INVESTIGATING LIFE HISTORY TRADEOFFS IN AN OPPORTUNISTIC BREEDING SONGBIRD, THE RED CROSSBILL (*LOXIA CURVIROSTRA*) IN GRAND TETON NATIONAL PARK

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✦ ABSTRACT

Because available energy is finite, organisms must be selective with how and when energetic resources are allocated to demanding physiological processes such as reproduction or self-maintenance like immune function. Historically, research to understand how organisms orchestrate their annual cycles with respect to these costly and conflicting processes has focused narrowly on seasonal breeders that constrain reproduction to times of year when thermoregulatory demand is low (i.e., summer), which provide limited opportunities to reveal how physiological costs of different processes may interact with environmental conditions to influence the evolution of investment strategies. In this study, we are examining seasonal and interannual variation in environmental conditions (temperature, precipitation, food supply) and investment patterns in survival and reproduction in a reproductively flexible songbird, the red crossbill (*Loxia curvirostra)*, which can reproduce opportunistically in both summer and winter in Grand Teton National Park. In addition, crossbills provide a perfect model to investigate these environmental and physiological interactions. Preliminary results from this study have indicated that food availability may play an important role in determining how much crossbills will invest in survival (specifically immune function) and reproduction; e.g., crossbills will invest more in innate immunity and reproduction when food availability is high. Overall, results from this study will provide information on how species in general and crossbills specifically respond to rapidly changing environments, which has become increasingly important in light of the effects of anthropogenic change.

✦ INTRODUCTION

Understanding how organisms allocate limited resources between survival and reproduction is one of the most fundamental problems in biology (e.g., Zera and Harshman 2001; Martin et al. 2008). Nearly all environments on earth are dynamic, thus organisms must adjust physiology, morphology and behavior to adaptively allocate resources as selective pressures shift (Sinclair and Lochmiller 1999; Nelson and Demas 1996). Seasonally breeding taxa provide insight into ways that multiple demanding processes can be maintained in the annual cycle (Zera and Harshman 2001). Generally, these species temporally segregate different components of the annual cycle and restrict the most demanding processes to times

Figure 1. Red crossbill on Lodgepole Pine at the AMK ranch (picture courtesy M. Drouilly).

when resource availability is high and environmental conditions are benign (Menaker 1971; Gwinner 1986; Lochmiller and Deerenberg 2000). However, such taxa provide limited opportunities to reveal how physiological costs of different organismal processes may interact with environmental conditions to influence the evolution of investment strategies, mainly because certain combinations of conditions and organismal activities never occur in these species (e.g., breeding in winter). Consequently, our knowledge of how harsh environmental conditions and reproductive effort may interact to shape investment in survival remains limited. Thorough evaluation of this interaction would benefit from a study system where investment in reproduction and survival is facultative across extremely divergent environmental conditions, allowing for a more direct assessment of how demands imposed by physiological processes and environmental fluctuations influence the evolution of life history-related investments. Additionally, more long-term field studies of free-living organisms are essential as they provide a more ecologically relevant context than the more common captive studies and may illuminate novel, transformative environmental or physiological variables that should be considered when designing future studies focusing on these tradeoffs.

Red crossbills (*Loxia curvirostra*, Figure 1) are temperate zone songbirds that display exceptional temporal flexibility of breeding, despite highly seasonal changes in weather (Adkisson 1996), and can be found in Grand Teton National Park every year (Kelsey 2009). In years of high food availability (i.e, conifer seed availability) these birds can breed on the shortest days of the year when conditions are extremely thermally challenging, and on the longest days of the year when thermal conditions are benign (Benkman 1987; Hahn 1998). In contrast, they may not breed at all in either season if food availability is low. Investment in reproduction is therefore facultative and is more closely related to annual changes in food availability (i.e., conifer seed abundance) than seasonal changes in thermoregulatory challenges (Benkman 1987, 1990; Hahn 1998). Energy costs and selective pressures, however, are sure to differ across seasons, making crossbills ideal for exploring how changing environmental conditions (i.e., temperature and food resources) and physiological costs (i.e., breeding, immune function, etc.) influence the balance of investment in reproduction versus survival.

✦ ENVIRONMENTAL CONDITIONS

Large seasonal fluctuations in day-length, temperature and precipitation characterize the north-temperate zone and contribute to low food availability during the short, cold days of winter. Energy demands of thermoregulation are higher in the winter and may prohibit investment in reproduction in many species (Nelson and Demas 1996). Crossbills, however, specialize on conifer seeds which typically increase in availability throughout summer as new cones develop, peak in early autumn as cones mature, and then decline throughout the winter and spring as seeds fall from the cones and are consumed by seed predators (Adkisson 1996). The quantity of new cones produced is highly variable across years (Fowells 1965). Crossbills, therefore, depend on a food supply that is variable and often uncoupled from seasonal changes in temperature or precipitation (Benkman 1987; Hahn 1998).

Reproduction

Reproduction is very energetically costly in birds and mammals but is essential to fitness (Nelson and Demas 1996; Speakman 2008). Significant energetic investment is required for attracting and keeping a mate, producing, laying and incubating eggs, and provisioning nestlings (Monaghan and Nager 1997). In addition, investing energy into increased fecundity or parental care in one breeding cycle might subsequently affect survival and future reproduction (Dhondt 2001).

Survival-enhancing processes

Many processes contribute to survival in animals. Some of these, however, are particularly sensitive to resource allocation adjustments. These include:

Immune Function: The immune system can be categorized along an innate (nonspecific)-acquired (specific) axis and a constitutive (noninduced)-induced axis (Schmid-Hempel and Ebert 2003). An organism's optimal immune defense strategies can vary among or within these axes depending on the current health of the individual and the current environmental conditions (Schmid-Hempel and Ebert 2003; Martin et al. 2008). For example, stress caused by inclement weather and low food availability during winter can be immunosuppressive, so animals may counteract these effects by investing more heavily in immunity and foregoing reproduction (Sinclair and Lochmiller 2000; Nelson and Demas 1996). Preliminary data on red crossbills indicate a trade-off between one aspect of innate immune function and reproduction in the summer during low cone years but not in high cone years. Thus, an interactive effect between reproduction and resource availability may be present even outside of thermally challenging conditions (Schultz unpublished data).

Plumage Molt: Animals must also allocate energy to the maintenance of the integument (e.g., plumage, pelage), which is critical for thermoregulation and predator avoidance. (Ling 1970). Approximately 30% of the entire body protein content is replaced in birds during molt.

Molecular and energy resources are in high demand and generally constrain molt to occur post reproduction and prior to the onset of migration or low winter temperatures (King 1978). Growth rates, however, can be adjusted if breeding occurs later in the summer or during times of food stress (Dawson 2004). Such adjustments may allow investment in other processes but may also affect survival if feather quality is diminished, particularly in non-migrant, north-temperate species that face harsh winters (Hinsley et al. 2003). These types of trade-offs are evident in crossbills. Preliminary data show that crossbills investing heavily in body molt have lower innate immunity than crossbills not in body molt (Schultz unpublished data).

✦ RESEARCH APPROACH

The Hahn lab has studied how cardueline finches orchestrate their annual schedules of various demanding and potentially conflicting processes to contribute to survival and/or reproductive success for over twenty years. To contribute to this ongoing long-term study of the annual schedules of cardueline finches, this project includes direct assessment of patterns of investment in immune function in red crossbills. How crossbills regulate investment in a survival-enhancing process like immune function when breeding, not breeding, and while molting under diverse environmental conditions is not currently known. To evaluate these hypotheses we are employing multiple field and lab techniques including: 1) longitudinal field survey of crossbills during two environmental extremes in winter and summer, 2) reproductive physiology measured by a) size of cloacal protuberances and brood patches in males and females, respectively, b) a lavage of the cloacal protuberance to collect semen and measure presence of spermatozoa, and c) utilizing hormone profiles (androgens and estradiol) extracted via a competitive binding radio-immuno assay (RIA) from blood samples, 3) two immune function assays to measure immunocompetence and to assess parasite load, and 4) investment in plumage molt measured by examining the presence of growing primary, secondary, and body feathers. This research addresses two hypotheses (described in detail below) including the environmental constraint and physiological constraint hypothesis- all of which aim to answer how both external environmental (Objective 1) and internal physiological states (Objective 2) affect the timing and nature of investment in reproduction and survival.

Hypotheses tested:

Environmental Constraint Hypothesis: Temporal and spatial variation in availability of resources and in environmental challenges are the primary determinants of the survival/reproductive investment balance.

Physiological Constraint Hypothesis: Limits to physiological capacity are the primary determinant of the survival/reproductive investment balance.

✦ STUDY AREA

In Grand Teton, crossbills can be located throughout the park, but tend to be concentrated in areas of specific conifer densities (Kelsey 2008). The park's dominant conifers are lodgepole pine (*Pinus contorta*), Douglas-fir (*Psuedotsunga menziesii*), Engelmann spruce (*Picea engelmanii*), blue Spruce (*Picea pungens*), and subalpine fir (*Abies lasiocarpa*). Specifically, we catch crossbills in areas that vary in the relative dominance of the conifers that are important food sources for types 2-5 of red crossbills: lodgepole pine, Douglas-fir, and Engelmann and blue spruce. Data were collected in 2010 and 2011 in the areas of Jenny Lake, Death Canyon, Signal Mountain, String Lake, and at the UW-NPS AMK Ranch.

✦ METHODS

The respective permitting authority has approved project methods. Animal capture and manipulation protocols have been approved by the University of California, Davis Institutional Animal Care and Use Committee (IACUC) and is conducted under a permit obtained from both Grand Teton National Park and the state of Wyoming in the summers of 2010 and 2011, and renewed for 2012.

Objective 1: How do external environmental conditions constrain the timing and nature of investment in reproduction or survival? To assess the effect of local environmental conditions on physiological investment patterns in the crossbill, we are measuring three key environmental variables: 1) average daily temperature, 2) precipitation levels, and 3) food availability during two environmental extremes where crossbills are likely to reproduce: winter and summer.

Capture Methods: We attract crossbills using live caged decoys. Decoys call loudly when they hear birds of their own type (Groth 1993), and birds are caught in mist nets when they approach the decoys (See Figure 2). We also supplement vocalizations from the decoy with playbacks of crossbill vocalizations. From each bird captured, we collect approximately 200 *u*L of blood into a pre-sterilized, heparinized capillary tubes and centrifuge the blood and freeze plasma at -20°C until hormone and immune assays.

Local Weather Conditions: Average daily temperatures and precipitation for the Grand Teton area are gathered from the NOAA High Plains and Western Regional Climate Centers. The NOAA/NWS Cooperative Observer 15-minute Precipitation Network is an example of a NOAA climate center that provides us with local weather information. The NOAA/NWS routinely collects 15-minute observations of precipitation from Fisher-Porter and Universal rain gages operated by cooperative observers located throughout the US (53 in Wyoming). These data are archived at NOAA/National Climatic Data Center (NCDC).

Figure 2. Mist Net setup with live decoys in winter and summer.

Cone Crop (food availability assessment)

Cone crop size is scored for all conifer species at each location and trap site (at 12 different long-term point-count sites established in 2006 by T. R. Kelsey and maintained annually since then) on a cone abundance index of 0 to 5 as used by the U.S. Forest Service. We score the cone crop on 10 trees of each species within each of four directional quadrants (NE, SE, SW, NW) from every place of capture.

Investment in Survival:

1. Immune Function: For this field study, we are measuring innate immune defense and constitutive adaptive defense using two different assays that probe different aspects of the immune system.

2. Plumage Molt*:* Pre-basic molt occurs seasonally in red crossbills (e.g., June through November) and may be arrested during summer breeding (Adkisson 1996). Molt of the nine primary flight feathers proceeds sequentially from wrist to wingtip. Molt progress will be scored as the nearest tenth of the most distally growing feather on a scale from 0.0 (not yet begun) to 9.0 (last primary fresh and finished growing) (Hahn 1995). We define active molt as having at least one feather growing (feather dropped,

Figure 3. Looking for the presence of a brood patch in a female crossbill.

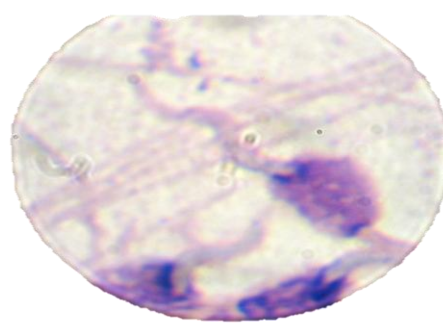

Figure 4. Male crossbill sperm taken from cloacal lavage.

in pin, or still growing).

Assessing Reproductive Investment:

Cloacal protuberance (CP) length in free-living male red crossbills significantly predicts testis length and therefore offers a non-invasive estimation of reproductive status (Cornelius 2009; Wingfield and Farner 1976). Males with cloacal protuberance lengths of 5 mm or larger are categorized as having high reproductive potential; males with cloacal protuberances of 3 to 5 mm are medium, and 3 mm or less are considered low (Cornelius 2009; Wingfield and Farner 1976). In female red crossbills, brood patch (BP) stage significantly predicts ovary condition (Cornelius 2009; Wingfield and Farner 1976). Females with brood patches > 0 are considered high, whereas females with brood patches=0 or below are considered low reproductive potential. Briefly, a dry and fully feathered breast scored a 0; a dry but bare (i.e., without feathers) breast scored a 1; a bare breast with increased vascularization and/or mild edema scores a 2; a bare, vascularized breast with full edema scores a 3; and a bare and wrinkly breast scored a 4 (i.e., post-full edema) (Cornelius 2009). Because estimations of cloacal protuberances and brood patches are not a perfect prediction of reproductive condition, we supplement this data with: 1) lavage of the cloacal protuberance to collect semen and measure presence of sperm (see Figure 4), 2) utilizing hormone profiles (androgens and estradiol) extracted via a competitive binding radio-immuno assay (RIA) from blood samples.

Objective 2: How does internal physiological state constrain the timing and nature of investment in reproduction or survival?

To measure the effect of an individual's internal physiological conditions on its investment in either reproduction or survival (these methods described in detail above), we use parasite load, body condition, and innate immune function.

Assessing Parasite Load: We use approximately 5 *u*L of blood to make one blood smear per individual, which is stained (Wright-Giemsa) for later inspection for blood parasites such as *Haemoproteus*, *Microfilaria*, and *Leukocytozoan*. Recent data have indicated that *Haemoproteus* is the most prevalent blood parasite and has wide variation in infection rate among individual red crossbills caught in Grand Teton National Park (Figure 5).

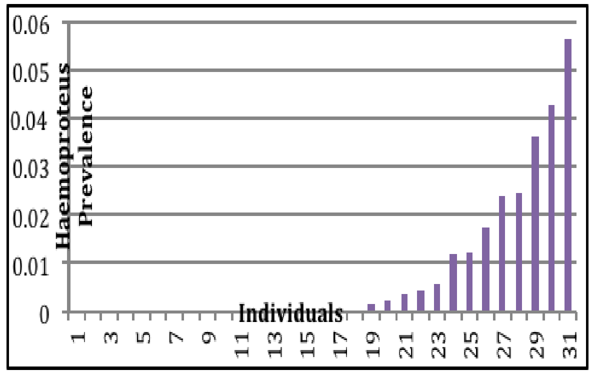

Figure 5. *Haemoproteus* prevalence across individuals in summer 2010.

Assessing Physical Condition: We calculate body condition by regressing body mass against physical size. Physical size is determined by measuring individuals for wing and tarsus length, keel, bill length, bill depth, and bill width using digital calipers and compiled by a principle component analysis (PCA). A positive residual between body condition and physical size is assumed to indicate higher body condition than negative residuals (Nolan and Ketterson 1983). Additionally we take measures of hematocrit from the blood, which can be interpreted

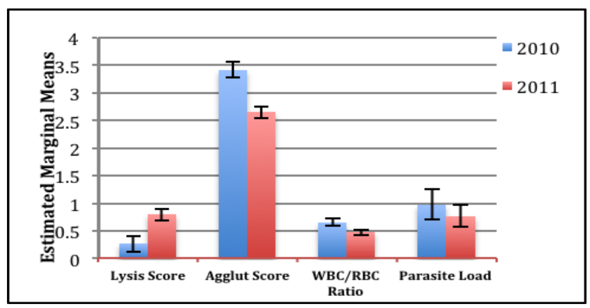

Figure 6. Immune Parameters from high (2011) and low (2010) cone years. Analyses corrected for Julian date and

as a measure of physiological condition and performance (Mills et al. 2008).

✦ Preliminary Results

Not all data collected from 2010 and 2011 has been analyzed. Hormone assays to measure androgens and estradiol as an assessment of reproductive condition will be completed funds pending. Data collected this winter will be analyzed this spring to be reported in next year's annual report.

How red crossbill physiological investment in immune function (survival) and reproduction are affected by food availability in a high (2011) and low (2010) cone year:

In summer of 2010 and summer and fall of 2011, Schultz (co-PI) ran a hemolysis-hemagglutination assay on the blood plasma of 32 and 68 red crossbills, respectively. 2010 was an extremely low cone year (cone crop score 0-1), while 2011 was a very high cone year (cone crop score 4-5). The hemolysis-hemagglutination assay uses a serial dilution of plasma and rabbit red blood cells to measure the activation of humoral component of constitutive innate immunity, specifically measuring complement levels via lysis ability and natural antibodies via agglutination level (Matson et al. 2005). When comparing a low to high cone year, in a low cone year (N=32), the average lysis score (complement level) of crossbill plasma was significantly lower (p=0.03) than in a high cone year (N=68), which could indicate that crossbills are able to maintain higher innate immunity in years with large cone crops (Figure 6). Agglutination levels were significantly lower in 2011 (p=0.001), which given that natural antibodies (agglutination score) serve as recognition molecules that initiate the complement enzyme cascade by agglutinating foreign cells, which ends in cell lysis, higher agglutination levels in 2010 do not equate to higher immunity (Matson et al. 2005). Crossbills caught in 2010 had significantly higher white blood cell/ red blood cell ratios (p=0.02). Elevated white blood cell/ red blood cell ratios can indicate an inflammatory response (Campbell 2007), which taken together with the lysis and agglutination scores can indicate that crossbills had lower innate immunity in 2010. Lastly, parasite loads (levels of *Haemoproteus*) were not significantly different between years (p>0.5), indicating that birds were similarly infected with these blood parasites regardless of year and immune status.

When comparing male reproductive potential and their average lysis score, males with high reproductive potential (large cloacal protuberances, see methods above) experienced a significant (p=0.04) tradeoff with innate immunity (lysis score) only in low cone years, suggesting that it may be more costly to breed in years with low cone availability for males (Figure 7). While female red crossbills are incubating eggs and nestlings, males feed not only themselves but also their incubating female (Adkisson 1996). Thus, having to spend significant more time foraging for food could increase the energetic demand placed on males during reproduction, which could potentially explain why this tradeoff is more pronounced in males than in females.

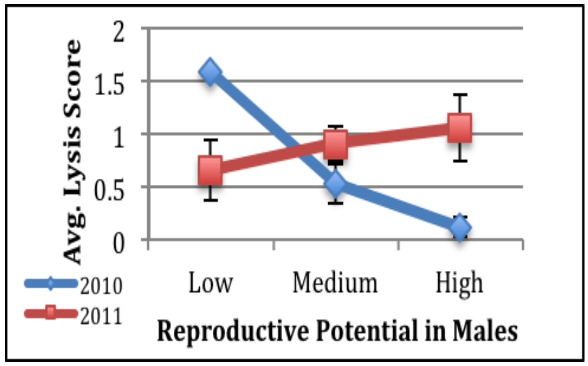

Figure 7. Average lysis score increases with male reproductive potential in 2011 and decreases in 2010 (p=0.04). No significant difference in females (p=0.469). Agglutination, WBC/RBC, and Parasite Load did not vary significantly (p>0.1) with reproductive condition in either year in males & females.

✦ CONCLUSIONS

The data presented above best support the **environmental constraint hypothesis**, which states that temporal and spatial variation in availability of resources and in environmental challenges are the primary determinants of the survival/reproductive investment balance. 2011 had higher food availability (higher cone crop score) than 2010, and crossbills caught during 2011 had overall higher innate immunity than those caught in 2010, suggesting that when resources are plentiful, crossbills are able to allocate more energy to survival (immune function), even while in reproductive condition.

How red crossbill physiological investment in plumage molt affects investment in innate immunity in a high cone year (2011). As mentioned above, plumage molt is an energetically expensive time for birds, particularly body molt. No significant differences in immune function were found among birds molting their primary or secondary feathers (p > 0.5), but significant differences were found among birds molting their body feathers (p=0.05, n=17) than those not molting their body feathers (N=50) in 2011 (Figure 8). Specifically, crossbills in body molt had significantly lower lysis scores than those not in body molt, indicating a potential trade-off between two survival-enhancing processes.

The data presented above best support the **physiological constraint hypothesis,** which states that limits to physiological capacity are the primary determinant of the survival/reproductive investment balance. Even during a year of high food availability (2011), crossbills molting their body feathers invested

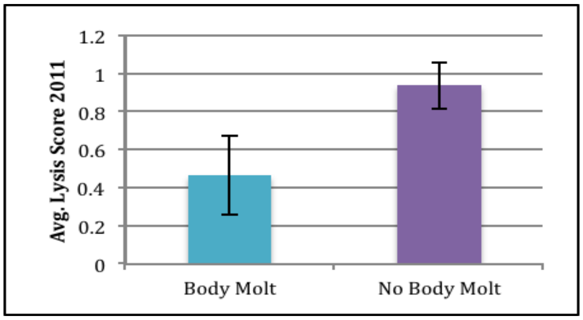

Figure 8: Average lysis score of both sexes affected by molting of body feathers in 2011 (p=0.05). No significant difference in 2010 (p=0.742).

less in innate immunity (lower lysis score) than those not molting their body feathers, suggesting that how much a crossbill invests in immunity (survival) is limited by this physiological process.

✦ BROADER IMPACTS

The timing and investment in various life history stages have been more extensively investigated in seasonally breeding organisms, with most of these studies focusing on captively breeding animals (Martin et al. 2008; Nelson and Demas 1996; Lee 2006). Historical emphasis on captive, seasonal breeders may have led to misconceptions regarding whether trade-offs alone can explain fluctuations in physiological processes such as immune function in natural systems (Martin et al. 2008). Thus, we are limited in our ability to answer questions that involve how demanding environmental conditions may affect investment decisions specifically in regards to reproduction because seasonally breeding animals typically breed only when environmental conditions are benign. By studying organisms that are able to reproduce in harsh environmental conditions such as opportunistic breeders, we will gain more insight into potentially alternative physiological mechanisms that regulate the timing and investment in survival and reproduction. Finally, understanding how species effectively allocate resources to competing physiological processes is becoming increasingly important in light of recent anthropogenic changes. Anthropogenic effects such as habitat and climate modification can either accelerate the rate at which life history strategies evolve or hasten the extinction of species that are not able to quickly adapt (Wuethrich 2000; Hughes 2000).

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