PC2^2	9	187.10	3.66	0.02	-83.86
Stage+Fat+Fat^2	9	187.48	4.05	0.02	-84.05
Stage+SMI+SMI^2	9	188.02	4.58	0.01	-84.32

Stage+HL+HL^2	9	188.15	4.71	0.01	-84.38
Stage+HL+Year	9	188.17	4.73	0.01	-84.39
Stage+Hb+Hb^2	9	188.34	4.90	0.01	-84.48
Stage+Year+Age	10	188.53	5.09	0.01	-83.41
Stage+HL+HL^2+Year	10	190.42	6.99	0.00	-84.36
Stage+PC3+Sex+Year	10	190.60	7.16	0.00	-84.45
Stage+Fat+Sex+Year	10	190.61	7.17	0.00	-84.45
Stage+PC3+$PC3^2$+Sex+Year	11	191.32	7.88	0.00	-83.63
Null	2	191.65	8.21	0.00	-93.78
Stage+Fat+Fat^2+Sex+Year	11	191.89	8.45	0.00	-83.91
Age	4	193.48	10.04	0.00	-92.59
Year	3	193.52	10.08	0.00	-93.67
Stage+TPP+Sex+(Sex xStage)	14	193.54	10.10	0.00	-81.09
Stage+SMI+Sex+(Sex xStage)+Time	15	194.10	10.67	0.00	-80.12
Stage+PCV+Sex+(Sex xStage)	14	194.16	10.72	0.00	-81.40
TPP+TPP^2+Sex+(Sex xStage)	15	194.25	10.81	0.00	-80.19
Year+Age	5	195.35	11.91	0.00	-92.45

	Stage+SMI+SMI^2+Sex+(Sex xStage)+Time	16	195.70	12.27	0.00	-79.64
	Stage+PCV+PCV^2+Sex+(Sex xStage)	15	196.20	12.76	0.00	-81.17
	Stage+PC1+Sex+(Sex xStage)+Year	15	196.78	13.34	0.00	-81.45
	Stage+Hb+Sex+(Sex xStage)+Year	15	196.87	13.43	0.00	-81.50
	Stage+PC1+PC1^2+Sex+(Sex xStage)+Year	16	198.56	15.12	0.00	-81.07
	Stage+PC2+Sex+(Sex xStage)+Year+Time	16	198.84	15.40	0.00	-81.21
	Stage+Hb+Hb^2+Sex+(Sex xStage)+Year	16	199.41	15.97	0.00	-81.49
	Stage+PC2+PC2^2+Sex+(Sex xStage)+Year+Time	17	199.58	16.15	0.00	-80.28
Number fledged	Year	3	65.62	0.00	0.18	-29.66
	Year+Age	4	66.35	0.73	0.12	-28.92
	Year+Age+(Year × Age)	5	66.92	1.30	0.09	-28.08
	Year+Age+(Year × Age)+SMI	6	67.19	1.57	0.08	-27.05
	Year+Age+(Year × Age)+HL+HL^2	7	67.98	2.35	0.05	-26.25
	Year+Age+(Year × Age)+PC2	6	68.78	3.16	0.04	-27.84
	Year+Age+(Year × Age)+Fat	6	68.82	3.20	0.04	-27.87
	Year+Age+(Year × Age)+TPP	6	68.91	3.29	0.03	-27.91

Year+Age+(Year × Age)+PC3	6	69.04	3.41	0.03	-27.97
Null	2	69.08	3.45	0.03	-32.46
Year+Age+(Year × Age)+Muscle	6	69.20	3.58	0.03	-28.06
Year+Age+(Year × Age)+Hb	6	69.21	3.59	0.03	-28.06
Year+Age+(Year × Age)+PC1	6	69.23	3.61	0.03	-28.07
Year+Age+(Year × Age)+PCV	6	69.23	3.61	0.03	-28.07
Year+Age+(Year × Age)+HL	6	69.23	3.61	0.03	-28.07
Year+Age+(Year × Age)+SMI+SMI^2	7	69.39	3.77	0.03	-26.96
Year+Age+(Year × Age)+Muscle+$Muscle^2$	7	70.12	4.50	0.02	-27.32
Year+Age+(Year × Age)+PC2+$PC2^2$	7	70.42	4.79	0.02	-27.47
Age	3	70.60	4.98	0.01	-32.15
Year+Age+(Year × Age)+Fat+Fat^2	7	70.72	5.10	0.01	-27.62
Year+Age+(Year × Age)+TPP+TPP^2	7	70.87	5.24	0.01	-27.70
Year+Age+(Year × Age)+Hb+Hb^2	7	70.99	5.37	0.01	-27.76
Year+Age+(Year × Age)+PC1+$PC1^2$	7	71.18	5.56	0.01	-27.85
Year+Age+(Year × Age)+PCV+PCV^2	7	71.26	5.64	0.01	-27.89
Year+Age+(Year × Age)+PC3+$PC3^2$	7	71.38	5.76	0.01	-27.95

Year+Stage	7	73.00	7.38	0.00	-28.76
Year+Age+Stage	8	73.20	7.58	0.00	-27.64
Stage	6	74.31	8.69	0.00	-30.61
Year+Age+Stage+(Year × Age)	9	74.33	8.71	0.00	-26.95
Age+Stage	7	75.27	9.65	0.00	-29.90
Year+Age+Stage+(Age × Stage)	12	78.34	12.72	0.00	-24.97
Fat+Sex+Stage	11	78.81	13.19	0.00	-26.57
Year+Age+(Year × Age)+PC3+Sex+Stage	11	78.97	13.35	0.00	-26.65
Year+Age+Stage+(Age × Stage)+(Year × Age)	13	80.58	14.95	0.00	-24.69
Age+Stage+(Age × Stage)	11	80.95	15.33	0.00	-27.64
Year+Age+(Year × Age)+Fat+Fat^2+Sex+Stage	12	81.31	15.69	0.00	-26.46
Year+Age+(Year × Age)+PC3+$PC3^2$+Sex+Stage	12	81.35	15.72	0.00	-26.48
Year+Age+(Year × Age)+SMI+Sex+Stage+(Sex × Stage)+Time	16	87.95	22.33	0.00	-23.92
Year+Age+(Year × Age)+TPP+Sex+Stage+(Sex × Stage)	15	89.03	23.41	0.00	-25.99
Year+Age+(Year × Age)+PC1+Sex+Stage+(Sex × Stage)	15	89.57	23.94	0.00	-26.25
Year+Age+(Year × Age)+Hb+Sex+Stage+(Sex × Stage)	15	89.57	23.95	0.00	-26.26
Year+Age+(Year × Age)+PCV+Sex+Stage+(Sex × Stage)	15	89.58	23.96	0.00	-26.26

	Year+Age+(Year × Age)+PC2+Sex+Stage+(Sex × Stage)+Time	16	90.78	25.16	0.00	-25.33
	Year+Age+(Year × Age)+SMI+SMI^2+Sex+Stage+(Sex × Stage)+Time	17	91.06	25.44	0.00	-23.89
	Year+Age+(Year × Age)+TPP+TPP^2+Sex+Stage+(Sex × Stage)	16	92.09	26.47	0.00	-25.99
	Year+Age+(Year × Age)+Hb+Hb^2+Sex+Stage+(Sex × Stage)	16	92.55	26.93	0.00	-26.21
	Year+Age+(Year × Age)+PCV+PCV^2+Sex+Stage+(Sex × Stage)	16	92.55	26.93	0.00	-26.22
	Year+Age+(Year × Age)+PC1+$PC1^2$+Sex+Stage+(Sex × Stage)	16	92.63	27.01	0.00	-26.25
	Year+Age+(Year × Age)+PC2+$PC2^2$+Sex+Stage+(Sex × Stage)+Time	17	93.24	27.62	0.00	-24.99
Number independent	Year+Age+(Year × Age)+SMI+SMI^2	7	145.10	0.00	0.44	-64.81
	Year+Age+(Year × Age)+SMI	6	146.15	1.05	0.26	-66.53
	Year+Age+(Year × Age)+PCV	6	148.33	3.23	0.09	-67.62
	Year	3	150.37	5.27	0.03	-72.04
	Year+Age+(Year × Age)+PCV+PCV^2	7	150.56	5.46	0.03	-67.54
	Year+Age	4	150.82	5.72	0.03	-71.16
	Year+Age+(Year × Age)+PC1	6	151.19	6.09	0.02	-69.05
	Year+Age+(Year × Age)+HL+HL^2	7	151.61	6.51	0.02	-68.07
	Year+Age+(Year × Age)	5	151.80	6.69	0.02	-70.51

Year+Age+(Year × Age)+Hb	6	153.00	7.90	0.01	-69.96
Year+Age+(Year × Age)+TPP	6	153.12	8.01	0.01	-70.01
Year+Age+(Year × Age)+PC3	6	153.24	8.13	0.01	-70.07
Year+Age+(Year × Age)+PC1+$PC1^2$	7	153.36	8.25	0.01	-68.94
Year+Age+(Year × Age)+HL	6	153.51	8.40	0.01	-70.21
Year+Age+(Year × Age)+TPP+TPP^2	7	153.57	8.46	0.01	-69.05
Year+Age+(Year × Age)+PC2	6	153.76	8.65	0.01	-70.33
Year+Age+(Year × Age)+Muscle	6	153.81	8.71	0.01	-70.36
Year+Age+(Year × Age)+Fat	6	154.08	8.98	0.00	-70.50
Year+Age+(Year × Age)+PC2+$PC2^2$	7	154.55	9.45	0.00	-69.54
Year+Age+(Year × Age)+Hb+Hb^2	7	155.28	10.17	0.00	-69.90
Year+Age+(Year × Age)+PC3+$PC3^2$	7	155.59	10.49	0.00	-70.06
Year+Age+(Year × Age)+Fat+Fat^2	7	155.97	10.86	0.00	-70.25
Year+Age+(Year × Age)+Muscle+$Muscle^2$	7	156.18	11.08	0.00	-70.36
Year+Stage	7	156.42	11.31	0.00	-70.47
Year+Age+Stage	8	157.66	12.55	0.00	-69.87
Year+Age+(Year × Age)+SMI+SMI^2+Sex+Stage+(Sex × Stage)+Time	17	159.28	14.18	0.00	-58.00

Year+Age+Stage+(Year × Age)	9	159.42	14.31	0.00	-69.49
Null	2	160.01	14.90	0.00	-77.93
Year+Age+(Year × Age)+PC3+Sex+Stage	11	160.55	15.44	0.00	-67.44
Year+Age+(Year × Age)+TPP+Sex+Stage+(Sex × Stage)	15	161.30	16.20	0.00	-62.12
Year+Age+(Year × Age)+Fat+Sex+Stage	11	161.44	16.34	0.00	-67.89
Age	3	161.71	16.61	0.00	-77.71
Year+Age+(Year × Age)+SMI+Sex+Stage+(Sex × Stage)+Time	16	162.17	17.06	0.00	-61.02
Year+Age+(Year × Age)+TPP+TPP^2+Sex+Stage+(Sex × Stage)	16	162.66	17.56	0.00	-61.27
Year+Age+Stage+(Age × Stage)	12	162.79	17.69	0.00	-67.20
Year+Age+(Year × Age)+PC3+$PC3^2$+Sex+Stage	12	163.20	18.10	0.00	-67.40
Stage	6	163.75	18.65	0.00	-75.33
Year+Age+(Year × Age)+Fat+Fat^2+Sex+Stage	12	163.83	18.73	0.00	-67.72
Year+Age+Stage+(Age × Stage)+(Year × Age)	13	164.95	19.85	0.00	-66.87
Age+Stage	7	165.59	20.49	0.00	-75.06
Year+Age+(Year × Age)+PCV+Sex+Stage+(Sex × Stage)	15	167.88	22.77	0.00	-65.41
Year+Age+(Year × Age)+Hb+Sex+Stage+(Sex × Stage)	15	168.65	23.55	0.00	-65.80
Year+Age+(Year × Age)+PC1+Sex+Stage+(Sex × Stage)	15	168.86	23.75	0.00	-65.90

Year+Age+(Year × Age)+PC2+Sex+Stage+(Sex × Stage)+Time	16	170.10	24.99	0.00	-64.99
Year+Age+(Year × Age)+PCV+PCV^2+Sex+Stage+(Sex × Stage)	16	170.50	25.39	0.00	-65.19
Year+Age+(Year × Age)+Hb+Hb^2+Sex+Stage+(Sex × Stage)	16	170.80	25.70	0.00	-65.34
Age+Stage+(Age × Stage)	11	171.52	26.42	0.00	-72.93
Year+Age+(Year × Age)+PC1+$PC1^2$+Sex+Stage+(Sex × Stage)	16	171.75	26.64	0.00	-65.81
Year+Age+(Year × Age)+PC2+$PC2^2$+Sex+Stage+(Sex × Stage)+Time	17	172.87	27.76	0.00	-64.80

CHAPTER V. CONCLUSION: WHAT DO BODY CONDITION INDICES TELL US ABOUT FITNESS?

Olga Milenkaya

That body condition influences fitness was first proposed by Darwin (1896) who suggested that individual health and vigor determines fecundity. How condition is interpreted today has consequences for many fields throughout animal ecology and evolutionary biology including the study of sexual selection (Cotton et al. 2004), carry-over effects where processes in one season impact the success of individuals the following season (Harrison et al. 2011), life history theory (Stearns 1992), and conservation biology (e.g., Milenkaya et al. 2013b; Chapter II). Here, I define body condition and condition indices, and then summarize how condition indices are employed in ecological studies. I do not focus on the various methodological considerations for calculating mass adjusted for structural body size because these have been discussed elsewhere (Jakob et al. 1996; Schulte-Hostedde et al. 2005; Peig and Green 2009, 2010). Instead, I focus on the broader ecological interpretation of a variety of condition indices as proxies for fitness. To evaluate this interpretation, I review the findings from my research (Chapters II−IV) and the ecological literature more broadly, and glean insights from poultry science in the interest of informing how condition indices can be interpreted in ecological systems. I conclude by questioning the pervasive interpretation of condition indices as indicators of individual quality or fitness and make recommendations for how condition indices are to be employed.

Defining body condition and its indices

Body condition (hereafter "condition") is defined in a variety of ways but is most often defined ambiguously if at all (Schulte-Hostedde et al. 2005; Schamber et al. 2009). A common definition is that condition is the pool of resources that an individual has acquired (and presumably assimilated) that can be allocated toward improving fitness (Rowe and Houle 1996; Hunt et al. 2004; Tomkins et al. 2004; Lailvaux and Kasumovic 2011). This definition is reflected in the terms that are used to describe condition including "energy capital" (Peig and Green 2009), "energetic state" (Schulte-Hostedde et al. 2005) and "relative fatness" (Jakob et al. 1996). For a more nuanced definition of condition that goes beyond energetic reserves, see Hill (2011) who proposed that condition is the relative capacity to maintain optimal functionality of essential cellular processes.

I emphasize that condition indices are not the same as condition itself (Green 2001); rather they are tools that measure aspects of condition. Here I consider mass adjusted for structural body size and indices of fat and muscle to be the traditional and most direct measures of condition because they quantify the stored energy that a bird has acquired, assimilated and can allocate to traits related to fitness. Additionally, I include in my discussion the wide range of hematological (e.g., mean corpuscular volume) and biochemical (e.g., triglycerides) indices because they are often interpreted broadly as condition indices. These indices do not measure energy capital but they reflect specific physiological systems and processes with potential implications for fitness. Finally, I also include performance measures (e.g., bacteria killing assays) and stress physiology (e.g., stress-induced or baseline corticosterone) which can be

interpreted as a combination of both condition and performance. Performance measures and stress physiology are not condition indices but are relevant here because performance measures reflect resource allocation decisions and corticosterone is involved in metabolism.

Condition indices in ecology

Although some consider condition to be tantamount to individual quality (e.g., Rowe and Houle 1996; Hõrak et al. 1998; Bearhop et al. 1999; Hanssen et al. 2009; Edler and Friedl 2010), Wilson and Nussey (2010) define individual quality as the axis of variation in genotype and phenotype that is positively correlated with fitness. Thus, individual quality, condition and fitness are related but are not synonymous. Condition is one aspect of the phenotype that might be a component of individual quality, and by definition, individual quality is positively (although not perfectly) correlated with fitness (Wilson and Nussey 2010).

Condition has generally been expected to reflect individual quality (e.g., Rowe and Houle 1996; Peig and Green 2009) because those of superior quality presumably will have more resources that can be allocated toward improving their realized fitness. Since neither condition nor individual quality can be directly measured, researchers have turned to the use of condition indices as their proxies. I refer to this common and often implicit interpretation of condition indices as the condition-quality hypothesis (Milenkaya et al. 2013a; Chapter III), which states that condition indices are meaningful indicators of individual quality and that they therefore predict fitness.

Applying the condition-quality hypothesis

The two assumptions of the condition-quality hypothesis are (a) that condition indices measure condition, and (b) that the relative condition among individuals reflects their quality. Although they seem intuitive, these assumptions may sometimes be violated. We know that condition indices vary by contexts such as sex, season, breeding stage, and age (Fair et al. 2007; Milenkaya et al. 2013b). When assessing condition, it is therefore important to compare individuals within the same contexts. Otherwise, condition indices may reflect the individual's circumstance (e.g., breeding stage) more than its condition or quality. I addressed this concern by assessing how condition indices in my population vary by sex, breeding stage, a sex by breeding stage interaction, age, time of day and year (Milenkaya et al. 2013b; Chapter II) and then controlling for this variance in my subsequent analyses (Milenkaya et al. 2013a; Chapters III, IV) such that I was comparing individual condition relative to others in the same context. If the condition-quality hypothesis is true then an individual's condition relative to others in the same context should be consistent across contexts. Other studies differ in whether or not such covariates are accounted for and if so, which ones are considered. Identifying the relevant contexts may not always be straightforward and I acknowledge that contexts other than the ones for which I controlled may also be important.

There are several other difficulties in applying the condition-quality hypothesis. First, because condition indices measure particular aspects of condition, the condition-quality hypothesis may not apply when an index does not capture the component of condition most relevant to fitness. That is, the condition indices being measured must reflect an animal's capacity to better survive and reproduce than its conspecifics in relation to natural and sexual

selection. Identifying the strongest selective pressure and the index that best reflects the individual's capacity to respond to it is challenging, and the indices become difficult to interpret in the absence of a specific and a priori justification for why a particular index is ecologically relevant. Perhaps for this reason, condition indices have an inconsistent relationship to fitness traits (see below). Second, strong selective events may be rare and their timing unpredictable, and condition indices need to be measured at a temporal scale appropriate to the selective event. For example, individual survival was predicted by condition indices measured prior to a disease epidemic (Wilcoxen et al. 2010), but not when measured at other times (T. Wilcoxen unpublished data). Studies that do not capture these less common, strong selective events may miss the occasion under which condition indices are most informative. Relative condition may therefore only reflect individual quality under particularly challenging circumstances and when the condition indices are relevant to the selective pressures.

Another difficulty in apply the condition-quality hypothesis is that condition may be confounded by habitat quality. Condition is interpreted by some as only a property of the individual, and by others only as a consequence of the environment. However, condition is instead a composite of both the individual and its environment (Rowe and Houle 1996; Cotton et al. 2004). One reason for failing to consider both factors in some studies may be that the intrinsic (individual quality) and extrinsic (environmental quality) effects are difficult to isolate. For example, stable isotope ratios correspond to wintering habitats of varying quality for black-throated blue warblers (*Dendoica caerulescens*) and migrating individuals with low δ13C signatures were fatter and had more muscle than birds with high δ13C signatures (Bearhop et al. 2004). Bearhop et al. (2004) therefore concluded that wintering habitat influences migrating condition, with potential downstream implications for fitness. However, they also noted that

since they inferred habitat selection remotely (via stable isotope analysis), they could not demonstrate that condition is a direct consequence of the habitat and, furthermore, that sorting by habitat type (i.e., high quality individuals outcompete low quality ones for high quality habitat) may also occur in this species (Bearhop et al. 2004). This demonstrates the challenge of separating the influences of inherent individual quality and habitat quality on condition, and the possibility of interaction between the two. Generally it is difficult to separate the effects of individual and habitat quality in species that hold territories because resources would necessarily vary between territories, and this may again be mediated by social interactions such that high quality individuals obtain the highest quality territories. In cases where individuals within a population have relatively comparable access to resources, then the variation in condition among individuals is more directly an expression of individual quality. Because my study population occupies a small site where individuals do not hold territories and forage in common areas, I largely avoided the confounding between individual quality and habitat quality that are found in other studies. My study population was therefore well suited for addressing the condition-quality hypothesis.

Finally, the condition-quality hypothesis does not apply when individuals vary in their reaction norms such that the optimal condition indices within a given context are different across individuals. If this is the case, then the condition-quality hypothesis is invalid because the condition index values that constitute "good" or "poor" condition differ between individuals.

Predictions of the condition-quality hypothesis

Two main predictions of the condition-quality hypothesis are (a) that condition indices should be repeatable within individuals (Milenkaya et al. 2013a; Chapter III) because aspects of individual quality are inherent and do not change in adulthood (Rowe and Houle 1996; Wilson and Nussey 2010), and (b) that condition indices predict realized fitness or its primary components (Chapter IV). The evidence in support of both predictions is mixed.

First, the repeatability of condition indices is not consistent across, or even within (e.g., Norte et al. 2008), studies. For example, total plasma protein was repeatable in great tits (*Parus major*) over four years (Norte et al. 2008) but not repeatable in upland geese (*Chloephaga picta leucoptera*) after just one year (Gladbach et al. 2010). In one study, heterophil to lymphocyte (H/L) ratio was repeatable over long time periods (Norte et al. 2008), while elsewhere it was only repeatable within a relatively short time period (Milenkaya et al. 2013a; Chapter III), only among females (Gladbach et al. 2010), or not at all (Ochs and Dawson 2008). Among crimson finches (*Neochmia phaeton*), I found that seven commonly used condition indices are repeatable over short, but not long time periods (Milenkaya et al. 2013a; Chapter III). This suggests that individuals have a physiological phenotype but that the phenotype is not consistent after more than a few months and that condition indices are therefore not likely to be meaningful indicators of individual quality. The prediction that condition indices are repeatable is not consistently demonstrated across studies and is not supported by my research.

The evidence in support of the second prediction of the hypothesis, that condition indices predict key components of fitness, is also mixed. There are clear examples of energy reserves positively influencing reproductive success among capital breeders (Ankney and MacInnes 1978; Ebbinge and Spaans 1995; Hanssen et al. 2003a) and migratory species (Kokko 1999). However,

the relationship between condition indices and fitness parameters in other species is not as straightforward. Condition indices predict fitness traits in some cases (Verhulst et al. 2004) but not others (Kilgas et al. 2006a; Wilcoxen et al. 2011), often within the same studies where some indices are meaningful while others are not (Bearhop et al. 1999; Ben-David et al. 2002; Kilgas et al. 2006b; Wilcoxen et al. 2010; Chapter IV) or an index predicts one fitness trait, but not another (Blomqvist et al. 1997; Hanssen et al. 2003b; Chapter IV). For example, the lymphocyte count of female common eiders (*Somateria mollissima*) failed to predict reproductive parameters such as laying date and clutch size, but predicted return rate, although only among the females that had abandoned their broods and not among those that cared for their young (Hanssen et al. 2003b). Similarly, I found that condition indices in crimson finches that reflect energy stores affect one fitness trait (annual reproductive success) but not another (survival; Chapter IV). Elsewhere, the social context is important in mediating the condition-fitness relationship as with great tits, where high fat score positively influenced survival of the subordinate, but not the dominant, classes (Gosler 1996), or with Siberian jays (*Perisoreus infaustus*) where the width of growth bars predicted annual reproductive success only among females, but not males (Gienapp and Merilä 2010).

Habitat can also impact whether condition has fitness consequences such as in great tits where fat scores predicted survival only when overwintering individuals were food limited but not otherwise (Gosler 1996). Burton et al. (2011) reviewed the large intraspecific variation in resting metabolic rate (RMR) and concluded that this variation likely persists because different environmental conditions may favor either low or high RMR, such that the relationship between RMR and fitness is context-dependent. Understanding the relevant context is important in interpreting condition indices, but this is not straightforward.

The lack of a clear relationship between condition and fitness is evident across orders and guilds, latitudinal gradients and life-history strategies with no obvious explanation for the inconsistency except that, where the relationship exists, it is context-dependent. My point that some condition indices, but not others, are sometimes, but not always, informative of some, but not all, fitness traits highlights that we lack predictive power to identify the relevance of condition indices. In light of this, the prudent approach is to avoid inferring fitness consequences from condition indices without first validating them. However, another complication with the condition-quality hypothesis is that condition indices are difficult to validate unambiguously. They are nearly impossible to test in isolation since they cannot be experimentally manipulated, CORT being an exception. One can manipulate work load, exposure to stressors, nutrition, and immune challenges, but one cannot alter muscle mass, hemoglobin concentration, or other condition indices in a direct way without simultaneously affecting other systems. The relationship between these indices and fitness, where it exists, is suggestive but correlative.

In applications of condition indices in ecological research, either as a measure of individual or habitat quality, the expectation is that condition indices predict fitness. However, this interpretation is poorly validated in ecological studies and is only partially supported by my research. Poultry science offers another venue for assessing the condition-fitness relationship. I do not imply that all aspects of the biology of poultry are directly transferable and applicable to wild birds. However, we may glean some useful insights from research done on condition indices among domesticated animals that may be informative in ecological systems.

Trade-offs

Poultry scientists focus on life-history theory and the trade-offs that animals face in allocating resources between different fitness traits (Rauw 2009). Examples of these trade-offs are evident in the artificially-selected lines of chickens bred for high and low response to sheep red blood cells (SRBC), an immunological assay used in both ecological and poultry research. Chickens from the line selected for high SRBC response have lower body mass (Gross et al. 2002), lower total plasma protein levels, more resistance to viruses but less resistance to bacterial infections compared to the low SRBC line (Gross and Siegel 1997). Not only is immune function costly and traded-off against other processes (Zhao et al. 2012), but an individual cannot simultaneously have a strong immune function against all possible diseases (Gross and Siegel 1997; Gross et al. 2002). Furthermore, selection for SRBC response resulted in trade-offs between reproductive traits, with chickens from the high SRBC line having higher quality eggs but a shorter period of fertility (Albrecht et al. 2012). It is challenging to interpret condition indices and immune function profiles in terms of fitness in this case because an individual that is functioning "well" in one capacity (e.g., SRBC response) may be functioning "poorly" in another (e.g., mass). And while SRBC response may be positively correlated with one fitness trait, it may be negatively correlated with another.

Individuals that perform above average across a suite of physiological processes and fitness parameters may meet the definition of high quality individuals. However, most individuals likely face trade-offs when allocating resources and cannot maintain all systems at their optimal. These individuals differ in fitness, such that some allocation strategies are ultimately more successful than others, but it is difficult to predict which strategy will incur the

highest fitness. Condition indices are difficult to interpret because a "high quality" individual based on one index may be of "low quality" based on another and inferring fitness consequences based on these indices therefore seems arbitrary. To address this concern, one would need to measure resource allocation decisions over a lifetime, as well as their associated trade-offs and fitness implications (Lailvaux and Kasumovic 2011).

Hematological and biochemical condition indices

Hematological and biochemical indices are used in poultry as early warning-signals of disease (Keçeci et al. 1998; Oğuz et al. 2000; Andretta et al. 2012) with particular attention to the relationship between packed cell volume and ascites syndrome. Selective breeding of chickens for high growth rate in the poultry industry has resulted in various physiological problems, especially when chickens are reared under extreme conditions such as cold temperatures. In these circumstances, chickens are susceptible to ascites syndrome which may be lethal and which coincides with decreased oxygen content in blood and increased packed cell volume due to increased erythropoiesis of large, immature red-blood cells which have low oxygen-carrying capacity (Luger et al. 2003). Thus, some have looked to high packed cell volume as an indicator of susceptibility to ascites (e.g., Shlosberg et al. 1996). Shlosberg et al. (1998) tested three lines of chickens that were selectively bred for low, medium and high packed cell volume and found that while individuals with high packed cell volume within each of the three lines had increased susceptibility to ascites, susceptibility to the syndrome did not differ between the lines. The interpretation of high packed cell volume as an early warning signal for ascites mortality has been questioned by Buys et al. (1999) who suggested that populations with high packed cell

volume are actually more resistant to ascites. Interestingly, body mass was a meaningful predictor of mortality from ascites with low weight individuals being more likely to die (Shlosberg et al. 1998). Thus, the interpretation of a common hematological index, packed cell volume, is inconsistent, and indeed simple body mass may be just as, or even more informative.

Where a particular disease is known to be a strong selective pressure, condition indices that reflect one's capacity to minimize the fitness costs of the disease may be meaningful. However, the lack of a consensus in poultry science over the interpretation of a common condition index in relation to a well-researched disease, in a highly-controlled setting, should give ecologists pause. It further underscores that condition indices need to be validated to confirm that they are meaningful and relevant.

Stress physiology

Indices that measure stress physiology are used in poultry science largely because of concerns over animal welfare. These are the same tools that are often employed in ecological research including CORT concentration (McFarlane and Curtis 1989; Gross and Siegel 1997; Kontecka et al. 1999; Estevez 2007; Quinteiro-Filho et al. 2012), H/L ratio (Maxwell 1993; Kontecka et al. 1999; Estevez 2007), and, to a lesser extent, eosinophils (Nowaczewski and Kontecka 2012). Their interpretation in poultry science also mirrors that found in ecological studies with elevated CORT, H/L ratios, and percent eosinophils generally taken to mean that an individual is stressed. However, stress indices among poultry are plagued by problems of interpretation. Maxwell (1993) found that while H/L ratios generally increase with stress they are

not reliable for all stressors and he therefore concluded that they cannot always be considered an accurate measure of stress. However, others suggest that H/L ratio is more reliable than CORT (McFarlane and Curtis 1989) and that CORT is difficult to interpret (Gross and Siegel 1997). While its relationship to stress may sometimes be unclear, CORT correlates with reproductive parameters in chickens (Schmidt et al. 2009) and predicts their mortality from experimentally induced ascites: individuals that died had higher concentrations than those that survived (Luger et al. 2003). Therefore CORT may predict fitness in at least some circumstances, but whether fitness consequences should be inferred from stress indices among wild birds remains unclear (Bonier et al. 2009).

The findings among poultry are relevant to ecologists because even in the highly controlled context of poultry research, generalizations about fitness based on condition indices, performance measures or stress physiology are difficult to make (Gross and Siegel 1997). Since ecological systems exhibit more variation than is found among poultry and are subject to uncontrolled and largely unknown stressors, it is unlikely that any condition index may invariably predict fitness of wild animals.

Conclusion

In this dissertation, I tested the condition-quality hypothesis by studying intraspecific variation in condition indices and fitness traits among crimson finches. I found that they vary widely in both reproductive success (Chapter I) and in condition indices (Chapter II), making them a suitable study system for addressing my research question. Furthermore, because they

occupy a relatively small site, do not hold territories and forage in common areas, I was able to evaluate whether condition indices reflect individual quality largely in the absence of confounding effects between habitat quality and individual quality.

Crimson finches are not a model species and because relatively little is known about these birds, I documented the life-history traits and breeding biology of my study population (Chapter I). My primary finding here was that crimson finches have relatively large clutch-sizes compared to other southern hemisphere and tropical species, and I hope this contributes to the broader discussion of the evolution of clutch-size (Milenkaya et al. 2011; Chapter I).

In Chapter II, I found that most condition indices vary by sex, breeding stage, and to a lesser extent year, age and time of day. Muscle score and H/L ratio were least variable by sex, breeding stage, age, and time of day, but exhibited significant annual variation, suggesting that they may be the best indicators of habitat quality because year effects may reflect differences in environmental conditions (Milenkaya et al. 2013b; Chapter II).

In Chapters III and IV, I tested the two predictions of the condition-quality hypothesis by asking if condition indices are repeatable within individuals and if they predict primary components of realized fitness, respectively. My results only partially support the two predictions because condition indices were repeatable within relatively short, but not long, time periods (Milenkaya et al. 2013a; Chapter III) and although some condition indices predicted reproductive success, others did not, and none predicted survival (Chapter IV). Interestingly, muscle score and other indices that reflect energy reserves were the most meaningful predictors of reproductive success, highlighting my results from Chapter II that muscle score may be one of the best condition indices in crimson finches (Milenkaya et al. 2013b; Chapter II). However, the

repeatability results suggest that this index may reflect environmental quality and resulting fitness potential, but not individual quality. Furthermore, because muscle score predicted reproductive success only within a multivariate framework in conjunction with other condition indices (Chapter IV), measuring only muscle score and inferring fitness consequences from it is not advisable. I draw two main conclusions from these findings: (1) that the condition-quality hypothesis may be valid and condition indices informative in highly specified contexts, but that condition indices (2) cannot be universally interpreted as indicators of individual quality or fitness and (3) need to be thoroughly validated to determine the appropriate context for their use.

Condition indices may be indicators of environmental and individual quality and I make the following recommendations for interpreting them correctly. (1) Because relative, instead of absolute, condition is the measure of interest, researchers should control for factors that influence condition indices in their study species such as sex, breeding stage, age, and year in order compare individuals in the same contexts. (2) The selective pressure that matters most to fitness in the study species should be identified, and both condition indices and the timing of sampling should be relevant to that selective event. For example, relevant indices include hemoglobin concentration prior to migration among long-distance migrants, immunological indices before a disease outbreak or energy reserves at the onset of breeding among capital breeders. (3) Researchers can then determine the relationship between condition and fitness to validate it within their study system. Because this relationship is affected by both individual and environmental quality, these effects should be isolated to determine which drives the condition-fitness relationship. In cases where these recommendations can be implemented, I expect condition indices to be informative. However, the recommendations highlight the challenges of using and interpreting condition indices because the relevant contexts and selective pressures

may be unknown and because individual and habitat quality effects may be nearly impossible to isolate. I therefore question the validity of the broad and over-arching interpretation of condition indices as proxies for individual quality and fitness, unless the indices have first been validated. The use of condition indices remains ubiquitous and the extrapolation from index to something grander seems to be both common and rarely challenged. I suggest that condition indices need to be used and interpreted more carefully and narrowly.

Finally, because of the challenges inherent to the condition-quality hypothesis, a new paradigm about condition and fitness may be needed. I am encouraged by Hill's (2011) suggestion for a new definition of condition where energy reserves are considered as just one component of condition while the ability to maintain optimal functionality of essential cellular processes is the primary focus (Hill 2011). Williams (2008; 2012) also offers a new approach where condition is less important than the mechanisms that individuals employ to regulate their condition. Either of these approaches, especially if considered over a life-time of resource allocation decisions (Lailvaux and Kasumovic 2011), will provide new insights into what the intraspecific variation in condition means for individual quality and fitness.

ACKNOWLEDGMENTS

I thank Jeffrey R. Walters for his advice, William A. Hopkins, Dana M. Hawley and Ignacio T. Moore for years of discussion on condition and Paul Siegel for insights on poultry.

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