Running Head: Status Badge Signaling

Functional importance of plumage badges as intraspecific signals in White-crowned sparrows (*Zonotrichia leucophrys oriantha*).

By

Zach Laubach

A Thesis Submitted in Partial Fulfillment of the

Requirements for the Degree of Master of Science (Natural Resources and Environment)

At the University of Michigan

August 2010

Thesis Committee:

Professor Johannes Foufopoulos, Chair

Professor Bobbi Low

Abstract

Status badges, such as bird plumage colors, are important parts of animal communication; they mediate intra- as well as intersexual interactions. Reliability of avian plumage badges is thought to be maintained by selective pressures, including social punishment. Costs, benefits, and resultant fitness tradeoffs are thought to maintain reliable status badges as evolutionarily stable signals. We tested this hypothesis during two breeding seasons (summers 2008-2009) in a population of Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*; MWCS) in Colorado (USA). Both sexes of this species possess a black and white striped crown that mediates interactions between juvenile and adult birds. Crown whiteness, expressed as the percentage of the crown that consists of white feathers, varies widely across individual sparrows.

To test whether the reliability (the consistent transfer of information relating signal design and content) of crown whiteness in males is maintained by social punishment, we examined cost and benefits associated with experimentally manipulated phenotypes. We predicted status badge related tradeoffs to sender condition and social interactions. We conducted a series of territory intrusions / call playbacks using male sparrow decoys with manipulated crowns to measure social punishment costs. Resident MWCS males received two simulated territorial intrusions by the same mounted decoy (once with a 'white-enhanced' and once with a 'white-reduced' crown treatment; these were presented in random order on different days). Males responded with significantly increased aggression when presented with white-enhanced decoys.

In a parallel experiment we tested the prediction that crown whiteness is (1.) associated with sender condition and variation in levels of corticosterone and (2.) under sexual selection. That is, we predicted that males with whiter crowns would gain reproductive benefits (measured as number of fledglings). In these experiments we experimentally enlarged or reduced the proportion of whiteness in males' crown feathers. Crown manipulations had no significant effect on baseline, nor on post-stress series corticosterone levels. While there was a trend for more offspring in males with white-enhanced crowns, this relationship was not significant due to small sample sizes of recovered nests. Our data provide support for the social punishment hypothesis, yet show no significant relationship between stress response and crown characteristics. Social costs are therefore at least partially responsible for maintaining the reliability of crown whiteness as a status badge in male MWCS.

Acknowledgements

There is a long list of people to whom I am greatly indebted for their patience and support throughout my research experience. Although a formal thanks is hardly enough I would like to express my most sincere appreciation to the following people who have been involved in some way with my research and pursuit of a degree: my advisor, Dr. Johannes Foufopoulos and the Foufopoulos lab, committee member Dr. Bobbi Low and the Bobbi lab, Greg Sampson for help collecting data, Kathy Welch for statistical support, Dr. Dan Blumstein for behavioral ecology advice, Dr. Michael Romero for lab use and hormone analysis advice, Laura Glassman for much help running hormone assays, Dr. Courtney Murdock for advice from her experience researching the MWCS system, Dr. Ian Billick and the staff at RMBL, Dr. Jim Diana for countless amounts of graduate school advice, Dr. Jacinta Beehner and Dr. Sushama Pavgi for hormone discussions, Dr. Elizabeth Tibbetts and Dr. Peter Bednekoff for behavioral ecology/signal discussions, my brother Isaac Laubach for volunteering with field work, my field assistants in 2008 and 2009, Rackham Graduate School for funding, The School of Natural Resources and Environment at University of Michigan for funding, and especially my family for continued support.

Table of Contents

1. **Introduction**
    a. *Basics of Signaling*
    b. *Interest*
    c. *Efficacy*
    d. *Costs*
    e. *Agonistic Signaling*
    f. *Status Badges*
    g. *Previous Similar Studies*
2. **Questions and Predictions about Costs**
    a. *Sender Condition: Morphologic and Physiologic Predictions*
    b. *Receiver Response: Cost of Reliability*
    c. *Female Choice: Signal Convention Reinforcement*
    d. *Hypotheses*
3. **Methods**
    a. *Field Site*
    b. *Study species: Mountain White-crowned sparrow (Zonotrichia leucophrys oriantha)*
    c. *General Field Methods*
    d. *Crown Painting Manipulations*
    e. *Blood sample collection and steroid hormone assays*
    f. *Decoy Challenges*
    g. *Isolation of Signal and Receiver-dependent Cost*
    h. *Reproductive success*
    i. *Statistical analyses*
4. **Results**
    a. *Sender Condition: RHP and Breeding Season Hormone Profile*
    b. *Behavioral Response to Decoy Challenge*
    c. *Effects of Crown Manipulation on Reproductive Success*
5. **Discussion**
    a. *Status Badges*
    b. *Interest and Efficacy*
    c. *Costs, Benefits and Resultant Fitness Tradeoffs*
    d. *Final Remarks*
6. **Tables and Figures**

Introduction

Basics of Signaling

Animal signaling functions as a means of communication between the signal sender and the receiver (e.g., Krebs & Dawkins 1984, Endler 1993, Johnstone 1997). By definition, signaling involves a transfer of information through an environment via olfactory, visual or aural communication (Endler 1993). A clear transfer of information between emitter and receiver occurs when signal exploitation is minimal (Otte 1974, Endler 1993; Fig. 1)**.** Signals are widespread in nature; they serve as important mediators of inter- and intra-species communication (Sebeok 1965). Signal evolution is maintained by selective pressures affecting individual fitness (Darwin 1859)**.**

Signals have two main components: the design or physical structure, and the content or information that influences sender and receiver strategies (Endler 1992)**.** The evolution of both design and content of signals is influenced by three factors: (1) signaling *interest,* the degree of conflict or cooperation between sender and receivers during signaling, (2) *efficacy*- the transmission efficiency, particularly in relation to receiver response, and (3) *costs*, benefits and resultant fitness tradeoffs associated with the signal (Dawkins 1993). These selective pressures shape the diversity of animal signals by relating signal design and content. The reliability of information communicated is affected by fitness tradeoffs associated with the signal, as well as differences in sender and receiver strategies (Smith 1974, Dawkins 1993, Searcy & Nowicki 2005). Using the three aforementioned selective factors (interest, efficacy, and costs), we can begin to organize and isolate aspects of signal function and evolution.

Interest

Senders and receivers have interests that are *similar*, as in predatory alarm signals, or *opposed*, as in aggressive or territorial disputes (Krebs & Dawkins 1984). The first step to investigating reliability and function of animal signaling involves clarification of interest; *why* signal in the first place? Aside from the possibility of true altruism, a signal sender's interest is to improve its own fitness (Alexander & Borgia 1978). The results of the signaling interaction may either improve or negate the receiver's fitness. When the fitness of both increases, we say the interest is similar. On the other hand, signals that improve emitter fitness but decrease receiver fitness involve opposed interest. Opposed interest is characteristic of agonistic contests (Caryl 1979, Enquist 1985, Senar 1990).

Efficacy

Efficacious signals communicate information efficiently; they will tend to elicit increased sensitivity and reaction in receiver response (Searcy & Nowicki 2005). Signals degraded through the environment or ignored by receivers are ineffective and will become vestigial over time (Guilford & Dawkins 1991). In addition to the cost necessary for signal detection (due to the signal efficacy), sender signal reliability is maintained through variable additional costs (Smith & Harper 2003). Signals are subject to a variety of marginal costs (e.g. physical condition or social status), and bigger signals pay higher prices. In other words, at equilibrium, the payoff resulting from signaling for evolutionarily fit individuals outweighs the marginal costs needed to send the signal (Johnstone & Grafen 1992). However, the costs associated with bigger signals constrain some portion of the population.

Costs

Costs, benefits, and the resultant tradeoffs matter because they underlie how a signal's design is tied to the information or content that the signal communicates. Some signals, such as sexually selected traits, convey information about the reproductive fitness of the sender. Weapons (such as antlers of a male deer) represent traits that involve high energetic expenses, but have high payoffs in life-and-death battles (Geist 1966). Similarly, sexual ornamentation (such as plumage on a peacock) also provides information regarding the sender's ability to pay nutritional, energetic, and physiological costs (Veiga & Puerta 1996, Keyser & Hill 1999, Viljugrein 1997). Signals directly related to production costs cannot be cheated (Guilford & Dawkins 1995, Smith & Harper 2003). Signal sender condition is also communicated through tradeoffs unrelated to signal production such as size, social status, immune function, and physiological characteristics (Røskaft et al. 1986, Hamilton & Zuk 1986, Veiga 1993, Qvarnstrom 1997, and Rowher 1975**)**. Costs, benefits and resultant tradeoffs which are related to sender condition limit signaling and support the handicap principle (Zahavi 1975, 1977). However, the tradeoffs associated with some signals are not exclusively dependent on emitter condition. In these scenarios different signaling strategies for individuals of varying physical condition will optimize fitness (Graffen 1990).

We can better understand signals after delineating the currencies in which different costs are paid and the variation in individual fitness tradeoffs (Johnstone & Grafen 1992). Multiple nomenclature schemes are used to describe differences in the information transferred when signals are used. Three terms reflect context-dependent interactions subject to change, based on condition and aggressiveness of signal senders and receivers: *choice actions* (Enquist 1985), *purely conventional signals* (Smith et al. 1988), and s*trategic choice handicaps* (Grafen 1990). On the other hand, resource-*holding power/potential* (RHP) (Parker 1974), *performance actions* (Enquist 1985), *assessment signals* (Smith et al. 1988), and *condition-dependent handicaps* (Graffen

1990) are all phrases that indicate invariable physical ability. A brief overview of signaling semantics reveals the bottom line; selective pressures relate signal designs and content for an Evolutionary Stable Strategy (ESS) (Smith 1974). ESS signals at equilibrium are influenced by fitness tradeoffs related both to performance constraints and to strategic choices that occur during contests (Hurd & Enquist 2005).

Agonistic Signaling

Agonistic signaling occurs during contests of conflicting interest over a resource (Caryl 1979, Krebs & Dawkins 1984, Enquist 1985). The costs, benefits, and resultant tradeoffs resulting from contests of agonistic signaling reinforce the system's reliability (Enquist 1985, Graffen 1990, Senar 1990)**.** Agonistic signals include what are referred to as 'cheap' or 'conventional' signals, due to their energetically inexpensive production cost (Smith et al. 1988, Guilford & Dawkins 1995). However, sender condition can still be communicated if previous experience or a pre-conditioned set of social norms imbue the 'cheap' signal with quality-relevant information (Dawkins 1993). Aspects of receiver psychology and contest asymmetries that include both motivation and fighting ability complicate the investigation of these signaling systems as evolutionarily stable strategies (Smith & Parker 1976, Guilford & Dawkins 1991). In conventional signaling involving strategic choice, reliability may derive from costs imposed by the receiver through social punishment (Smith et al. 1988, Dawkins 1993, Guilford & Dawkins 1995, Deag & Scott 1999).

Status Badges

Status badges (Krebs & Dawkins 1984) are considered conventional signals (Smith et al. 1988, Guilford & Dawkins 1995) that involve resource discrepancies between sender and receiver (Dawkins 1993, Searcy & Nowicki 2005). Status badges are relatively cheap to produce, with costs that are primarily dependent on social contexts, like receiver punishment (Rowher 1975). Examples of such badges include color markings or other subtle designs that convey social status (Rowher 1977). Badges mediate agonistic contests by signaling asymmetries in intent or motivation to fight, as well as genuine fighting ability (Smith 1976). Reliable badge variation provides a signaling convention which mediates contests and minimizes costs (Smith et al. 1988). Status badges are an ESS if they reliably relate signal design and content in terms of receiver-dependent costs and correlated aspects of sender condition (Enquist 1985, Johnstone & Norris 1993, Hurd 1997). Badges are an interaction handicap involving sender's fitness tradeoffs including costs inflicted by receivers (Hurd & Enquist 2005). Status badge variation promotes a social hierarchy communicated through signal size or intensity (Rowher 1975, 1977). However, the badge itself is not an assessment signal; that is; it is not solely constrained by physical or physiological costs to the sender, leaving the system susceptible to cheating (Smith & Harper 2003).

Why then do animals not display unreliable badges in lieu of self-propagation during agonistic interactions? Understanding badge reliability requires distinguishing different costs, benefits and resultant fitness tradeoffs. Status badges may involve fitness tradeoffs related to sender-dependent conditions and receiver-dependent social interactions (Johnstone & Norris 1993, Searcy & Nowicki 2005). Such tradeoffs involve correlated individual-emitter conditions (behaviors or a physical quality like size or hormone levels), social punishment from receivers, and preferential female choice (Smith et al. 1988, Johnstone & Norris 1993, Johnstone 1997). Costs and benefits fluctuate depending on the context of the signaling interaction continually changing the contested resource's relative value.

Context dependence is influenced by the *value* of the contested resource and an individual's *ability* to access that resource, known as RHP (Resource Holding Potential;

Parker 1974). Increasing resource value means greater incentive to pay higher cost (Gherardi 2006, Tibbetts 2008). For each individual, access costs and payoffs underlie fitness, making context important for interactions involving status badges (Tibbetts 2008). Put in lay terms, a resource of low value gives a low potential payoff. Thus, for resources of low value, escalating costs would be detrimental to both contestants as it quickly negates potential benefit to either party. On the other hand, when contesting high value resources, the interaction may no longer rely on badge signaling and often resort to tests of RHP and aggression. In contexts where high costs and payoffs exclude all but fit individuals, status badge cheaters will be detected through an incongruence of signal and emitter condition (Rohwer 1977, Tibbetts 2008).

In a reliable system, individuals displaying the biggest or most elaborate badges possess the highest value resources (Ketterson 1979, Rowher 1985, Studd & Robertson 1985, Møller 1987a, b, Røskaft & Rowher 1987, Whitfield 1987). Status badge cheaters are detected when resource value is high and similar signals meet because increased aggression exposes the cheater's weaknesses (Smith et al. 1988). The best fighters inflict costs on similar signaling competitors in a test of signal legitimacy termed like-versus-like social punishment (Rohwer 1975, 1977). Escalated challenges occur most commonly between senders and receivers of similar signals (Enquist 1985). When challenges escalate beyond conventional signaling, detection of incongruence between RHP and signal status can occur (Rowher 1977). Thus, reliability derives from tradeoffs that expose and minimize cheating in an ESS. A reliable system of badge status signaling requires a demonstration of like-versus-like social punishment (Rohwer 1975, 1977, Ketterson 1979, Enquist 1985, Smith et al. 1988).

In summary status badges are reliable because signal cheating entails paying the maximum cost (Ketterson 1979, Slotlow et al. 1993). Signals that disclose information about aggressiveness and RHP prior to escalating a challenge prevent both contestants- especially the one with less RHP- from paying unnecessary costs (Rowher

1982). At equilibrium, there are lower marginal costs to signaling for higher quality individuals (Johnstone & Graffen 1992). Only the highest-quality individuals can afford to pay the highest costs (Smtih et al. 1988, Searcy & Nowicki 2005). Tradeoffs related to social punishment and possible injury prevent cheaters from entering the population (Studd & Robertson 1985), and maintain the ESS. Contexts inciting social punishment and that test the correlation between the signal and sender condition uphold signal reliability (Rohwer 1985, Hurd 1997, Searcy &Nowicki 2005, (Gehardi 2006). Status badges are an ESS at equilibrium if signaling is reliable, and cheating is prevented through tradeoffs effecting fitness (Grafen 1990, Smith & Harper 2003).

Previous Similar Studies

Preliminary information from white-crowned sparrows and related taxa suggest that crown traits are critical mediators of social interactions (Parsons & Baptista 1980, Fugle et al. 1984, Watt 1986, Fugle & Rothstein 1987, Keys & Rothstein, 1991, and Slotlow et al. 1993, Slotlow & Rothstein 1995a,b). In wintering flocks of Gambel's white-crowned sparrows (*Z. l. gambelii)* crown characteristics- and not age- were found to be the main communicator of social status (Parsons & Baptista 1980). Another study found that painting brighter crowns on juvenile and adult female sparrows resulted in modified birds being more successful in aggressive encounters than controls (Fugle et al. 1984). Fugle's experiments suggest that crown brightness is an indicator of relative RHP between different ages, as well as sex groups. In a later experiment, painting crowns of immature birds brighter aided in successful status cheating within their age group. However, successful cheaters did not appear to receive more aggression from dominant adult males, making successful cheating 'cost-free' (Fugle & Rothstein 1987). Finally, in a study that evaluated dominance hierarchy in un-manipulated birds within their wild wintering flocks, it was found that white-crown sparrows showed dominance hierarchy at feeding sites. Adult males were the most dominant, followed by adult female, juvenile male, and juvenile female, respectively (Keys & Rothstein 1991).

These studies demonstrate that crown signals may be beneficial in terms of resource access without any obvious cost to cheaters. In the context of wintering social groups, there are no apparent tradeoffs for signaling that would maintain reliability. The status signaling hypothesis is not upheld among white crown sparrows (Slotlow et al. 1993). However, these studies do demonstrate that crown characteristics of white crowned sparrows are involved in the communication of resource holding potential (RHP) as related to age and sex during winter flocking (Watt 1986, Slotlow & Rothstein 1995a,b). We suspect that the proportion of white to black coloring on Mountain white-crowned sparrows (referred to as ‘crown whiteness’) (Fig. 2) will be associated with tradeoffs during the breeding season confirming the reliability of this signal as a status badge.

Here, we investigated whether there was a phenotypic signal design that mediated intraspecific communication during the breeding season for the MWCS. If so, is this status badge maintained with minimal exploitation or cheating. Specifically, we were interested in the *reliability of the content of crown whiteness* as a functional communication device. We investigated the costs, benefits and resultant tradeoffs acting as selective pressure on the evolution of crown whiteness. To achieve these aims we evaluated correlates of emitter condition, receiver response, and reproductive success as related to female choice for male crown plumage during the breeding season.

To determine whether the proportion of crown whiteness signaled by male MWCS meets the requirements of status badge theory within the limits of an evolutionarily stable strategy, we considered the influence of principle selective pressures, including contestants’ interests, efficacy, and tradeoffs associated with crown whiteness as a signal. Because fitness tradeoffs were the greatest unknown, we devised a series of experimental questions and predictions grouped into three logical categories. These categories include emitter conditions (measures of morphology and physiology), receiver response (measured as behavioral focal observations), and reproductive success. The costs and benefits were studied in a population of MWCS independently during two consecutive field seasons. Each of the three aspects of our study hypothetically demonstrates how costs affecting fitness influence the content underlying a signal design in a functional signaling system (Fig. 3). Figure 3 ties together the three different experiments we conducted and helps explain how signal *design* is related to signal *content* in an evolutionarily stable status-signaling system. Before discussing questions and predictions, we need to justify the signal system as a logical choice to study.

Crown plumage is a signal used to delineate social hierarchies (Keys & Rothstein 1991). Crown whiteness is used in competitive situations where sender and receiver demonstrate opposing interests. Furthermore, signals confined to head or breast suggest intraspecific communication in birds (Rohwer 1975). Based on previous work and general observations of crown use, we presumed that crown whiteness acted as a signal of opposing interest for MWCS in the context of a breeding season.

Next we asked, was crown whiteness efficacious? Crown stripes are a pattern of contrasting colors located on the head, the highest and most visually accessible part of the bird. Previous work showed receiver recognition of crown manipulations as demonstrated by adjusted behavioral response towards painted crowns (Fugle et al. 1984, Fugle & Rothstein 1987). This was coupled with field observations that noted MWCS flare their crown to exaggerate the whiteness during various signaling scenarios. With this evidence we presumed crown whiteness to be pervasive between individuals in their natural environment. Thus the most basic qualifications of a signal would be met, and crown whiteness would be detected by the receiver. Confirming the first two of three principle selective forces acting on signals, we were then prompted to investigate further possible costs, benefits, and resultant tradeoffs that would maintain the reliability of crown whiteness.

Questions and Predictions about Costs

Sender Condition: Morphologic and Physiologic Predictions

Status badges have condition-dependent correlated costs, in addition to evoking receiver-dependent punishment (Johnstone & Norris 1993, Guilford & Dawkins 1995). In other words, signal design is associated with information (content) related to sender condition. We predicted that condition-dependent tradeoffs would be correlated with crown plumage whiteness. Crown whiteness would be related to morphologic and physiologic fitness tradeoffs.

We considered possible correlations between crown whiteness and costly physical traits that provide an agonistic advantage for male MWCS. Larger physical size, coupled with physiologic adaptations provides an advantage when competing for territories (Røskaft et al. 1986, Goymann & Wingfield 2004). For example, increased size, while it facilitates higher RHP, presents a tradeoff between the costs of energetic expenses and the benefis of social status (Brown et al. 2005). Similarly, we expected hormonal response to be related to the signal design (Zuk et al. 1995, Douglas et al. 2009).

We predicted that naturally white-enhanced crowns would have lower baseline corticosterone levels and an attenuated corticosterone response to a stress treatment. Our prediction was based on the rationale that whiter crowns- associated with more physically fit individuals- should be better adapted to handle stressful situations (Wingfield et al. 1992, Roberts et al. 2007). Stress responses inhibit reproductive behavior while activating survival instincts (Wingfield & Silverin 1986). In the occurrence of a stressful event, plasma corticosterone (which has a higher binding affinity than testosterone to corticoid binding globulin) increases and enables unbound testosterone to be cleared from the system hepatically (Swett & Breuner 2008). We predicted that individuals with the highest RHP and the whitest crowns would have a down-regulated stress response in order to maintain high levels of testosterone (which is known to be associated with aggressive behavior) (Wingfield 1985). Sender condition reliability derives from enduring costs of reduced stress response inhibiting survival mechanisms, as well as testosterone related immunocompetence (Zuk et al. 1995, Douglas et al.2009). However, during a short and unpredictable breeding season, the ability to cope with hormone-related costs while focusing energy towards mating effort would imply a higher level of reproductive fitness (Schwabl et al. 1988)**.**

We also experimentally altered male MWCS crowns and measured corticosterone levels after releasing birds back into the wild population. We predicted that changing a male's social status from lower status to higher status would induce a stress response and increase baseline corticosterone levels. In this scenario, males whose crowns were painted whiter were put in a more permanent aggressive signaling state (they were basically cheaters). These males should have higher levels of plasma corticosterone, reflecting inability to handle increased social punishment.

Receiver Response: Cost of Reliability

We also measured receiver response to variations in crown whiteness during agonistic challenges. It was predicted that territory-holding males would recognize differences in crown whiteness, and that receivers would respond differently to different proportions of white in the crown. Different responses to variations in crown whiteness should confirm efficacy.

Additionally, we were interested in the type of reaction elicited from territory-holding males towards experimental variations in our decoys' crown whiteness. We anticipated that whiter and more aggressive-signaling crowns would elicit a more aggressive response. If receivers view enhanced crown whiteness as a signal of RHP, we expect them to respond more aggressively towards whiter crowns in a breeding season context. White-reduced crown signal would represent less of a threat to territory-holding males. We expected increased social punishment for enhanced crown whiteness, because fitness payoffs are heightened and territories are especially valuable during the breeding season. We predicted like-versus-like social punishment (Rohwer 1977, Slotlow et al. 1993). Territory-holding males would respond more aggressively towards other phenotypes which threaten their resource access (Møller 1987 a,b). Detection of behavioral incongruence and heightened aggressive response in a breeding season context provides evidence of crown whiteness reliability and verifies social status signaling.

Reproductive Success: Female Choice

Female choice suggests signaling as a strategy in sexual selection (Andersson 1994 and Barraclough et al. 1995). We evaluated the influence of female choice on crown whiteness and reproductive success. High quality males might attract higher quality females, and experience greater reproductive success (Andersson 1994, Anderholm et al. 2004, Yasukawa et al. 2009). If sender condition is reliable, conspecific selection may tie back into the signaling system (Johnstone & Norris 1993) (Fig. 3). We predicted that whitest-crown signals would offer direct benefits in the form of better territories or resources, which would improve reproductive success (Røskaft & Rowher 1987, Veiga 1993). Higher-quality and higher-status individuals may also increase indirect benefits for females who selected them as mates, such as improved heterozygosity and other genetic benefit**.**

To investigate these possibilities we looked for indication of female choice and reproductive success based on males signals (Lemon et al. 1992). Females vary in their reproductive potential; higher quality and more experienced females are able to fledge more offspring (e.g., Langston et al. 1990, Weimerskirch 1992,). We predict that these higher-quality females would select males with the most prominent signal. From this we expected a relationship between male crown whiteness and male reproductive success.

To evaluate other possibilities of sexual selection in addition to female choice, a number of morphological traits were investigated. Literature on the sexual morphology of MWCS is conflicting: some references assert they are monomorphic, while others claim they are dimorphic in terms of plumage (Parsons & Baptista 1980, Morton 2002). We aimed to investigate this further. We predicted that if sexual selection is indeed involved in the evolution and maintenance of this signal, then proportion of crown whiteness would be sexually dimorphic between sexes.

Hypotheses

To test these questions and verify our predictions, we developed three null hypotheses and complementary field experiments:

(1) Males with greater proportion of crown whiteness will demonstrate the same sender condition as the rest of the population. There will be no relation between badge size and RHP. Stress hormone levels and morphological correlates will not be related to badge size.

(2) Males with a greater proportion of crown whiteness will elicit the same

behavioral response as other males in terms of receiver-dependent social punishment.

(3) Males with higher proportion of crown whiteness will have no difference in terms of reproductive success compared to other males. Signal conventions will not influence female choice, which will be unrelated to badge signaling.

To test these hypotheses we looked at the proportion of crown whiteness as a signal during the breeding season in a high elevation MWCS population in Gothic, Colorado. Through a combination of physiological and morphological measures, behavioral observations, and experimental plumage manipulations we aimed to gain insight into the design and content of proportion of crown whiteness as a badge of status. This study addressed questions concerning the efficacy along with the costs, benefits and fitness tradeoffs of a status badge used when the interest of emitters and receivers are opposed**.** If indeed crown whiteness were a status badge and if the information communicated were reliable, signaling in a breeding season context would represent an ESS.

Here, we describe three experiments designed to understand the significance of crown whiteness as a badge of status for breeding MWCS and to elucidate how crown plumage mediates social interactions. The purpose of these experiments was to determine if this signaling system complimented the status badge theory and was maintained as an ESS.

Methods

Field Site

This study was conducted in the vicinity of Rocky Mountain Biological Laboratory located in Gothic (Gunnison Ct.), in central Colorado [38°57’33’N, 106°59’21’W]. Four pre-established study plots were situated along the East River within the Gunnison National Forest at an approximate elevation of 2,950m above sea level. Each plot was 600m long by 150m wide, following the natural contour of the meandering river valley and bisected by a seasonal road. Vegetation consisted primarily of alpine meadows interspersed with low willow thickets and bordered along the slopes of the valley by encroaching stands of aspen (*Populus tremuloides*) and coniferous forest (*Picea engelmanni* and *Abies lasiocarpa*).

Study species: Mountain White-crowned sparrow (Zonotrichia leucophrys oriantha)

To investigate factors that shape the evolution of a plumage trait as a possible status badge, we focused on the crown plumage of mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*; MWCS), a common passerine bird species. The species has emerged in recent years as an important model organism for avian physiology and a large number of studies have investigated various aspects of its life history (review in Morton 2002). Of particular interest was the specie’s striking black and white crown stripe pattern, and its potential to act as status signal. We investigated proportion of crown whiteness (Fig. 2) as a signal of status. Behavioral response was measured during agonistic contests between male MWCS during the breeding season context. We also measured morphologic, physiological, and reproductive correlates of crown manipulations.

We conducted this study on a population of Mountain white-crowned sparrows (MWCS - *Z. l. oriantha)* breeding in the high elevations of the Colorado Rocky Mountains. A migratory species, MWCS arrive from wintering grounds in Mexico and the Southwestern United States at breeding grounds in early to mid-May. Birds arrive in groups; males arrive first followed by females 2-3 weeks later (Morton 2002). Mate choice is determined by male competition and female selection after arrival at the breeding grounds (Morton 2002). MWCS are short-lived passerines with a median age of 1.94 yrs for males and 1.91 yrs for females. The mean breeding age for this species is 2.12 yrs for males and 1.88 yrs females (Morton 2002). Thus most birds will breed only once suggesting strong selection pressure for optimal mate choice and setting the stage for intense agonistic challenges.

General Field Methods

Study birds were caught in Potter traps that were baited with white Proso millet. Trap lines were opened from late May to late July on a daily basis from 6:00am to 12:00pm. We collected morphological measurements from all captured birds. Each bird was weighed to the nearest 0.5g in a small mesh bag with a Pesola® spring scale (Foufopoulos 2010). Wing cord and tail length were measured using a hand-held ruler. The proportion of white in the crown was calculated by measuring crown width (distance between the two outer edges of a sparrow's black 'eyebrows') and stripe width (width of the mid-crown white stripe) along the line connecting the two eyes (Fig. 2). The proportion of crown whiteness was expressed as:

$$(\text{Stripe Width} / \text{Crown Width}) \times 100$$

We also quantified tarsus length, cloacal protruberance (both in *mm*), as well as subcutaneous fat deposits at the furcula and the abdomen. All birds were banded using both a single numbered FWS metal band, and a unique combination of 3 colored plastic leg bands facilitating visual identification in the field. Because the majority of birds on the study plots are captured every year and MWCS are short-lived and strongly philopatric, we assumed that unbanded birds were new recruits to the study population.

Crown painting manipulations

We manipulated proportion of crown whiteness in similar fashion for two different experiments: first to understand the relationship of crown whiteness on the avian stress response, and secondly to understand the effect of crown whiteness on reproductive success.

Following standard data collection, we modified crown traits in all male birds captured on the study plots using black and white paint (Fig. 4a, 4b.), that were opaque, permanent, easy to apply, and quick drying. For white we used a white Artline® paint marker and either a black ZIG Painty® or black Deco Color® paint markers.

Some passerine bird species can see beyond the range of visible electromagnetic radiation into the ultraviolet part of the electromagnetic radiation spectrum (Odeen & Hastad 2003). Therefore, we tried to select a white paint that would match the reflectance of the white portions of the crown both in the visible and the UV section of the spectrum (Fig. 5). In addition to matching closely the natural color of the plumage we also tried to select a paint that had the right consistency and would bind well to the bird's feathers. After multiple trials, we settled on Artline ® paint marker because it met all of these criteria. While the paint reflectance did not fit perfectly across the whole spectrum (Fig. 5), it nonetheless provided a reasonably close match in the central portions of the spectrum that are most likely to be cued upon during signaling (Qvarnstrom 1997).

Prior to paint application, all crown sections were cleaned with 70% isopropyl ethanol to remove any dirt and oil residues that might prevent paint from binding to the feathers. In this study we had two experimental groups, one with white-enhanced crowns and a second with white-reduced crowns. To achieve these effects we used either white paint to expand the white midstripe of the crown laterally (White-enhanced), or black paint to expand the two black eye-brows and reduce the white midstripe (white-reduced; Fig. 4a, b.) In the control group, the existing coloration of the crown was covered with paint without changing the distributions of the black and white plumage sections (Fig. 4a, 4b). We also made sure that experimental phenotypes remained within the limits of natural crown variation. Following application and before the paint dried, we picked apart all painted feathers with a pair of forceps to avoid plumage clumping and a subsequent loss of structural integrity and displaying functionality. Birds were then released onto their territories. If a previously painted bird happened to be recaptured we touched up any portions of the paint that might have lost the original pigment.

Blood sample collection and steroid hormone assays

Blood samples were collected from all birds in the study population to obtain a DNA sample and to identify infection with hemoparasites. These samples were collected from each bird by puncturing the brachial vein between the radius and the ulna using a fine tipped (27G) syringe and collecting blood in microcapillary tubes.

To determine blood corticosterone concentrations we used a modified trapping protocol to collect blood samples from a subset of birds that were included in a crown manipulation experiment. Because excessive time confined in a trap can raise bird corticosterone levels and obscure underlying patterns (Wingfield & Farner 1976) we followed Romero's (2005) recommendations and minimized the amount of time the study birds spend in the traps to <15 minutes. To achieve this, we shortened the standard trapline to 12-15 traps so that we could check every trap in less than 15minutes. Following the recommendations of previous literature, we would collect a blood sample in <3 minutes after opening a trap (Wingfield et al. 1982, Romero & Reed 2005). Because food uptake has the potential to influence corticosterone concentrations (Astheimer et al. 1992), only the minimal amount of seed was used when birds were being captured to obtain corticosterone samples.

Hormone sample collection followed the standard passerine stress series protocol that requires two samples to be collected, one pre-stressor and one following a 30min stressor (Wingfield & Farner 1976, 1992; Romero & Reed 2005). After the initial blood sample was drawn, the birds were placed in a dark cloth bag and were left in a quiet, shady location. After 30min the bird was removed from the bag and a stress-induced blood sample was drawn (Romero & Reed 2005). We collected 60-120µl of blood from each bird so that there was sufficient plasma to run the corticosterone assay.

Blood samples were stored on ice and centrifuged later the same day to separate the plasma from the cellular components. Plasma was extracted into NUNC™ tubes using a Hamilton™ syringe and stored at -80°C. Frozen samples were processed to the laboratory of one of the authors (MR) and plasma corticosterone levels were measured using standardized radioimmuno assays (Romero 2010). We extracted hormones from plasma samples in distilled dichloromethane, which after evaporating were mixed in a phosphate buffer solution. Then we separated samples into duplicates along with a scintillation recovery. Radioactive corticosterone, antiserum, and finally charcoal were added to each sample. Radioactive corticosterone competes with naturally occurring corticosterone for binding with the antiserum on the charcoal substrate that acts as a non-specific binding site (Romero 2010). Consequently, birds with higher natural corticosterone levels had higher scintillation counts, because more of the naturally occurring corticosterone occupies antiserum binding sites, leaving more of the radio-labeled antigen to be detected. Samples were run in duplicate and were compared against a series of radioactive corticosterone standards of varying concentrations.

Painted males were recaptured within approximately one to two weeks of having crowns manipulated. Males that we were able to recapture had two additional blood samples drawn; we extracted a second baseline and second 30-minute stress response blood. For these birds, we compared baseline, peak stress response, and difference in stress response after treatment among the three paint treatment groups to determine whether signal altercation was implicated by plasma corticosterone levels.

Decoy Challenges

To identify subjects for the decoy challenges, we surveyed the study plots for territory-holding males. Males were assumed to be occupying a territory if they were seen repeatedly at a specific location singing or paired with a female. Once a territory-holding male was located, we recorded a two minute baseline song to estimate song rate (Table 1). After this baseline recording was obtained, we approached the focal bird's perch (typically the upper branches of a willow or conifer), and one of three mounted sparrow decoys was randomly chosen and set up as the challenger. Decoys were prepared from resident male MWCS that were found dead from exposure or vehicular collision. All decoys had been mounted in a neutral perching posture to avoid inadvertently signaling aggression or subordination. During each challenge, the decoy's crown whiteness was either enhanced or reduced by combing the natural crown feathers to expose more or less whiteness (Fig. 6). Enhanced white crowns had whiteness values ranging between 45-55% while reduced-whiteness crowns ranged from 10-15%. Both enhanced and reduced whiteness crowns fell within the range of natural variation (10-55%) seen in this population.

Isolation of Signal and Receiver-dependent Cost

Every territorial male included in our analysis (n=33) was subjected to two intrusion trials: a whiteness-enhanced decoy and a whiteness-reduced decoy. The responses to each trial were compared. To correct for seasonal changes and differences in individual receiver aggression, we used a paired sampling design. Paired sample data were collected within a day or two to reduce effects of environmental changes, which are unpredictable and severe during high elevation summers and are also known to influence MWCS behavior and physiology (Wingfield & Farner 1978 a,b, Morton 2002, Morton et al. 2004). To avoid circadian fluctuations of hormones that affect bird behaviors, paired trials were run at approximately the same time each day (Breuner et al. 1999). Our data were collected in the field and slight variations in daily weather patterns were not controlled for, and may have altered behaviors. The risk of slight weather variation occurring between consecutive, was considered to be a better option than presenting decoy challenges on the same day, and risking lack of independence between trials (a challenged male may recall the previous challenge without sufficient time in between trials). Our paired design also enabled each territory-holding male to be presented with both a white ('aggressive') and black ('subordinate') decoy treatment. Measuring responses in this paired fashion was done to reduce intrinsic (age and experience) and extrinsic (territory quality) variations among individuals in a population (Hyman et al. 2004). Paired-trial focal observations helped us to detect differences in individual behaviors (Table 1; also Andrew 1961, Morton 2002)**.** We also used experimental manipulations to test for costs of signal reliability. Controlling the variable of interest was done instead of merely ascertaining an observational correlation between social punishments in response to natural crown whiteness (Altmann 1974). We were also able to control number of other possible confounding factors, isolating proportion of crown whiteness as the only variant.

To reduce variation stemming from the type of decoy used even further, we used the same decoy for both trials: once with its crown feathers combed to enhance whiteness and once to reduce it. We alternated between initial presentations with white-enhanced and white-reduced treatments to avoid familiarity or order effects (Jarvi & Bakken 1984).

The territory intrusion setup entailed a decoy clipped to a branch near where the territory-holding male was perched. The speaker and decoy were no greater than 10m from the territory-holding male (in 2008). To streamline the presentation a decoy was clipped to a willow branch that was permanently affixed to a speaker in 2009. The same presentation method was used for both the crown enhanced and crown reduced trials administered to a given male. In either case, the speaker was located directly under the decoy. The advantage of affixing a decoy to the speaker was that there was little disconnect between the visual (mounted decoy) and aural (recorded song) signals. This combination of decoy, branch, and speaker was placed in the resident's territory as close to the resident male as possible. Effort was made to clip the decoy at the same height, in case elevation or position within a bush has social or dominance significance (cf. Campos et al. 2008).

For the playbacks we used MWCS songs belonging to the local dialect and recorded in the previous year in the general vicinity of the study valley. One of four possible songs, normalized at 85dB, was randomly chosen and played on an endless loop at a rate of four songs per minute, for a period of two minutes out of a SONY SRS-77G speaker. The song from the same individual was played during each two-trial pair.

To avoid pseudo-replication effects, we used four different decoys and four different songs which were randomly paired together for each resident male. Because songs were recorded from the same population of MWCS from recent generations there was little chance of introducing an unfamiliar dialect and complicating territory-holding males' response by some novel effect (Marler & Tamura 1964, Milligan & Verner 1971, Baker et al. 1984, Cunningham et al. 1987).

All behaviors listed in the species ethogram (Table 1) were recorded into an Olympus (VN-5200PC) digital voice recorder. We started recording the resident male's behaviors as soon as it approached the decoy and continued scoring all behaviors for an additional five minutes after the end of the two-minute playback period. During the 2009 field season only, immediately following this seven minute focal sample, the resident male was observed for five more minutes (now totaling 12 minutes) to determine whether an attack would occur. During these additional five minutes the regular ethogram was not scored; only attacks were noted. Data recorded in 2009 included some additional behavioral data compared to data from 2008. Spoken focal sample data were later replayed and scored in JWatcher [v. 1.0 Blumstein 2000-2010] before they were incorporated into a spreadsheet and organized for statistical analysis.

Occasionally female sparrows (presumably mated with the resident male) would appear at the site of the trial. Because their presence tended to heighten the intensity of the response of the focal male, we repeated the analyses using female presence as a covariate in our model.

Data were also analyzed accounting for timing of the reproductive cycle. Behavioral responses tend to change as the resident population transitions from territory establishment phase to the nesting phase (Wingfield & Farner 1978a,b, Morton 2002, Morton et al. 2004). To account for this shift, and given that we found nests at a relatively constant rate over the course of the nesting season, we used a conservative cut-off for this seasonal change based on the time at which we had found 75% of the nests on the study plot. From our experience from previous years, this point coincided with the period at which the majority of the population made this behavioral shift.

In addition to behavioral counts we obtained data on latency of a male's first response, his closest approach to the decoy, the total behavioral response time during a trial, number of attacks, and duration of attacks if they did occur.

Reproductive success

During our 2008 field season, we captured male MWCS and randomized crown manipulations to one of three groups (white-enhanced, white-reduced or control). We used the painting technique described previously (Fig. 4a, 4b.). Males had their crowns painted the first time they were captured and had their paint touched up in subsequent recaptures. We tried to paint males as early as possible (our initial paintings were mostly in June but continued from end of May through part way into July) so that the altered crown was visible for the territory establishment and female choice. Once males had been painted, they were released with the intent of observing their reproductive success.

To determine the effects of crown manipulations on reproductive success, we found nests by observing and following parents returning to their nests to incubate eggs or to feed nestlings. This task was facilitated by the conspicuous nest return call that female MWCS give when in the immediate vicinity of the nest. Other nests were found by flushing birds off their nest during systematic vegetation surveys. When we found a nest we marked its location using flagging and a GPS, and then determined the identity of the parents. Each nest was checked every other day until it either failed or fledged. Reproductive success was determined based on the number of nestlings that fledged

(Lemon et al. 1992, Morton 2002). A nest was assigned to a particular male if that bird was observed guarding or tending that nest.

Statistical analyses

i. Morphological and reproductive success data.

To understand whether morphological traits relating to RHP were associated with enhanced crown whiteness, we ran correlation analyses between crown whiteness and several morphological measurements made on all captured birds (Zahavi 1975, Badyaev & Qvarnstrom 2002). Crown whiteness was compared between males and females using a two-sample t-test in the R GUI statistics package. We tested all morphological data for violations of normality using the Shapiro-Wilk test. Whenever assumptions of normality were not met, we used a non-parametric test (Spearman rank correlation) as opposed to parametric tests (Pearson's product-moment correlation). Effects of experimental crown manipulations on reproductive success data were analyzed using a one-way ANOVA in SPSS. During 2008 we enhanced the crown whiteness of 68 males and reduced the crown whiteness of 55 males in addition to 77 control birds. We found the nests of 4 control birds, 3 white-enhanced males, and 5 white-reduced. To determine if crown treatment affected the ease of nest location we ran a chi-square test cross-tabulating the number of males painted in each group and the number of painted males whose nests we located. We used nQuery Advisor to determine minimum samples needed to obtain the necessary statistical power for this comparison. Assuming a standard deviation of 1.5, and a sample size of 51 individuals in each of the three groups, a one-way analysis of variance will have 80% power to detect a difference in means with an $\alpha = 0.05$.

ii. Hormone assays

Stress response ΔC, thus the change from baseline to stressed state after 30 minutes of confinement, was calculated as:

$$\Delta C = (C_{Stress} - C_{baseline}).$$

Corticosterone concentrations were not normally distributed, so we used a natural log-transformation on baseline, stressed state, and ΔC values. We analyzed plasma levels of corticosterone in relation to proportion of natural crown whiteness, using a simple linear regression in SPSS. For males for which we had baseline information and which were crown-manipulated and then recaptured, we had data on initial and acute stress response levels of corticosterone for two catches, before and after paint treatment. These were compared to each other in the three paint treatment groups using a series of One-way ANOVAs in SPSS 17.0.

iii. Decoy presentations

Paired count data of different behaviors were compared using a Generalized Estimating Equation model in SPSS 17.0 with a negative binomial probability distribution and a log link function. For this model we set the offset (a predictor variable in our model) as the natural log of the amount of time a resident male was visibly present. Latency of first response and total response times were analyzed in SPSS using a Wilcoxon Sign Rank test. Closest approach categories were analyzed in SPSS using a McNemar test. Binary attack data were analyzed using a McNemar test, and attack durations using a Mann-Whitney U test. To account for possible seasonal shifts in reproductive effort we also analyzed the data by splitting them in an early and late subset based on observed behavioral shifts and previous work (before and after the date that 75% of the nests were located) (Morton 2002). To reduce variation due to environmental seasonality or shifting breeding phenology, we included only those birds where we were able to administer both intrusion challenges within the period of 2-3 days (Wingfield & Farner 1978a,b, and Morton 2002, Morton et al. 2004). In addition we excluded three trials in which the resident male never appeared to recognize the deployed decoy. Data were analyzed separately for 2008 and 2009 seasons due to small modifications in the experimental protocol. In 2009 we added ‘puffing’, an aggressive posturing behavior, to our ethogram (Table 1).

Latency and total response time were both recorded as duration of time and analyzed using Wilcoxon Sign Rank Test. The territory holder’s closest approach to the decoy was categorized into three distance categories. These distances were estimated to the closest tenth of a meter (1 - <1m; 2 - 1-2m; and 3 - >2m).

Attacks in which physical contact was made by the territory-holding male to our decoy were rare events in both seasons. The occurrence was so infrequent during 2008 that we did not run any statistical analysis on attacks. In 2009, although still a rare occurrence (7 occurrences out of 42 total trials), we examined attacks as binary data of either occurring or not, and also for duration of time. For all paired trials in 2009 we categorized our attack data as ‘yes’ an attack occurred during the trial, or ‘no’ an attack did not occur. These data were then analyzed using a McNemar test. We then made a subset of our data that included only those trials during which an attack occurred; for these, we analyzed duration of attack using a Mann-Whitney U test.

Results

Sender Condition: RHP and Breeding Season Hormone Profile

When comparing crown whiteness to various morphological traits we found that it was positively related to tarsus length (Fig.7) (*p=0.00025, rho = 0.243, n=222, Spearman)*, but no other traits (tail length: *p = 0.6524, rho = -0.030, n=218, Spearman;* wing chord: *p = 0.3942, rho = 0.057, n=220, Spearman; and body mass p = 0.8203, t = -0.2274, n = 213, Pearson*).

Baseline plasma corticosterone of unmanipulated male MWCS ranged from below radio-immunological detection levels, (<0.52ng/ml), to a very high baseline concentration of 42.01ng/ml. Thirty minute stress-induced sample concentrations ranged 0.85ng/ml to 104.2ng/ml. Peak stressed concentrations were significantly higher than baseline plasma corticosterone levels *(p<0.001 t=-9.593, n=47, Paired T-test)*.

Corticosterone Versus Natural Crown Variation

In a comparison between naturally occurring crown whiteness and three measures of plasma corticosterone (baseline, thirty minute stress and difference from baseline to stressed coriticosterone). We found that crown whiteness does not significantly predict baseline corticosterone levels *(p > 0.1, b = 0.081, t (45) =0.547, Simple Linear Regression),* stressed state corticosterone levels *(p > 0.1, b = 0.102, t(45) =0.689, Simple Linear Regression)*, or the amount of change in corticosterone levels which occur when a bird is stressed *(p > 0.1, b = -0.040, t(45) = -0.266, Simple Linear Regression)*

Corticosterone Versus Experimental (painted) Crown Variation (post-manipulation)

Baseline and stress-induced corticosterone concentrations differed in birds before treatment (*p<0.0001, t=-5.572, df=20, paired t-test*), as well as after recapture (*p<0.0001, t=-4.284, df=20, paired t-test*. The significant differences indicated that birds were responding to our stress protocol in a biologically relevant nature both before and after receiving painted crown treatments. While these results were expected based on general endocrine function, we were particularly interested in the differences in corticosterone levels resulting from different crown painting manipulations. Does changing the signaling state affect the underlying stress response?

Our analysis of plasma corticosterone levels indicates no significant difference among any of the corticosterone measures for the different treatment groups (7 black, 5 white and 9 controls) as a response to our plumage painting. We found no significant difference among any of the paint groups when recaptured after having interacted in the wild with their manipulated crown: baseline corticosterone *($F_{(2,18)}$= 2.291, p=0.998, One-way ANOVA)* and 30-min stressed state corticosterone *($F_{(2,18)}$= 0.491, p=0.620, One-way ANOVA)* for paint treated birds. To observe a corticosterone response to signal manipulations we compared the before and after paint treatment corticosterone measures for white, control, and black groups. We looked at Δ baseline [initial – after treatment] *($F_{(2,18)}$= 0.002, p=0.998, One-way ANOVA)* and Δ stress-induced [initial - after treatment] *($F_{(2,18)}$= 0.687, p=0.516, One-way ANOVA*) states but found that baseline and 30 minute stressed state levels of corticoserone were not significantly different for any of the paint groups do to the treatment.

We also looked at the painting effect on stress response measured as the after treatment baseline subtracted from the after treatment stress induced corticosterone: Δ difference after treatment [stress – baseline] ($F_{(2,18)}$= 2.061, p=0.156*, One-way ANOVA*). To account for individual variation we subtracted the initial corticosterone values from the after paint treatment values and compared the effect of enhancing or reducing crown whiteness. There were no significant differences between treatments in any of our measures of corticosterone.

Behavioral Response to Decoy Challenge

The results of the decoy manipulations indicate that in adult male sparrows, enhanced crown whiteness elicits increased levels of aggression and social punishment. In both the 2008 and 2009 trials, resident males produced significantly more aggression behaviors ('chink' calls: 2008: *p=0.007, Wald Chi-square=7.233, df=1* [Fig. 8a]*; 2009:*

p=0.005, Wald Chi-square=7.733, df=1) [Fig. 8b] when challenged with decoys with white-enhanced crowns, versus when challenged with the same decoys with white-reduced crowns.

We found that males exhibited elevated rates of puffing when presented with white-enhanced decoys, (*p=0.028, Wald Chi-square=4.857, df=1)* [Fig. 9]. Being an inconspicuous behavior which often occurred in conjunction with more obvious behaviors, 'puffing' however was relatively rare in our recorded data and was observed only 13 out of 40 trials (three times against white-reduced and 10 times against white-enhanced decoys).

In 2008 males exhibited decreased rates of strutting when presented with a white-enhanced decoy (*p=0.024, Wald Chi-square=5.078, df=1)*. However, because this behavior was relatively rare (observed in only 4 out of 12 trial pairs), interpretation of this pattern was difficult. This behavior was not significant in 2009 when we increased sample size. Strutting in males is a highly energetic and coordinated display which likely advertises vigor to females and probably confidence to other males.

We did not discern any statistical differences between the two crown treatments for any other behaviors scored in our ethogram (flights, perch changes, and song behaviors). These behaviors were analyzed with the GEE separately for 2008 and 2009 (Table 2) because focal trials were timed differently. Using female presence and Julian date on which 75% of nests were found as covariates in our model, we found no significant differences. Of these behaviors flights, perch changes, songs, and strutting were not found to be significantly different when females were present, or between these different seasonal time periods (Table 2).

Using the McNemar test we found no significant difference in attack occurrence between white-enhanced and white-reduced decoy treatments. We found no significant difference in whether or not a territory-holding male engaged in a physical attack based on decoy crown treatments. After running a Mann-Whitney U test we found no significant difference between duration of attack time by territory-holding males on white-enhanced decoys as compared to the duration of time they spent in a state of attack on white-reduced decoys (p= 0.480, *U=4.00, Z=0.707, df=1 Mann-Whitney U)*.

We found no difference in territory-holding males' closest approach distance towards white and black decoys (*p=0.160, Chi-square=3.667, df=2, McNemar Bowker*) in 2008 and (*p=0.506, Chi-square=2.333, df=3, McNemar Bowker*) in 2009. In 2009 closest approach data was also grouped into subsets for before and after when 75% of the nests were found and again no significant difference was detected. We found no significant difference in either year for latency or total response time in relation to decoy crown whiteness.

Effects of crown manipulation on reproductive success:

Crown whiteness in MWCS is a sexually dimorphic trait: males (n=223) have significantly whiter crowns than females (n=160) (Fig. 10) *(p = 0.0018, t = -3.1399;* independent sample t-test*)*. This effect is body-size independent- whereas males are on average bigger and have larger absolute crown sizes than females, because crown whiteness is expressed as a fraction of two linear dimensions it is independent of absolute size.

Crown treatment did not affect the probability of finding a nest (p=0.199, χ^2=6.0, df=4, 68 males enhanced crown whiteness, 55 males reduced crown whiteness, and 77 control birds). There were no significant differences in reproductive success between treatment groups *($F_{(2,13)}$= 0.485, p=0.627, One-way ANOVA).* However, white-enhanced (WE) birds produced on average more nestlings than control (C) and white-reduced

(WR) males (WE: mean =3.33, S.E.- 0.816497, range= 2, n=3; C: mean =2.88, S.E.- 0.4406772, range= 4, n=8; WR: mean =2.4, S.E.- 0.678233, range= 4, n=5) [Fig. 11].

Discussion

Status Badges

We found that crown whiteness, measured as the proportion of white to black plumage, acts as a status badge in MWCS. Our data suggest that during agonistic disputes in the breeding season, crown whiteness communicates information regarding male resource holding potential (RHP). In the context of high resource value, competitions confirm opposing interest of signaling contestants and signal efficacy. Costs, benefits and resultant tradeoffs related to crown whiteness confirm the reliability of this signal for MWCS. Thus, our results suggest that crown whiteness as a status badge is an ESS.

Interest and Efficacy

Recall that there are three selective criteria relevant to the evolution of a particular signal design: interest, efficacy, and cost (Dawkins 1993). During staged scenarios of agonistic signaling, territory-holding males heightened aggression to deter the resource access of challengers (in this case our decoys). These aggressive responses confirmed opposed interests between male MWCS. In the wild, successful exclusion of a challenger entails a fitness gain for the winner at a cost to the other contestant. Experimental territory intrusions during the breeding season elicited aggressive male versus male interactions, supporting the assumption of opposing interests for male MWCS in a competitive context.

Our results also confirmed the efficacy of crown morphology as a communication signal. The decoy challenge experiments revealed clear differences in receiver response with crown whiteness. Signal distinction demonstrates that, at minimum, the receiver can detect varying proportions of crown whiteness. This finding dovetails with the results of previous studies that show that *Z. leucophrys* dominance hierarchies are maintained in part by crown characteristics; confirming the efficacy of this badge (Fugle et al. 1984, Watt 1986, Fugle & Rothstein 1987, Keys & Rothstein 1991, Slotlow et al. 1993). Despite the importance of understanding interest and efficacy, it is also necessary to demonstrate the costs and benefits that underlie the communicated content of a signal. Without incurring tradeoffs, the signal can be subverted by ‘cheaters’ rendering it unreliable and evolutionarily unstable.

Costs, Benefits and Resultant Fitness Tradeoffs

This work documents several costs, benefits and resultant fitness tradeoffs associated with crown whiteness, suggesting that this is a reliable or ‘honest’ status badge of individual quality and RHP.

Sender Condition: Morphological associations

Correlation of crown whiteness with a number of morphological traits indicated a positive relationship with tarsus length but not mass, tail length, or wing length. Longer tarsi reflect longer legs. Longer tarsi provide an important advantage in aggressive bouts, usually resulting in higher RHP (Parker 1974, Monkkonen 1990). Like many other morphological traits, tarsus length is a good proxy for overall frame size, and is not subject to within-season fluctuation (Andersson & Andersson 1994). Because a larger body frame is inherently associated with elevated energetic expenditure costs (Searcy 1979), long tarsi represent an expensive lifelong investment. In turn, males that can afford the elevated energetic cost of supporting a larger body frame also have an increased chance of winning contests for resources (Searcy 1979, Monkkonen 1990). Consequently, while production of a large white crown itself requires few extra production costs, it does reflect the ability of an individual to invest in an energetically expensive trait, namely a larger frame size.

Costs to the Sender: Crown whiteness and corticosterone profiles

Various activity patterns (e.g., aggression, territoriality, or breeding behaviors) are closely tied to underlying endocrine responses (e.g., Wingfield 1985)**.** Aggressive interactions associated with agonistic signaling and territoriality, such as chasing and other forms of social punishment, are likely to increase adrenaline. The adrenaline release is part of a hormonal cascade that induces a stress response. The result is higher baseline levels of plasma corticosterone (Harvey et al. 1984). Binding site competition between corticosterone and testosterone may influence reproductive activities (Swett & Breuner 2008). We expected that males having the whitest crowns would also have lower baseline corticosterone levels. A down-regulated stress response would allow frequent exposure to stressful breeding season contests, while maintaining reproductive behaviors. Contrary to what we expected, we found no significant correlation between naturally occurring crown whiteness and baseline corticosterone levels.

We found no clear pattern between naturally occurring crown whiteness and the stress response in male MWCS. It seems that even if males with the whitest crowns would have increased numbers of agonistic interactions, they have a physiological habituation to minor stressors. Such a coping mechanism or habituation to a stress stimulus, demonstrated by males with the whitest crowns would mean inhibition of the stress response and would result in lower peak corticosterone levels (Harvey et al. 1984). Males with less prominent crown whiteness may also maintain low levels of corticosterone simply by avoidance strategies. Not participating in stressful situations or competitions with males displaying the whitest crowns could prevent some males from experiencing detrimental stress levels. Our results failed to support our original predictions and crown whiteness does not relate to corticosterone levels.

Sender Condition: Stress Response from Signal Cheating

We compared stress hormone information between baseline and stressed (holding for 30 min. in a dark bag) state. We also evaluated over a period of 1-2 weeks, changes in circulating corticosterone levels in response to an experimentally manipulated crown. Corticosterone concentrations changed significantly between baseline to stressed state. However, we were unable to detect significant differences in corticosterone levels between initial capture and second capture, suggesting that crown manipulations had little effect on the stress response. There was no difference between white-enhanced, white-reduced, or control paint groups; signal cheaters showed no fitness tradeoffs related to stress response.

Our original prediction was that social punishment for crown cheating would elicit a stress response. The results instead suggest that changed crown whiteness does not alter a receiver's stress response in a manner that is reflected in plasma corticosterone concentrations. There is no increase in corticosterone levels associated with experimentally manipulated crowns. Thus, we did not find that reliability of crown signaling was maintained through costs related to the sender's stress hormone profile. Crown whiteness manipulations and the resultant aggressive interactions incurred may not be sufficient to increase corticosterone levels. It may be that stress responses are reserved for catastrophic events. MWCS may have an adapted stress response to tolerate agonistic signaling in high elevation breeding grounds (Wingfield et al. 1992,1995, Roberts et al. 2007).

In summary, males with whiter crowns did not have lower baseline or peak corticosterone levels than less white males. Experimentally altered crown whiteness also showed no influence on the signal sender's corticosterone levels. Therefore we have no evidence to suggest that the reliability of crown whiteness is maintained by fitness tradeoffs related to corticosterone levels. Future investigations of the costs and benefits of the MWCS stress response and its relation to badge status signaling should also consider measuring testosterone.

Even if all males demonstrated the same corticosterone response, other hormones could alter tradeoffs related to crown whiteness. Corticosterone does not cause a significant decline in testosterone (Wingfield & Silverin 1986). Because corticosterone does not limit production of testosterone, males with whiter crowns may still have higher-than-average levels of testosterone (Searcy & Wingfield 1980). Individuals with increased testosterone often gain resource access through higher aggression (Searcy & Wingfield 1980). However, high testosterone levels mean there are chances of immunological and energetic costs (Zuk et al. 1995, Buchanan et al. 2001). The complexity of hormonal contribution to status badge signaling is evident. More work is needed to determine if crown whiteness reliability is related to tradeoffs associated with the sender's endocrinology.

Receiver-dependent Cost: Aggressive Response

During the breeding season, territory-holding males demonstrated increased aggressive behavior towards male decoys with whiter crowns. The specificity of the experimental crown manipulation enabled us to isolate the role of crown whiteness during agonistic encounters, because all other aspects of each decoy's plumage and song remained unchanged between trials.

Heightened aggressive behaviors from resident birds were shown towards white-enhanced decoys, in the form of increased rates of aggressive ‘chink’ calls and ‘puffing’ behaviors. Therefore possessing a larger badge resulted in costs of exclusion, condescending attention, and social persecution by territory-holding male MWCS. When high social status males impose a cost on potential cheaters, they reveal an inconsistency between signal design (crown morphology) and content (fighting ability). The results of territory intrusions indicate that social punishment towards male MWCS with whiter crowns is an important cost of displaying a bigger badge. Along with other fitness tradeoffs, the results from our decoy challenges suggest that crown whiteness is an evolutionarily stable signaling system. Further, reliable information is communicated between senders and receivers (Smith et al. 1988 and Guilford & Dawkins 1995).

Slight morphological differences and subtle behaviors often convey information between senders and receivers (Whitfield 1987, Chaine & Lyon 2008). Decoys in a fixed perching position held variables such as posture, subtle movements, and other behaviors constant. Using decoys also ensured that morphologically associated RHP signals, such as overall size remained the same. Each territorial male was presented with the same decoy and same song playback. The only difference between paired trials was crown treatment. Hence, we isolated the signal of interest and found that adult males recognized variation in crown whiteness according to their responses. We were also interested in how the proportion of crown whiteness was perceived by territory-holding males.

Costs to Intruders Inflicted by Receivers (Territory Holders)

Our results showed a difference in the response of territory-holding males to different decoy treatments. There was a significantly heightened aggressive response to white-enhanced decoys, recognized by MWCS as the aggressive more threatening status badge. White-enhanced decoys also received higher puffing rates (only measured in 2009). This result demonstrates social punishment in the form of aggression towards white-enhanced badges. Our findings support the status badge theory because crown whiteness is subject to these like-vs-like social punishment costs. It is possible that the proportion of crown whiteness evolved as a social mediator in resource disputes (Johnstone & Norris 1993). Status badge signaling with crown whiteness would prevent confrontations from escalating into a more costly physical attack. The association between the signal *design* and underlying *content* relates crown whiteness as a reliable plumage status badge, resistant to cheating.

Based on our findings, we conjecture that crown whiteness in male MWCS is a status badge conveying information about the signalers RHP. However, as a conventional signal, there are no obvious costs in its production (cf. Guilford & Dawkins 1995). Crown whiteness may seem vulnerable to mutant phenotypes disrupting an evolutionarily stable strategy at equilibrium (Rohwer 1981 & Ewald, Smith et al. 1988), but recall that dishonest signaling of crown whiteness entails a cost (in this case, social persecution or elevated aggression) from receivers (Rowher 1975). Signal reliability is maintained through social punishment. Signalers that cannot support the RHP they advertise pay higher marginal costs (Johnstone & Norris 1993).

Status badges mediate agonistic confrontations. As costs and benefits change with social context and relative resource values senders and receivers are influenced (Rowher 1977, Tibbetts 2008). To understand status badges it is important to consider context of both the signaling interaction and the resource value. The social punishment costs demonstrated in this study along with the results of other studies bring to attention two critical aspects of signaling; context and resource value. The more similar are resident and intruder during agonistic signaling, the more aggression escalates (Clutton-Brock et al. 1979). Status badge reliability requires such like-vs-like social punishment costs (Møller 1987 a, b, Slotlow et al. 1993). Previous literature has not reported costs associated with cheating crown signaling in this species. Our study demonstrated that there *are* receiver-dependent costs associated with senders displaying the most aggressive signal. The balance between costs and payoffs imposes selection pressures that maintain evolutionarily stable signals (Arnqvist & Rowe 2005). Costs of social punishment occurring in a breeding season context suggest the importance of resource value. Other studies on white crown sparrows have shown that crown signaling convention delineates resource access in wintering groups but without cost (Parsons & Baptista 1980, Fugle et al. 1984, Watt 1986, Fugle & Rothstein 1987, Keys & Rothstein, 1991, and Slotlow et al. 1993, Slotlow & Rothstein 1995a,b). The important distinction is that previous studies and the results of our experiments indicate that high value resources may be required to test the reliability status badge convention. The context in which agonistic signaling occurs influences whether there is a reliance on convention or an escalation towards costly social interactions and tests of RHP (Tibbetts 2008). For male MWCS, the high value resources involved with breeding season competitions elicit costly receiver responses for signals of high RHP. An inability to match ones signal with their actual RHP could result in the detection of incongruence between signal state and sender condition; cheaters would further suffer increased aggression (Rohwer 1977, Tibbetts 2008).

We also investigated other aspects of this signal convention (cf. Smith et al. 1998). More specifically, if the receivers realize the association between signal design and emitter condition, we anticipated signals to affect a larger audience beyond male-male challenges, and that badges of status would also affect female choice (Johnstone & Norris 1993).

Female Choice: Reinforcement of Signal Convention

Our third aim was to measure how an established conventional signal functions with respect to receiver preference. Both intrasexual (male-male competition) and intersexual (female choice) interactions have the potential to work as a selective forces on animal signals (Møller 1992). In particular, status badges can be selected for through male competition as well as through female choice (e.g., Griggio et al. 2007). Specifically, we assessed signal-related bias in reproductive fitness by evaluating shifts in female preference in males with experimentally manipulated crowns.

As with many socially monogamous species, MWCS use less conspicuous signals rather than extreme ornamentation (Kirkpatrick et al. 1990). However, if females do select their mates by using plumage badges, then this will be a powerful selective force shaping signal design (Møller 1992). We quantified reproductive success in nesting pairs in which the male's crown was manipulated. We found that male crowns manipulated to have a higher proportion of crown-whiteness did not result in an increase in the number of fledglings. We were unable to make inference on female quality as it relates to number of fledglings and higher quality females' choice for male crown whiteness. This lack of significance was probably in part the result of small sample sizes - additional sampling effort will be needed to achieve sufficient statistical power.

Sexual Selection: Other Evidence

Two indirect lines of evidence suggest that crown whiteness is important in MWCS sexual selection. First, sexual dimorphism in a trait is generally considered to be result of sexual selection (Andersson 1994). Indeed we found that in white-crowned sparrows such dimorphism exists as males tend to have a larger proportion of crown whiteness than females do.

Second, if a trait is sexually selected, one would predict that it develops at or after sexual maturation. In accordance with this prediction, the white and black crown coloration in MWCS is a trait that develops after sexual maturity; these birds possess a brown and tan crown as juveniles (Morton 2002). While both of these lines of evidence further suggest that crown whiteness play a role in sexual selection, they are not conclusive evidence that crown whiteness is a sexually-selected signal. Further investigation of crown whiteness in a reproductive context is needed to determine the role, if any, that sexual selection has played in this badge of status.

Final Remarks

For the migratory MWCS, breeding at high elevations in the Rocky Mountains entails resource competition in a harsh and generally unpredictable environment. The evolution of a plumage badge, such as male crown plumage whiteness, mediates communication between signal emitters and receivers during agonistic disputes. We found evidence suggesting that crown whiteness is a badge of status, signaling a male's RHP through a positive correlation to tarsus length which is an energetically expensive trait associated with fighting ability. In addition to these findings our work supports the badge of status hypothesis by providing examples of like-versus-like cost. Receiver-dependent costs, in the form of preferential discrimination against cheaters, further indicate reliability in aligning signal design and content. In summary, social punishment of incongruence between signal and RHP during the breeding season suggests that crown whiteness is an evolutionary stable badge of status in White-crowned sparrows. Future studies can now build on the recognition that in White-crowned sparrows this badge, though cheap to produce and maintain, is associated with signaler RHP and is subject to costs associated with social punishment.

Tables and Figures

Table 1. Ethogram used during focal trials to score territory-holding males' response to decoy challenge/call playbacks. Each behavior is listed, defined, and the data type which was collected is noted.

Behavior	Definition	Data Type
Flight	A bird flies through the air for a distance of >2 meters.	count
Perch	The bird relocates by walking, hopping or fluttering over a total distance of less than 2 meters.	count
Chink	An agitated aggressive call which includes a variety of notes: notes for mobbing or scolding during an intrusion (chink, chip, pink); and during conflicts (whine).	count
Sing	Production of melodious sounds including whistles, buzzes, various syllables, and trills which start high and loud and fade off.	count
Strut	Trill/twittering call with simultaneous drooping of the wings tips, puffing of the body plumage and rapid body vibration. Display is used by males in territorial disputes and same-sex attacks. Also used by females to solicit copulations.	count
Attack	Resident male engages in physical contact with the decoy.	count/state
Puff	Body posture is changed by erecting body (in particular breast) plumage and drooping the wings, to make the bird appear bigger than normal. Aggressive behavior.	count
Out	Resident male leaves the trial area and disappears out of the view of the observer.	state
Latency	Time elapsed from start of playback to first response by resident male.	state
Closest Approach	Distance of closest approach (in meters) from decoy.	distance

Table 2. Three aggressive response behaviors [highlighted in bold] from territory holding males were directed with significantly greater frequency towards decoy intruders displaying white-enhanced crowns. Additional covariates [female presence and date on which 75% nest were found] which might have altered the underlying aggressive state of male territory holder were also considered but were not significant (explanation of these covariates is given in the Methods section). Empty cells were not analyzed with covariates because this was expected to only further increase observed differences.

Behavior	2009	2009 - female presence	2009 - 75% nests found	2008
chink	**Wald Chi-square=7.733, df=1, p=0.005**	-	-	**Wald Chi-square=7.233, df=1, p=0.007**
puff	**Wald Chi square=4.857, df=1, p=0.028**	-	-	-
perch	Wald Chi-square=0.350, df=1, p=0.554	Wald Chi-square=0.411, df=1, p=0.521	Wald Chi-square=0.205, df=1, p=0.650	Wald Chi-square=1.347, df=1, p=0.246
fly	Wald Chi-square=0.042, df=1, p=0.838	Wald Chi-square=0.079, df=1, p=0.779	Wald Chi-square=0.116, df=1, p=0.734	Wald Chi-square=2.984, df=1, p=0.084
strut	Wald Chi-square=0.296, df=1, p=0.586	Wald Chi-square=0.298 df=1, p=0.585	Wald Chi-square=0.007, df=1, p=0.935	Wald Chi-square=5.078, df=1, p=0.024
sing	Wald Chi-square=0.312, df=1, p=0.576	Wald Chi-square=1.121, df=1, p=0.290	Wald Chi-square=0.135, df=1, p=0.714	Wald Chi-square=0.306, df=1, p=0.580

Figure 1. Diagram of a Functional Signaling System as proposed by Endler (from Otte 1974) to explain a signaling system in terms of signal senders (emitters) and signal receivers. A functional or evolutionarily stable strategy has little cheating/exploitation of signal communication.

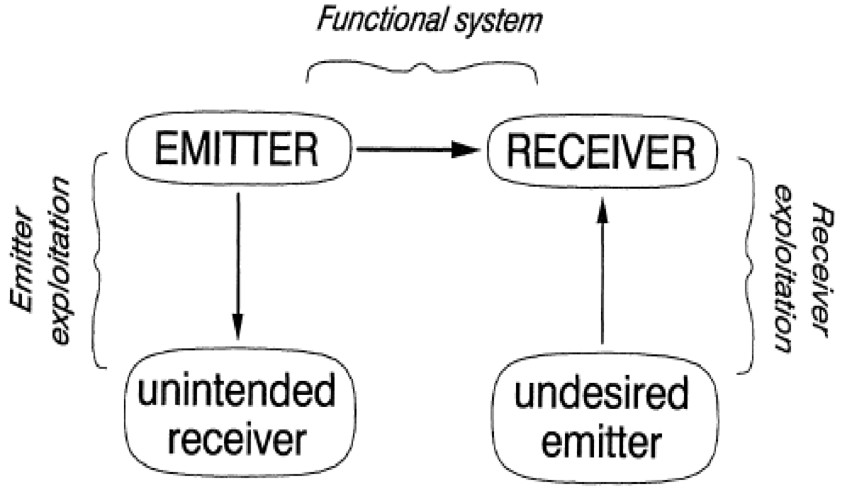


Figure 2. In Mountain white-crowned sparrows, crown width is determined by measuring from the outer edge of one black eyebrow to the edge of the other black eyebrow (red bar) while stripe width is determined by measuring the width of the white mid-crown stripe (yellow bar). Whiteness of crown (i.e. percent white of the crown) is calculated by dividing the width of the yellow bar by the width of the red bar, and is independent of absolute head size.

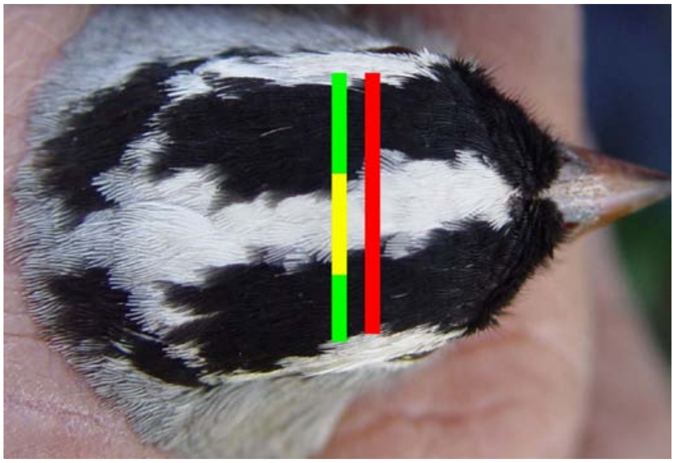


Figure 3. . This schematic represents the general principles underlying signal design and content: how the different selective forces interact to shape the evolution of a functional status system such as the proportion of crown whiteness in male MWCS. The small red triangle represents the interaction of various costs, benefits and resultant fitness tradeoffs that maintain the system's reliability.

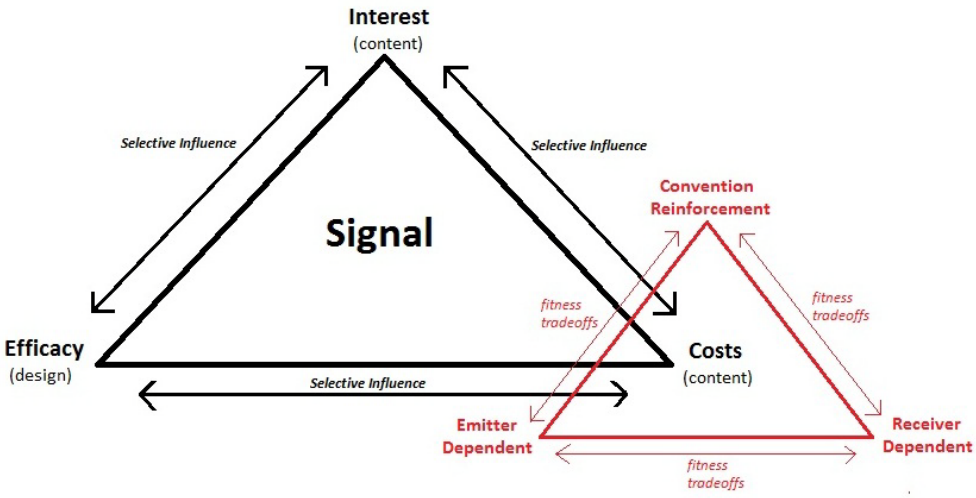


Figure 4a. Schematic of treatment and control groups in the experimental plumage manipulation experiment. Birds assigned to the white-enhanced (Enlarged) crown treatment group (B.) had the central white stripe of their crown expanded laterally, using white paint. Birds in the white-reduced (Reduced) crown treatment group (C.) had the width of the central white stripe narrowed by expanding the black ‘eyebrows,’ using black paint. Control birds had the central white stripe painted with white paint but the width of the original stripe was not altered.

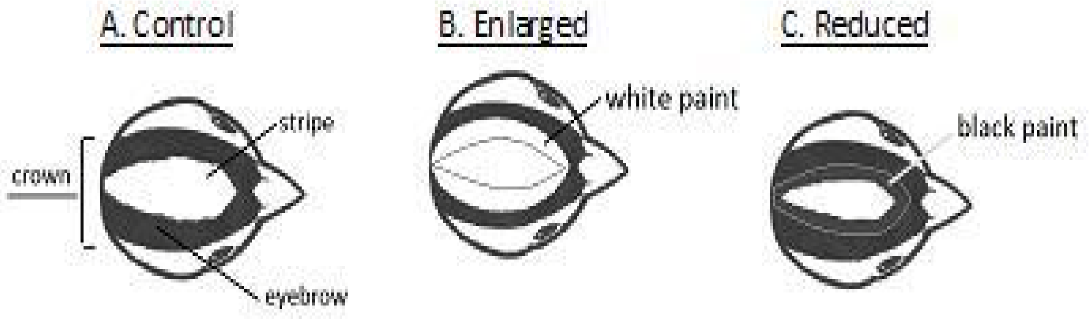


Figure 4b. These images include, in series, *a.)* crown cleaning, crown painting *b.)* crown enhanced (whiter) crowns, and *c.)* crown reduced (blacker) crowns. The last image, *d.)* shows crown plumage being picked apart for structural and functional integrity after painting.

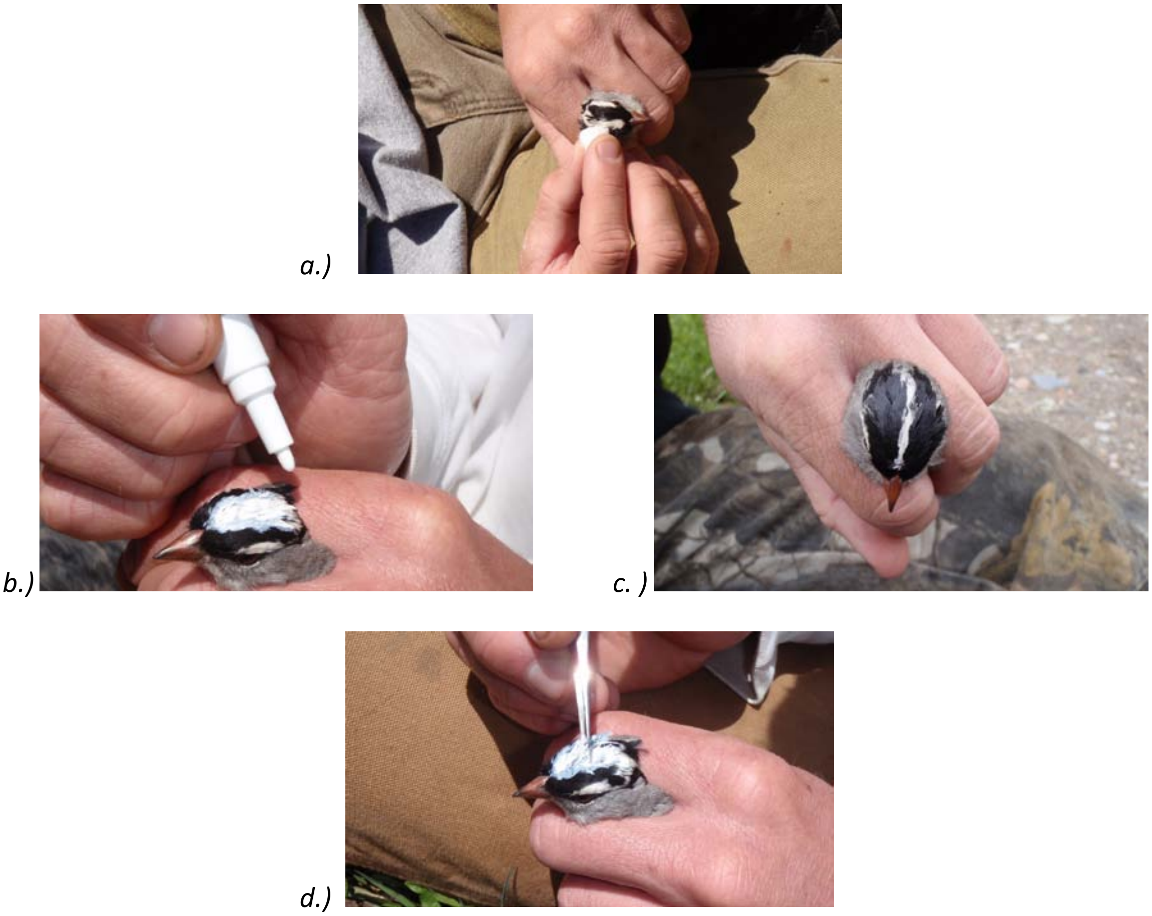


Figure 5. Spectrometer measurements of UV reflectance for natural sparrow plumage, and for the white paint employed in the plumage manipulations. Green, purple, turquoise and orange lines represent reflectance across the electromagnetic spectrum of the white crown feathers of four sample sparrows. Blue line represents the reflectance of the white paint (Artline ® paint marker) when used on white paper; the red line represents reflectance of the same white paint applied to sparrow crown feathers. The highest reflectance of natural white crown plumage occurs at wavelengths above the UV-spectrum. When placed on the feathers, the paint marker matches the higher percent transmission of natural feathers near the middle wave lengths. This is likely more important for visual cueing than matching the tails of the distribution where percent reflectance is lowest.

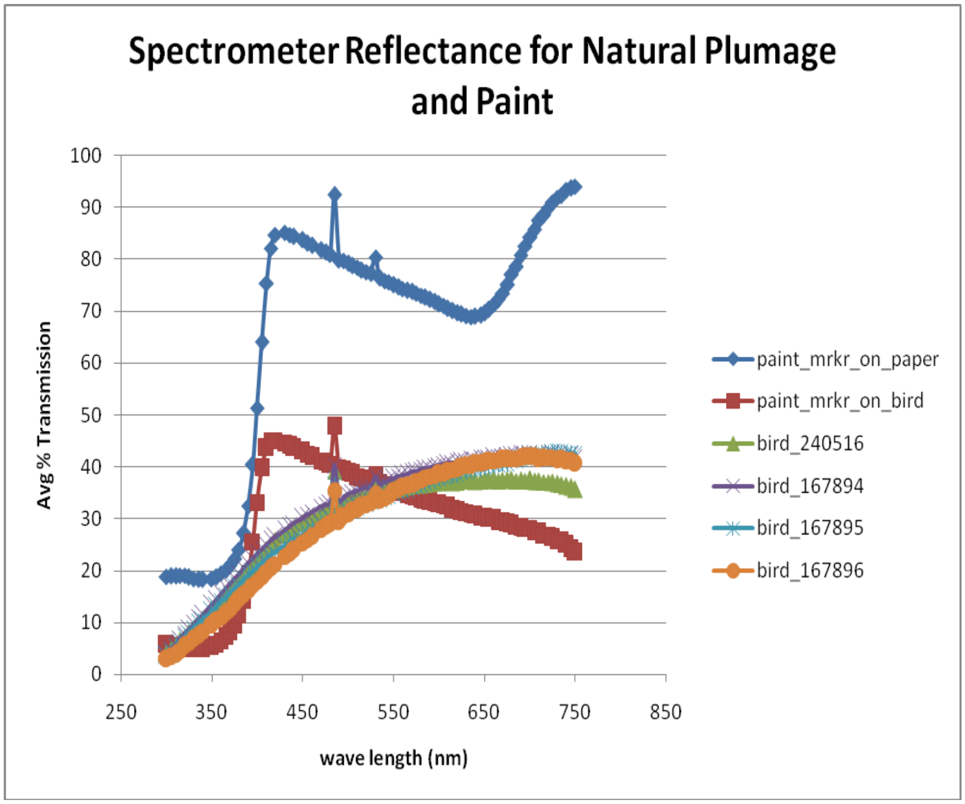


Figure 6. The decoy on the left has the crown plumage combed to a white-enhanced signal; the decoy on the right shows a white-reduced signal.

Figure 7. In male MWCS tarsus length is positively, but loosely (*p=0.00025,* Spearman's rho = 0.243), correlated to proportion of crown white.

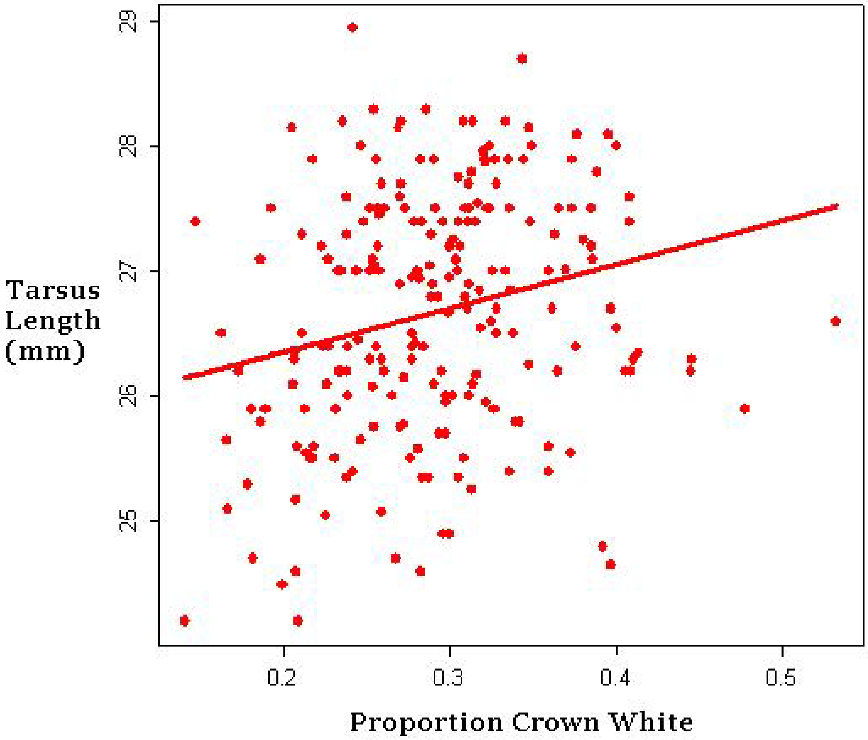


Figure 8a. In 2008, male MWCS performed a chink response (Table 1) significantly more often towards whiter (crown whiteness enhanced) decoy intrusions than towards black (crown whiteness reduced) decoy intrusions.

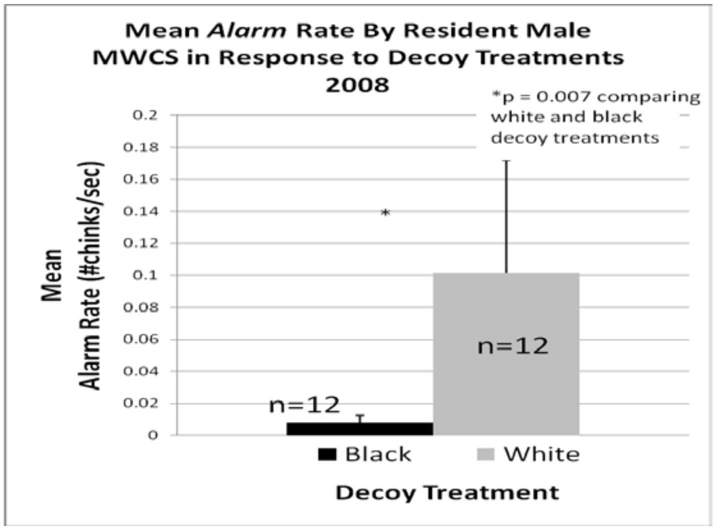


Figure 8b. In 2009, male MWCS performed a chink response (Table 1) significantly more often towards whiter (crown whiteness enhanced) decoy intrusions than towards black (crown whiteness reduced) decoy intrusions.

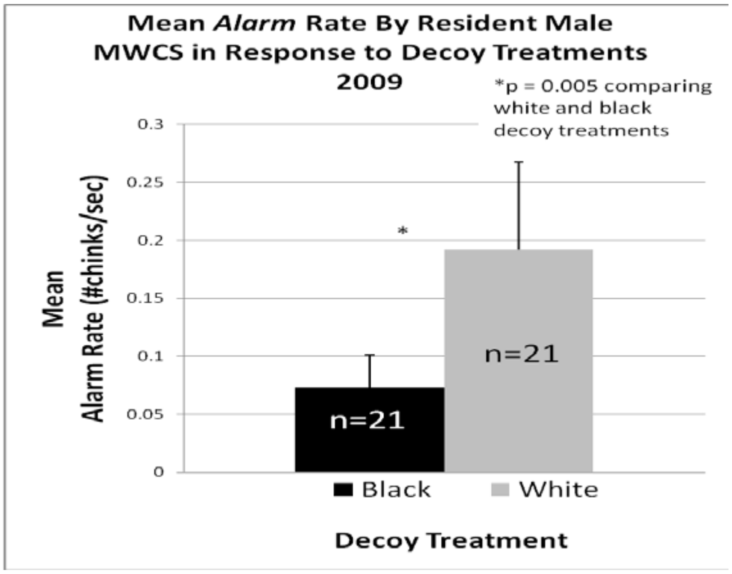


Figure 9. In 2009, male MWCS performed an aggressive puff response (Table 1) significantly more often towards whiter (crown whiteness enhanced) decoy intrusions than towards black (crown whiteness reduced) decoy intrusions.

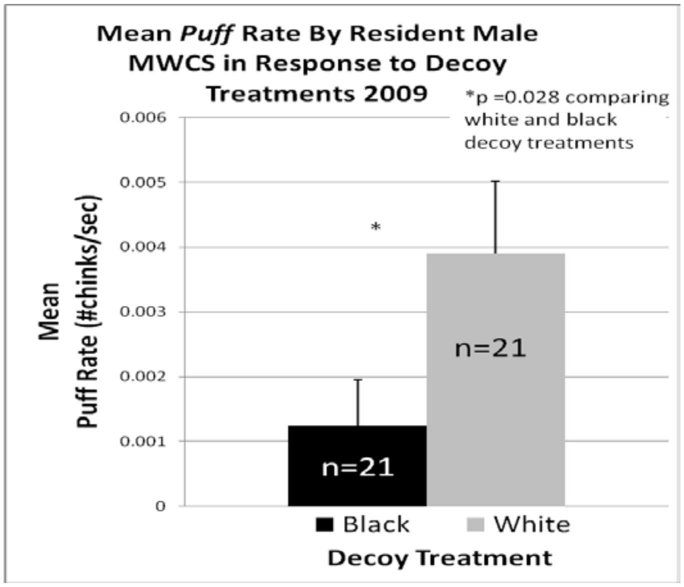


Figure 10. MWCS are sexually dimorphic; males have a greater proportion of white in the crown than females.

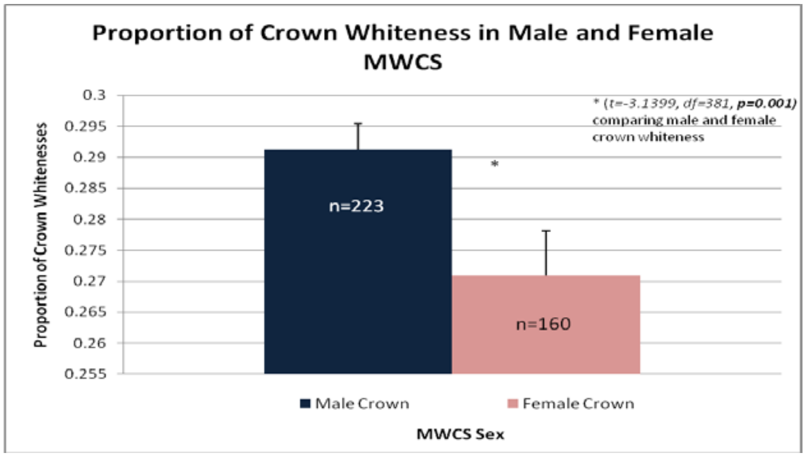
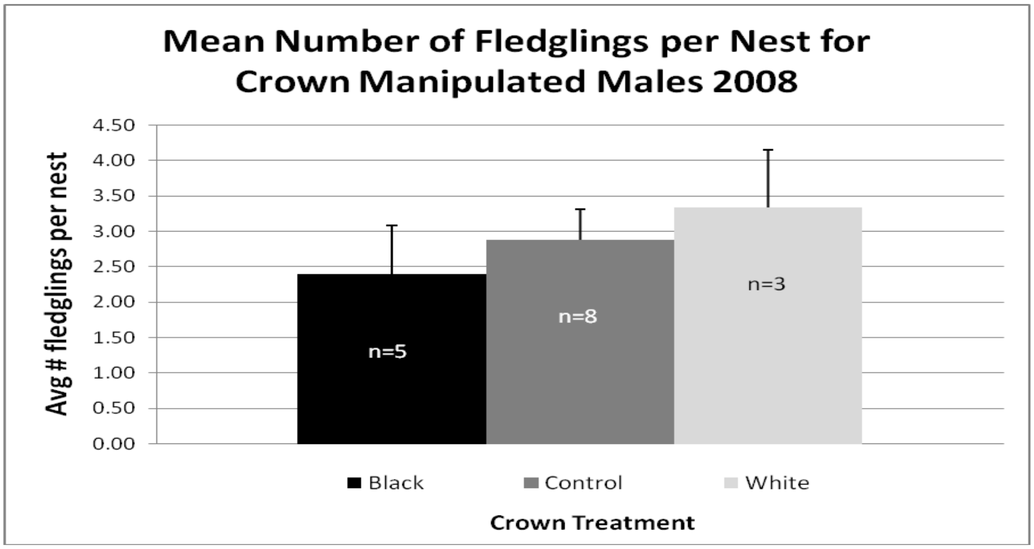


Figure 11. Reproductive success (defined as average number of fledglings per nest) of male MWCS belonging to the three different treatment groups (black = crown whiteness reduced, control = crown whiteness remains the same, and white = crown whiteness enhanced). Differences are not statistically significant (P> 0.1).



Literature Cited

Altmann, J. 1974. Observational study of behavior sampling methods. *Behaviour*. **XLIX:** 227-266.

Alexander, R. D. and Borgia, G. 1978. Group selection, altruism, and the levels of organization of life. *Review of Ecology and Systematics*. **9**: 449-474.

Anderholm, S., Olsson, M. Wapstra, E. and Ryberg, K. 2004. Fit and fat from enlarged badges: a field experiment on male sand lizards. *Proceedings of the Royal Society of London-B*. **271**: S142-S144.

Andersson, M. 1994. Coloration and other visual signals. In *Sexual selection: monographs in behavior and ecology.* (ed. J. R. Krebs & T. Clutton-Brock), pp. 315-348. Princeton, NJ: Princeton University Press.

Andersson, S. Andersson M., 1994. Tail ornamentation, size dimorphism and wing length in the genus Euplectes (Ploceinae). *The Auk*. **111**: 80-86.

Andrew, R. J. 1961. The displays given by passerines in courtship and reproductive fighting: a review. *The Ibis*. **103a**: 315-348.

Arnqvist, G. and Rowe, L. 2005. Sexual selection and sexual conflict: history, theory and empirical avenues. In *Sexual Conflict*. (ed. J. R. Krebs & T. Clutton-Brock), pp. 14-43. Princeton, NJ: Princeton University Press.

Astheimer, L. B., Buttemer, W. A., and Wingfield, J. C. 1992. Interactions of corticosterone with feeding, activity, and metabolism in passerine birds. *Ornis Scandinavica*. **23**: 355-365.

Badyaev, A. V. and Qvarnstrom, A. 2002. Putting sexual traits into the context of an organism: a life-history perspective in studies of sexual selection. *The Auk*. **119**: 301-310.

Baker, M. C., Cunningham, M. A. and Thompson, A. D. Jr. 1984. Cultural and genetic differentiation of two subspecies of white-crowned sparrow. *The Condor*. **86**: 359-367.

Barraclough, T. G., Harvey, P. H. and Nee, S. 1995. Sexual selection and taxonomic diversity in passerine birds. *Proceedings of the Royal Society of London-B*. **259**: 211-215.

Breuner, C. W., Wingfield, J. C. and Romero, M. L. 1999. Diel rhytms of basal and stress-induced corticosterone in a wild, seasonal vertebrate, Gambel's white-crowned sparrow. *Journal of Experimental Zoology*. **284**: 334-342.

Brown, W. D., Smith, A. T., Moskalik, B. and Gabriel, J. 2005. Aggressive contests in house crickets: size motivation and the information content of aggressive songs. *Animal Behaviour*. **72:** 225-233.

Blumstein, D. T., Daniel, J. C. and Evans, C. S. 2000-2010. JWatcher. http://www.jwatcher.ucla.edu/

Buchanan, K. L., Evans, M. R., Goldsmith, A. R., Bryant, D. M., Rowe, L. V. 2001. Testosterone influences basal metabolic rate in male house sparrows: a new cost of dominance signaling? *Proceedings of the Royal Society of London-B*. **268**: 1337-1344.

Campos, D. P., Bander, L. A., Raksi, A. and Blumstein, D. T. 2008. Perch exposure and predation risk: a comparative study in passerines. *Acta Ethologica*. **12**: 93-98.

Caryl, P. G. 1979. Communication by agonistic displays: what can game theory contribute to ethology? *Behaviour*. **68**: 136-139.

Chaine, A. S. and Lyon, B. E. 2008. Intrasexual selection on multiple plumage ornaments in the lark bunting. *Animal Behaviour*. **76**: 657-667.

Clutton-Brock, T. H., Albon, S. D., Gibson, R. M., and Guinness, F. E. 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus l.*). *Animal Behaviour*. **27:** 211-225.

Cunningham, M. A., Baker, M. C. and Boardman, T. J. 1987. Microgeographic song variation in the Nuttall's white-crowned sparrow. *The Condor*. **89**: 261-275.

Darwin, C. 1859. Natural Selection. In *On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life.* (ed. E. O. Wilson), pp 501-533. New York, NY: W. W. Norton and Company.

Dawkins, M. S. 1993. Are there general principles of signal design? *Proceedings of the Royal Society of London-B*. **340**: 251-255.

Deag, J. M. and Scott, G.W. 1999. 'Conventional' signals in avian agonistic displays: integrating theory, data, and different levels of analysis. *Journal of Theoretical Biology*. **196**: 155-162. *Journal of Physiology B*. **179:** 297-304.

Douglas, H. D. III, Kitaysky, A. S., Kitaiskaia, E. V., Maccormick, A., and Kelly, A. 2009. Size of ornament is negatively correlated with baseline corticosterone in males of a socially monogamous colonial seabird.

Endler , J. A. 1992. Signals, signal condition, and the direction of evolution. *The American Naturalist*. **139**: 125-153.

Endler, J. A. 1993. Some general comments on the evolution and design of animal communication systems. *Proceedings of the Royal Society of London-B*. **340**: 215-225.

Enquist, M. 1985. Communication during aggressive interaction with particular reference to variation in choice of behaviour. *Animal Behaviour*. **33**: 1152-1161.

Fugle, G. N., Rothstein, S. I., Osenberg, C. W. and McGinley, M. A. 1984. Signals of status in wintering white-crowned sparrows, *Zonotrichia leucophrys gambelii*. *Animal Behaviour*. **32**: 86-93.

Fugle, G. N. and Rothstein, S. I. 1987. Experiments on the control of deceptive signals of status in white-crowned sparrows. *The Auk*. **104**: 188-197.

Foufopoulos, Johannes. 2010. Ornithological field protocol. http://sitemaker.umich.edu/jfoufop/lab_resources. 1-20.

Geist, V. 1966. The evolutionary significance of mountain sheep horns. *Evolution*. **20**: 558-566.

Gherardi, F. 2006. Fighting behavior in hermit crabs: the combined effect of resource-holding potential and resource value in *Pagurus longicarpus*. *Behavioural Ecology and Sociobiology*. **59:** 500-510.

Goymann, W., and Wingfield, J. C. 2004. Allostatic load, social status and stress hormones: the costs of social status matter. *Animal Behaviour*. **67:** 591-602.

Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology*. **144**: 517-546.

Griggio, M., Serra, L., Licheri, D., Monti, A. and Pilastro, A. 2007. Armaments and ornaments in the rock sparrow: a possible dual utility of a carotenoid-based feather signal. *Behavioural Ecology and Scociobiology*. **61**: 423-433.

Guilford, T. and Dawkins, M.S., 1991. Receiver psychology and the evolution of animal signals. *Animal Behaviour*. **42**: 1-14.

Guilford, T. and Dawkins, M.S., 1995. What are conventional signals? *Animal Behaviour*. **49**: 1689-1695.

Hamilton, W. D., and Zuk, M. 1986. Heritable true fitness and bright birds: a role for parasites? *Science.* **218:** 384-387.

Harvey, S. Phillips, J. G., Rees, A., and Hall, T. R. 1984. Stress and adrenal function. *The Journal of Experimental Zoology*. **232**: 633-645.

Hurd, P. L. 1997. Is signaling of fighting ability costlier for weaker individuals? *Journal of Theroretical Biology.* **184:** 83-88.

Hurd, P. L., and Enquist, M. 2005. A strategic taxonomy of biological communication. *Animal Behaviour.* **70:** 1155-1170.

Hyman, J., Hughes, M., Searcy, W. A. and Nowicki, S. 2004. Individual variation in the strength of territory defense in male song sparrows: correlates of age, territory tenure, and neighbor aggressiveness. *Behaviour*. **141**: 15-27.

Jarvi, T., and Bakken, M. 1984. The function of the varioatn in the breast stripe of the Great Tit (*Parus major*). *Animal Behaviour*. **32**: 590-596.

Johnstone, R. A. and Grafen, A. 1992. Error-prone signaling. *Proceedings of the Royal Society of London-B*. **248**: 229-233.

Johnstone R. A. and Norris, K. 1993. Badges of status and the cost of aggression. *Behavioural Ecology and Sociobiology*. **32**: 127-134.

Johnstone, R. A. 1997. The Evolution of Animal Signals. In *Behavioural ecology: an evolutionary approach Fourth Edition.* (ed. Krebs, J. R. and Davies, N. B.), pp. 155-178. Oxford, England: Blackwell Science Ltd.

Ketterson, E. D. 1979. Status signaling in dark-eyed juncos. *The Auk.* **96:** 94-99.

Keys, G. C. and Rothstein, S. I. 1991. Benefits and costs of dominance and subordinance in white-crowned sparrows and the paradox of status signaling. *Animal Behaviour*. **42**: 899-912.

Keyser A. J. and Hill G. E. 1999. Condition-dependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament. *Proceedings of the Royal Society of London-B*. **266**: 771-777.

Kirkpatrick, M. Price, T., Arnold, S. J. 1990. The Darwin-Fisher theory of sexual selection in monogamous birds. *Evolution*. **44:** 180-193.

Krebs, J. R. and Dawkins R. 1984. Animal signals: mind-reading and manipulation. In *Behavioural ecology: an evolutionary approach Second Edition*. (ed. Krebs, J. R. and Davies, N. B.), pp. 380-402. Sunderland, Massachusetts: Sinauer Associates.

Langston, N. E., Freeman, S., Rowher, S., and Gori, D. 1990. The evolution of female body size in red-winged blackbirds: the effects of timing of breeding, social competition, and reproductive energetic. *Evolution*. **44**: 1764-1779.

Lemon, R. E., Weary, D. M. and Norris, K. J. 1992. Male morphology and behavior correlate with reproductive success in the American redstart (*Setophaga ruticilla*). *Behavioral Ecology and Sociobiolog*y. **29**: 399-403.

Marler, P. and Tamura, M. 1964. Culturally transmitted patterns of vocal behavior in sparrows. *Science*. **146**: 1483-1486.

Milligan, M. M. and Verner, J. 1971. Inter-populational song dialect discrimination in the white-crowned sparrow. *The Condor*. **73**: 208-213.

Møller, A. P. 1987a. Social control of deception among status signaling house sparrows *Passer domesticus*. *Behavioural Ecology and Sociobiology.* **20**: 307-311.

Møller, A. P. 1987b. Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signalling. *Animal Behaviour.* **35**: 1637-1644.

Møller, A. P. 1992. Frequency of female copulations with multiple males and sexual selection. *The American Naturalist*. **139**: 1089-1101.

Monkkonen, M. 1990. Removal of territory holder causes influx of small-sized intruders in passerine bird communities in northern Finland. *Oikos*. **57:** 281-288.

Morton, M. L. 2002. The mountain white-crowned sparrow: migration and reproduction at high altitude. *Studies in Avian Biology*. **24**: 1-236.

Morton, M. L., Pereyra, M. E., Crandall, J. D., MacDougall-Shackleton, E. A. and Hahn, T. P. 2004. Reproductive effort and return rates in the mountain white-crowned sparrow. *The Condor*. **106**: 131-138.

Odeen, A. and Hastad, O. 2003. Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Molecular Biology and Evolution*. **20**: 855-861.

Otte, D. 1974. Effects and functions in the evolution of signaling systems. *Annual Review of Ecology and Systematics.* **5:** 385-417.

Parker, G. A. 1974. Assessment strategy and the evolution of fighting behavior. *Journal of Theoretical Biology.* **47:** 223-243.

Parsons, J. and Baptista, L. F. 1980. Crown color and dominance in the white-crowned sparrow. *The Auk*. **97**: 807-815.

Qvarnstrom, A. 1997. Experimentally increased badge size increases male competition and reduces male parental care in the collared flycatcher. *Proceedings of the Royal Society of London-B*. **264**: 1225-1231.

Roberts, M. L., Buchanan, K. L., Bennett, A. T. D. and Evans, M. R. 2007. Mate choice in zebra finches: does corticosterone play a role? *Animal Behaviour*. **74**: 921-929.

Rohwer, S. 1975. The social significance of avian winter plumage variability. *Evolution*. **29**: 593-610.

Rohwer, S. 1977. Status signaling in Harris sparrows: some experiments in deception. *Behaviour*. **61**: 107-129.

Rowher, S. 1982. The evolution of reliable and unreliable badges of fighting ability. *American Zoologist*. **22:** 531-546.

Rowher, S. 1985. Dyed birds achieve higher social status than controls in Harris' sparrow. *Animal Behaviour*. **33:** 1325-1331.

Romero, M. L. and M. J. Reed. 2005. Collecting baseline corticosterone samples in the field: is under 3 min good enough? *Comparative Biochemistry and Physiology*. **140**: 73-79.

Romero, M. L. 2010. Corticosterone RIA protocol.

Røskaft , E., Jarvi, T., Bakken, M., Bech, C., Reinertsen, R. E. 1986. The relationship between social status and resting metabolic rate in great tits (*Parsus major*) and pied flycatchers (*Ficedula hypleuca*). *Animal Behaviour*. **34:** 838-842.

Røskaft , E. and Rohwer, S. 1987. An experimental study of the function of the red eapualettes and the black body colour of male red-winged blackbirds. *Animal Behaviour*. **35**: 1070-1077.

Searcy, W. A. 1979. Morphological correlates of dominance in captive male red-winged blackbirds. *The Condor*. **81:** 417-420.

Searcy, W. A. and Wingfield, J. C. 1980. The effects of androgen and antiandrogen on dominance and aggressiveness in male red-winged blackbirds. *Hormones and Behavior*. **14**: 126-135.

Searcy, W. A. and Nowicki, S. 2005. The evolution of animal communication: reliability and deception in signaling systems. *Monographs in Behavior and Ecology.* (ed. Krebs, J. R. and Clutton-Brock, T.) Princeton: Princeton University Press.

Sebeok, T. A. 1965. Animal communication. *Science*. **147**: 1006-1014.

Senar, J. C. 1990. Agonistic communication iin social species: what is communicated? *Behaviour.* **112**: 270-283.

Slotlow, R., Alcock, J. and Rothstein, S. I. 1993. Social status signaling in white-crowned sparrows: an experimental test of the social control hypothesis. *Animal Behaviour*. **46**: 977-989.

Slotlow, R. and Rothstein, S. I. 1995a. Influence of social status, distance from cover, and group size on feeding and vigilance in white-crowned sparrows. *The Auk*. **112**: 1024-1031.

Slotlow, R. and Rothstein, S. I. 1995b. Importance of dominance status and distance from cover to foraging white-crowned sparrows: an experimental analysis. *The Auk*. **112**: 107-117.

Smith, J. M. 1974. The theory of games and the evolution of animal conflicts. *Journal of Theoretical Biology*. **47**: 209-221. (ed. Harvey, P. H. and May, R. M.) Oxford: Oxford University Press.

Smith, J. M. and Parker, G. A. 1976. The logic of asymmetric contests. *Animal Behaviour*. **24**: 159-175.

Smith, J. M., Harper, D.G.C. and Brookfield, J.F.Y. 1988. The evolution of aggression: can selection generate variability? *Proceedings of the Royal Society of London-B*. **319**: 557-570.

Smith, J. M. and Harper, D. 2003. Animal Signals. *Oxford Series in Ecology and Evolution.*

Studd, M. V., Roberstson, R. J. 1985. Evidence for reliable badges of status in territorial yellow warblers (*Dendroica petechia*). *Animal Behaviour*. **33**: 1102-1113.

Schwabl, H. Ramenofsky, M., Schwabl-Benzinger, I., Farner, D. S., Wingfield, J. C., 1988. Social status, circulating levels of hormones, and competition for food in winter flocks of the white-throated sparrow. *Behaviour*. **107:** 107-121.

Swett, M. B., Breuner, C. W. 2008. Interaction of testosterone, corticosterone and corticosterone binding globulin in the white-throated sparrow *(Zonotrichia albicollis)*. *Comparative Biochemistry and Physiology-A.* **151**: 226-231.

Tibbetts, E. A. 2008. Resource value and the context dependence of receiver behaviour. *Proceedings of the Royal Society of London-B*. **275**: 2201-2206.

Veiga, J. P. 1993. Badge size, phenotypic quality, and reproductive success in the house sparrow: a study of honest advertisement. *Evolution.* **47**: 1161-1170.

Veiga, J. P., Puerta, M. 1996. Nutritional constraints determine the expression of a sexual trait in the house sparrow, *Passer domesticus*. *Proceedings of the Royal Society of London-B.* **263:** 229-234.

Viljugrein, H. 1997. The cost of dishonesty. *Proceedings of the Royal Society of London-B*. **264**: 815-821.

Watt, D. J. 1986. A comparative study of status signaling in sparrows (genus *Zonotrichia)*. *Animal Behaviour*. **34**: 1-15.

Weimerskirch, H. 1992. Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction, and survival in the wandering albatross. *Oikos*. **64**: 464-473.

Whitfield, D. P. 1987. Plumage variability, status signaling and individual recognition in avian flocks. *TREE*. **2**: 13-18.

Wingfield, J. C. and Farner, D. S., 1976. Avian endocrinology: field investigations and methods. *The Condor*. **78**: 570-573.

Wingfield, J. C. and Farner, D. S., 1978a. The annual cycle of plasma irLH and steroid hormones in feral populations of the white-crowned sparrow, *Zonotrichia leucophrys gambelii*. *Biology of Reproduction*. **19**: 1046-1056.

Wingfield, J. C., Farner, D. S., 1978b. The endocrinology of a natural breeding population of the white-crowned sparrow (*Zonotrichia leucophrys pugetensis*). *Physiological Zoology*. **51**: 188-205.

Wingfield, J. C., Smith, J. P. and Farner, D. S. 1982. Endocrine responses of white-crowned sparrows to environmental stress. *The Condor*. **84**: 399-409.

Wingfield, J. C. 1985. Short-term changes in plasma levels of hormones during establishment and defense of a breeding territory in male song sparrows, *Melospiza melodia*. *Hormones and Behavior*. **19**: 174-187.

Wingfield, J. C. and Silverin, B. 1986. Effects of corticosterone on territorial behavior of free-living male song sparrows *Melospiza melodia*. *Hormones and Behavior*. **20**: 405-417.

Wingfield, J. C., C. M. Vleck, M. C. Moore. 1992. Seasonal changes of the adrenocortical response to stress in birds of the Sonoran Desert. *The Journal of Experimental Zoology*. **264**: 419-428.

Wingfield, J. C., O’Reilly, K. M. and Astheimer, L. B. 1995. Modulation of the adrenocortical response to acute stress in arctic birds: a possible ecological basis. *American Zoologist*. **35**: 285-294

Yasukawa, K. Butler, L. K. and Enstrom, D. A. 2009. Intersexual and intrasexual consequences of epaulet colour in male red-winged blackbirds: an experimental approach. *Animal Behaviour*. **77**: 531-540.

Zahavi, A. 1975. Mate selection-a selection for a handicap. *Journal of Theoretical Biology*. **53**: 205-214.

Zahavi, A. 1977. The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology*. **67**: 603-605.

Zuk, M., Johnsen, T. S., and Maclarty, T. 1995. Endocrine-immune interactions, ornaments, and mate choice in red jungle fowl. *Proceedings of the Royal Society of London-B.* **260**: 205-210.