



2012

The role of social interactions on the development and honesty of a signal of status

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THE ROLE OF SOCIAL INTERACTIONS ON THE DEVELOPMENT AND
HONESTY OF A SIGNAL OF STATUS

DISSERTATION

A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in the
College of Arts and Sciences
at the University of Kentucky

By
Sanh Kin Diep

Lexington, Kentucky
Director: Dr. Westneat, Professor of Biology
Lexington, Kentucky
2012

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ABSTRACT OF DISSERTATION

THE ROLE OF SOCIAL INTERACTIONS ON THE DEVELOPMENT AND HONESTY OF A SIGNAL OF STATUS

Badges of status are supposed to have insignificant production costs, so use costs are thought to be most important in ensuring signal reliability. Use costs arise from the use of the status signal in social interactions. Social experiences that arise from the use of inappropriate signals in social interactions may drive mechanisms that result in reduced fitness for inappropriate signalers. The role of social control, probing and familiarity in producing use costs was explored. There was no evidence that social control by dominants produced a cost for cheaters and no evidence that social control by subordinates produced a cost for inappropriate signaling by Trojans. Probing produced a cost for cheating when resource value was high but not when resource value was low. Familiarity had some effect on the cost and benefit of cheating but in patterns that were not predicted. Familiarity both eliminated a benefit of cheating and reduced a cost of cheating; therefore it is uncertain how familiarity affects honest signaling. The status signal of the receiver had no effect on the cost or benefits of cheating, and there was no evidence of punishment. Social experiences have the potential to affect signal development to produce a correspondence between signal and status. The effects of social experience on signal production were examined and there was little evidence that social experience influenced bib development. Neither aggression expressed nor aggression received was not predictive of bib size. Additionally, tests on the different measures of winning experience produced conflicting conclusions regarding the relationship between winning experience and bib development.

KEYWORDS: House sparrow, *Passer domesticus*, Status signal,
Social control, Probing

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September 27, 2012

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HONESTY OF A SIGNAL OF STATUS

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ACKNOWLEDGEMENTS

I would like to thank my husband, Xabier, for all the emotional support he provided during our many years together. I would like to thank Dr. David Westneat, my advisor, for the all the guidance and enthusiasm through the life of this dissertation. I would like to thank past Westneat lab members, for providing many insights that helped improve the design of the experiments. I would like to send a big thank you to all the undergraduates that worked on the experiments- without your contribution I wouldn't have been able to perform the experiments. I would also like to thank the University of Kentucky, Department of Biology and the Graduate school for the financial support provided.

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Chapter One: Introduction

Background

Rohwer (1975) observed that some winter birds showed a high amount of intraspecific variability in appearance and hypothesized that some morphological traits that show high variation provide information on the approximate social status of an individual within a group. That is, the magnitude of the trait corresponds with the signaler's resource holding potential (RHP), the ability to win an all out fight. Rohwer (1975) called these traits "status signals" and reasoned that they would allow subordinates to avoid fights they are likely to lose and reduce the frequency of fighting by dominants, thereby reducing the time and energy needed to establish dominance relationships. Fighting should only be necessary in cases in which the dominance relationship is unclear because opponents are signaling similar status (Rohwer 1975). Potential status signals have been found in a variety of taxa, including lizards (Fox et al. 1990a), insects (Tibbetts and Dale 2004) and birds (reviewed in Senar 1999).

Signaling should be evolutionarily stable when cost –benefit tradeoffs result in higher quality individuals benefiting more from an enhanced advertisement (Zahavi 1975, 1977, Grafen 1990, Getty 1998). An integral part of understanding this tradeoff is identifying the costs. "Badges of status" are a type of status signal that are hypothesized to have insignificant production cost (Dawkins and Krebs 1978). The reliability of badges is therefore dependent on other types of costs, such as costs arising from the use of status signals in social interactions (Rohwer and Rohwer 1978, Maynard Smith and Harper 1988 , Owens and Hartley 1991a). These use costs can arise through a variety of mechanisms including social control, probing and punishment. Rohwer (1977) used the term "social control" to described added costs that arose from interactions between the inappropriate signaler and conspecifics. Rohwer (1977) suggested that costs for signaling inappropriately arose due to attacks by true dominants and the need to fight subordinates when subordinates should yield. I will use the term "social control" to describe the costs that arise due to attacks by true dominants and to describe the costs that arise from the need to fight subordinates when subordinates should yield. Probing occurs when a subordinate tests the ability or motivation of an apparent dominant to defend a resource.

Punishment of inappropriate signalers occurs when the aggression displayed by familiar opponents to inappropriate signalers exceeds the aggression displayed by familiar opponents to both individuals that are the same rank as that signaled by the inappropriate signaler and individuals that are the same rank as the true rank of the inappropriate signaler. There is some evidence that the production of black feather patches is independent of condition (Hill and Brawner 1998a, Gonzalez et al. 1999, McGraw et al. 2002) (but see Veiga and Puerta 1996, Griffith et al. 1999a, Fitze and Richner 2002, Griffith et al. 2006); therefore black feather patches may function as badges of status.

Social control by dominants

Some models of signaling show that reliable signaling using conventional signals can be stable if cheaters, individuals that signal higher RHP than their true RHP, pay the cost appropriate for the level signaled (Maynard Smith and Harper 1988). These costs reduce the fitness benefits of exaggerating RHP and individuals experience the highest fitness benefit when they signal appropriately. Aggression by dominants can result in cheaters paying the cost appropriate for the level signaled. The social control hypothesis suggests that cheating is controlled by encounters between cheaters and true dominants. A key prediction for the social control hypothesis is that cheaters fight more frequently with true dominants than controls fight with true dominants. Support for the existence of social control by dominants is mixed and difficult to interpret due to problems in experimental design or small sample sizes. Birds dyed to appear as dominants experienced an increase in frequency of attacks by dominants (Rohwer 1977) and interacted more frequently with dominants than did unmodified controls (Moller 1987a). However, Rohwer's (1977) study lacked a sham treatment to control for the effects of handling and Moller (1987a) pseudosampled. Moller (1987a) introduced multiple birds of the same treatment type to the same flock and then used the introduced birds, instead of the flock, as the unit of observation. Other birds dyed to appear as dominants did not receive more aggression from dominants than did controls (Fugle and Rothstein 1987b, Gonzalez et al. 2002b) and introduced dominants and subordinates received similar levels of aggression from resident dominants (Slowtow et al. 1993). However in some of these studies, small sample size (Slowtow et al. 1993) and effects of familiarity (Gonzalez et al.

2002a) make the results difficult to interpret. A well designed test of the predictions of the social control by dominants hypothesis, in which opponents are unfamiliar and the appropriate units of observation are used has yet to be performed.

Social control by subordinates

Most empirical studies of status signaling have focused on how cheating is controlled and have largely ignored the other type of inappropriate signaling, signaling a lower RHP than actual RHP. Both types of inappropriate signaling can result in unreliable signals. These types of inappropriate signalers are named “Trojans” (Owens and Hartley 1991a). Trojans are non aggressive when food is abundant but aggressive as food becomes scarce. Owen and Hartley (1991a) show that Trojans can invade a population of reliable signalers, replacing individuals signaling high aggression when food is abundant and replacing individuals signaling low aggression when food is scarce. However some conditions of the model are unrealistic, for example, individuals signaling low aggression can share the resource without costs and Trojans can win contests against individuals signaling low aggression without paying a cost though there is no difference in aggression signaled (Maynard Smith and Harper 2003). For status signaling to remain reliable, Trojans should incur costs that individuals of the same rank who are signaling appropriately do not. These costs are likely to come about because Trojans experience increased aggression from subordinates that should defer, but do not. This idea has rarely been tested. Dominant Harris’ sparrows made to appear as subordinates experienced an increase in the ratio of active to passive wins, indicating that more fighting was needed to win the same number of interactions (Rohwer 1977). However, the sample size for this study was low ($n=3$) and a test with a larger sample size needs to be performed before it can be determined if Trojans have added costs that honest signalers do not.

Probing of cheaters by subordinates

Another type of use cost can arise through probing, in which individuals display aggression to assess the ability and motivation of opponents to defend a resource. The level of aggression used to probe opponents that signal high rank may be higher than that used in encounters with opponents that signal the same rank because individuals

anticipate that more aggression will be required to overcome opponents signaling high RHP. Probing by females may be especially important in imposing costs on cheaters. Female house sparrows were more aggressive to males signaling high RHP than to males signaling low RHP (Hein et al. 2003). The authors suggest that females may be using probing to gather information for use in mate choice. Cheaters will likely receive more aggression when probed by females than will honest subordinates and cheaters may be discriminated against in mate choice. Though probing can potentially produce a cost for cheating, it is a controversial type of use cost. Subordinates that probe true dominants pay a high cost; therefore probing is thought to be an unstable strategy (Dawkins and Guilford 1991, Szamado 2000). But value asymmetry, a situation in which one opponent values the resource more than the other, can affect the benefits gained by probing and make probing more likely to occur. The role of probing in imposing costs on cheaters has not been tested though value asymmetry is likely to be common in the natural environment.

Punishment of cheaters

Familiarity may affect the cost and benefits of signaling inappropriately because information gained from repeated interactions or from observing others interacting can enforce or reduce the veracity of the status signal of an opponent. Unfamiliar opponents may use status signals to settle contests and cheaters may be able to dominate opponents they would have likely lost to in a fight. However cheating may be revealed among familiar opponents and the benefits of cheating could be eliminated. Furthermore, cheating may result in punishment. Subordinate paper wasps modified to appear as dominants received more post contest mounts than did controls (Tibbetts and Dale 2004). However it is not clear if punishing cheaters is a stable strategy because punishment is spiteful since the effort put into punishing opponents by an individual may exceed any fitness benefits gained (Nakamaru and Iwasa 2006); this is especially true as once cheating is revealed, the individual will no longer defer to cheaters, thereby minimizing any benefits of punishment. The effects of familiarity on the cost and benefits of cheating have not been examined though birds often interact repeatedly and individuals can observe neighbors interacting.

Development of status signals

If signaling inappropriately is costly, then a mechanism must exist to ensure a match between signal level and RHP during signal development. For badges of status this does not involve condition dependence but instead might be influenced by social interactions. Social experiences such as winning interactions, losing interactions, receiving high aggression or displaying high aggression may be important in signal development. These social experiences may occur in the context of social interactions such as probing. A study by McGraw et al (2003b) provides some initial support. Male house sparrows in the beta rank molted a larger bib than those in the gamma rank, however there was no difference in the bib size of alpha and gamma rank males. Additionally, aggression rate experienced by the house sparrows was positively correlated with bib size; however it is not known if aggression displayed or aggression received affected signal production and more importantly, it is not known if aggression affects bib size or if it only correlates with it. The effects of status are conflated with the effects of aggression as beta birds were both more dominant and experienced more aggression than gamma birds. To examine the effects of social experience on bib development, social rank will need to be applied as an effect in an experiment on bib development.

Study Organism

I propose to use the house sparrow (*Passer domesticus*) as my study organism. Male house sparrows have a dark bib on the throat and breast area that is absent in females (Lowther and Cink 1992). Bib size has been shown to be positively correlated with dominance among males and females (Hein et al. 2003). The size of the bib size is not correlated with condition (McGraw et al. 2002, Poston et al. 2005a) (but see Veiga and Puerta 1996, Griffith et al. 1999a) so the bib likely functions as a badge of status. Aggression among individuals is modulated by the sex of the opponents and bib size of males (Hein et al. 2003). Modifications to bib size affect aggression received but do not result in changes in status (Moller 1987a), suggesting the presence of mechanisms to identify cheaters. In the winter, House sparrows can form large mixed sex flocks that consist of hundreds of individuals (personal observation), so birds may meet unfamiliar

individuals frequently. House sparrows molt once a year in the fall and the bib developed at that time is worn until molt next year (Lowther and Cink 1992).

Aims

I propose to test several hypotheses regarding the role of use costs in maintaining signal reliability and the effects of social interactions on signal development in house sparrows.

1. I propose to test for the existence of social control by dominants by enlarging the bib of house sparrows and observing interactions between the modified birds and known dominants.
2. I propose to test for the existence of social control by subordinates by reducing the bib of house sparrows and observing interactions between the modified birds and known subordinates.
3. I propose to test for the effects of probing on cheaters by enlarging the bib of house sparrows and observing interactions between the modified birds and subjects that have been deprived for different lengths of time.
4. I propose to test for the effects of familiarity on the costs and benefits of cheating by enlarging the bib of house sparrows and observing interactions between the modified birds and subjects over a long period.
5. I propose to test that social experiences at molt can affect signal development by manipulating the social status of juveniles and measuring the size of the bibs developed.

By completing these test I will be able to determine if use costs exist and if so which are important in maintaining reliable signaling. Information about the different types of use costs can be used to refine our models of status signaling. These tests will also be an important first step in understanding how reliable signals are developed and maintained.

Chapter Two: Review of ultimate and proximate mechanisms for maintaining informative status signals

Introduction

Variation in appearance exists between members in many species. Rohwer (1975) proposed that the variation of some morphological traits evolved to signal the approximate status of an individual within a group. The central topic in the study of status signaling is understanding how status signaling remains evolutionarily stable. Signaling high resource holding potential (RHP) allows individuals to dominate conspecifics, therefore it appears beneficial for all individuals to signal high RHP regardless of actual RHP. If all individuals signal high RHP, the signal becomes uninformative and individuals stop attending to it. Zahavi (1977) suggests that evolutionary stability of honest signaling requires that inappropriate signalers bear added costs. These costs can result from the production of the signal, bearing the signal or displaying the signal to conspecifics. Since signaling inappropriately is likely to be costly, mechanisms to ensure a match between status and signal must exist. Hormones may play a role in mediating the match between signal and status because hormones can potentially affect or respond to social experience. I will discuss the role of each type of cost in maintaining the evolutionary stability of honest signaling and the mechanisms that ensure the match between status and signal.

What are Status Signals?

Status signals are ornaments that signal RHP and allow members of a group to establish a dominance hierarchy without a round robin of fights. RHP is indicated by signal level; and qualities that contribute to winning, such as condition and skill, determine RHP. Individuals signaling low RHP (subordinates) should defer to opponents signaling high RHP (dominants). Status signaling allows subordinates to avoid fights they are likely to lose and allow dominants to reduce the number of fights they engage in; thereby reducing time and energy spent establishing dominance relationships. Fighting should only occur in instances when opponents indicate similar RHP. Status signals are most useful when individuals are interacting with strangers frequently and when it is difficult to assess the traits that contribute to winning (e.g. skill). Status signals are found

in species that live in flocks or species that are territorial; and the evolution of at least one type of status signal, the breast patch, has been shown to be significantly associated with winter sociality in new and old world sparrows (Tibbetts and Safran 2009). Status signals are most commonly studied in birds (reviewed in Senar 1999), though they have been found in other taxa, including lizards (Fox et al. 1990b) and insects (Tibbetts and Lindsay 2008). Generally, status signals are ornaments that show variation among individuals and do not contribute to fighting ability. Ornaments that are status signals in birds include combs, black, white or red feather patches, feather tufts and UV reflecting feather patches (Eckert and Weatherhead 1987, Moller 1987b, Evans and Hatchwell 1992, Part and Qvarnstrom 1997, Parker and Ligon 2002, van Dongen and Mulder 2008, Vedder et al. 2010).

The status signaling hypothesis predicts that signaling high RHP is beneficial, as subordinates should defer to individuals signaling high RHP. Individuals signaling high RHP are more likely to dominate conspecifics and are more likely to be avoided by conspecifics. The effects of signal level on the behavior of opponents can be studied using individuals who have been modified to appear as dominants. The results of these manipulation studies show mixed support for the benefits of signaling high RHP. Male house sparrows and female paper wasps modified to appear as dominants did not become more dominant (Moller 1987a, Tibbetts and Dale 2004). However, subordinate siskins and model paper wasps modified to appear as dominants were avoided (Senar and Camerino 1998b, Tibbetts and Lindsay 2008) and subordinate male house sparrows modified to appear as dominants won a larger proportion of fights (Gonzalez et al. 2002b). The differences in the findings of these studies may be due to differences in methodology. In the latter two studies, subordinates were used, and in the former two studies, randomly chosen individuals were used. The effects of change in signal level on agonistic behavior may be more apparent when using subordinates than using randomly chosen individuals, as the change in RHP signaled would be greatest when using subordinates.

Evolutionary stability of status signals

Signaling theory provides a plausible explanation for why variation in appearance may have evolved and attempts to explain how variation is maintained. Specifically, the theory attempts to explain why subordinates do not “cheat” by signaling high RHP though they could potentially benefit from falsely signaling high status. Cheating refers to situations where the perceived RHP of the signaler is higher than their actual RHP. There is another type of incongruous signaling, where individuals (Trojans) signal a RHP that is lower than their true RHP, that can also result in unreliable signaling; however the benefits of signaling a lower quality are not clear (although see Owens and Hartley 1991b). Signaling theory suggests that honest signals are only evolutionarily stable when additional costs are imposed on individuals that signal inappropriately (Zahavi 1975, 1977, Grafen 1990). When individuals of low RHP signal high RHP, they incur costs that an individual with high RHP signaling high RHP would not. Bearers of status signals “chose” a signal level based on the relative costs and benefits of performing each signal level. Because these costs vary with the RHP of the performer, the signal level that maximizes fitness will vary with the RHP of the performer. Individuals maximizing fitness signal at a level that is appropriate for their true RHP, resulting in honest signaling. Since it is the out of equilibrium costs that are important in maintaining evolutionary stability, studying the costs that maintain honest signaling requires the experimenter to ‘force’ an individual to produce a signal that it would otherwise not produce (Szamado 2011b). Maynard Smith and Harper (1995) termed the cost needed to ensure the reliability of a signal “strategic cost”. Strategic cost may result from production costs, bearing costs or use costs (Johnstone 1998b). Signals that are honest because of production or bearing costs are called classic handicaps (sensu Hurd and Enquist 2005) and those that are honest because of costs that result from interactions between the receiver’s response to the signal and the performer’s state are called conventional signals (sensu Hurd and Enquist 2005).

Production Costs of Status signals

Production costs come about because producing a signal requires resources that are scarce and are used for other purposes, so allocating them to signal production results in negative effects on other components of fitness. The degrees to which other components of fitness are negatively affected depend on the condition of the individual; individuals in good condition should be less affected than individuals in poor condition. Because condition likely contributes to RHP, signals that are condition dependent may also act as status signals. A tradeoff between signal production and other components of fitness may occur because material or energy needed to produce the signal are needed for other functions or because the signal can only be produced in the presence of a compound that has negative effects on other functions.

Material costs of signal production

Carotenoid based ornaments are commonly thought to be signals that are condition dependent (reviewed in Olson and Owens 1998) and brighter ornaments are thought to indicate better condition. Carotenoid based ornaments function as status signals in some territorial species (Pryke et al. 2001, Pryke and Andersson 2003), and in at least one flocking species (Pryke and Griffith 2006). Investigations of the carotenoid based ornament of house finches show no or even negative correlations between the signal and status (Belthoff et al. 1994, McGraw and Hill 2000d, b). However, in Gouldian finches, the carotenoid based ornament does appear to function as a status signal (Pryke and Griffith 2006). The red morphs dominate both the yellow and black morphs; and reddening or blackening the head resulted in a change in the proportion of active supplants (Pryke and Griffith 2006). Production of carotenoid based ornaments are commonly thought to be costly because carotenoids, which are needed for signal production, also have immune enhancing effects (reviewed in Hill 1999) and carotenoids can not be manufactured de novo. Carotenoids must be obtained through the diet and the amount of carotenoid in the environment is commonly thought to be limited. Carotenoid displays may reveal stress on the immune system, as carotenoid allocation must be partitioned between the immune system and signal production (Lozano 1994).

Individuals in poor condition are thought to have dull signals because they have inferior immune function and must allocate a larger portion of their carotenoid reserve to bolster the immune system, resulting in an equal reduction in carotenoids available for signal production. The amount of carotenoids needed by the immune system is dependent on the condition of the individual; this sets up a condition dependent tradeoff between signal production and immune function. Support for a condition dependent tradeoff between carotenoid based ornament production and immune function is weak. It is not known if immune systems in wild birds are carotenoid limited (Hill 1999, Lozano 2001) and though studies of mate choice signals show carotenoid supplementation enhances display quality and immune function (Blount et al. 2003, McGraw and Ardia 2003) and immune challenges reduced signal quality (Faivre et al. 2003, Alonso-Alvarez et al. 2004), a condition dependent trade off between carotenoid display production and immune function has not been demonstrated. If a condition dependent tradeoff exists, bright individuals on a low carotenoid diet should mount a stronger immune response than dull individuals on a low carotenoid diet. The immune response of American goldfinches on a low carotenoid diet was independent of signal quality (Navara and Hill 2003). Carotenoid signal production and immune function do appear to tradeoff, but thus far, the tradeoff does not appear to be condition dependent.

Melanin based ornaments are commonly thought to be inexpensive to produce because melanin is synthesized from a common amino acid, tyrosine. Tyrosine can be obtained in the diet or can be synthesized from phenylalanine, another amino acid (Lerner 1953). It has been suggested that melanin based ornaments may have production costs because tyrosine may be limited in the diet and a tradeoff may occur between the use of tyrosine in signal production and the use of tyrosine to form proteins used for other functions (Jawor and Breitwisch 2003). There is some evidence that melanin based ornaments are condition dependent (Griffith et al. 1999b) and access to high quality food affect the signaling component of the melanin based ornament (Tibbetts 2010). It is unknown what aspect of the diet is important in melanin signal production. The signaling component of melanin based signals does not appear to be affected by dietary restriction of tyrosine and phenylalanine (Poston et al. 2005b). However, other compounds, such as metal cofactors of tyrosinase, the enzyme that catalyzes the rate-limiting step in

melanogenesis, may also limit the production of melanin based ornaments and may be important in other functions (Jawor and Breitwisch 2003). For example, coenzyme copper is needed for the production of hemoglobin; and the coenzyme iron is needed for the production and maintenance of red blood cells (reviewed in Jawor and Breitwisch 2003). At low levels, the use of copper and iron in these functions may trade off with use in melanin based ornament production. Additionally, it has been suggested that dietary minerals may be important in melanin based ornaments (McGraw 2003), and there is some evidence that calcium may play this role (McGraw 2007); however a calcium limited diet did not result in the reduction of a melanin based ornament in House sparrows (Stewart and Westneat 2010). It is unknown if access to an unknown compound in the diet is linked to the development of the signaling component for all melanin based signals, or if diet is important for only those species that develop the signal only once and prior to social interactions, as is the case with paper wasps (Tibbetts 2010). Birds that renew the signal at molt annually may use alternative methods of matching social status to signal, e.g. through social experience.

Energetic cost of signal production

Though energetic costs may affect signal production there are few studies that have addressed this hypothesis. Hill (2000) found that access to food affected the quality of the carotenoid signal produced, with house finches on unrestricted diets growing brighter and redder plumage than house finches on restricted diets. However the effect of caloric intake were conflated with the effects of other nutritional components as no attempts were made to control the intake of other nutritional components.

Costs of signal production mediated by hormones

The immunocompetence handicap hypothesis suggests that high levels of testosterone are needed for the production of traits signaling good condition and high levels of testosterone negatively affect immune function (Folstad and Karter 1992). Testosterone has been shown to affect melanin based signals (Evans et al. 2000), and the production of spurs, combs and wattles are testosterone dependent (reviewed in Owens and Short 1995); however effects of testosterone on immune function are mixed. No correlation between testosterone level and antibody response to keyhole limpet

hemocyanin was observed in testosterone implanted red wing blackbird (Hasselquist et al. 1999). Similarly, cell mediated response to phytohaemagglutinin and humoral response to sheep red blood cell were not correlated with testosterone level in testosterone implanted house sparrows (Evans et al. 2000, Buchanan et al. 2003b). However, testosterone level was related to humoral response in intact house sparrows (Buchanan et al. 2003b) and testosterone implants suppressed humoral response in female, but not in male, *Geopelia cuneata* (Casagrande and Groothuis 2011). There is little support that production of melanin displays trade off with immune function. Immune challenges in American goldfinch (McGraw and Hill 2000c) and house finch (Hill and Brawner 1998b) do not affect melanin pigmentation; however the melanin based ornament studied was not known to act as a signal and therefore no tradeoff was expected. There does not appear to be a testosterone-mediated tradeoff between melanin based status signal production and immune competence; however there is some evidence that high levels of testosterone can affect basal metabolic rate, another component of fitness (Buchanan et al. 2001). Male house sparrows implanted with high levels of testosterone had higher basal metabolic rate and greater increase in bib size. It is not clear if an increase in basal metabolic rate positively or negatively affects fitness as higher metabolic rate result in larger energy demands but may also increase foraging activity.

Bearing Costs of Status Signals

Traits that signal status may attract predators and individuals signaling higher RHP may be more conspicuous to predators. Increased exposure to predators may control cheating from spreading (Fugle and Rothstein 1987b). If condition were positively correlated with the ability to defend against predators, only individuals in good condition would be able to survive while bearing a signal of high RHP. If predation is important in controlling cheating, cheaters will have higher predation rates than honest subordinates or honest dominants. No studies that have tested this prediction. Studies on conspicuousness and predation suggest that conspicuous individuals suffer higher predation rates (Gotmark and Olsson 1997) (but see Gotmark 1993). Fledgling great tits colored red suffered more predation than yellow colored controls, though both were reared in the same nest (Gotmark and Olsson 1997). However parents also fed red fledglings more

frequently, therefore red fledglings may have been larger and therefore preferred by predators. No studies have addressed the effect of status signal levels on predation attraction or determined if status signal predicts ability to defend against predators. Reyer et al. (1998) found a positive correlation between signal level and intensity of nest defense in house sparrows; but the study did not measure success of defense.

Use Costs of Status Signals

Conventional signals appear to be vulnerable to cheating because the signals are inexpensive to produce or bear, however selection should favor precise and accurate conventional signals because costs from conventional signals arise from errors between what the receiver perceives the signal to mean about the state of the signaler and the actual state of the signaler, and selection should act to minimize those costs (Lachmann et al. 2001). Game theory models suggest that honest signaling can be an evolutionarily stable strategy when cost of the fighting increases steeply with respect to the benefits of winning and cheaters pay the cost appropriate for the level signaled (Maynard Smith and Harper 1988). Cheating then would not spread because cheaters would experience high costs when they encounter individuals that are aggressive. Aggressive individuals fight other individuals signaling high aggression and the cost of fighting increases with aggression. When fighting costs are high relative to the value of the resource, the net benefit of cheating is sharply reduced. This idea is supported by the models of Szalai and Szamado (2009), which suggest that honest signaling is most likely to evolve when resource value is low in comparison to cost of fighting. Maynard Smith and Harper (1988) models also suggest that for signaling to remain honest, cheaters should fight more often with individuals signaling high aggression and fighting among individuals signaling high aggression should be more costly than fighting among individuals signaling low aggression. However, signaling aggressiveness requires assumptions that are not likely to be met (Hurd 2006), suggesting that it is likely that other characteristics are being signaled. If it is RHP that is signaled, these requirements for evolutionary stability are congruent with Rohwer's (1977) proposal that status signaling remains evolutionarily stable as a result of social control of deception. Social control of deception results when dominants direct more aggression at individuals signaling high RHP than at individuals

signaling low RHP. The increased cost of fighting a dominant outweighs benefits of cheating.

Aggression from dominants

Rohwer (1977) argued that it was not logical for dominants to attack cheaters, as efforts put into “persecuting” cheaters seem to exceed any fitness loss that dominants experience due to successful cheaters. However Maynard Smith and Harper (1988) suggest that highly aggressive individuals always fight vigorously against other individuals signaling an equally high value, because in an honest population vigor is usually needed to win. In an honest population, vigor is also required to overcome opponents signaling high RHP, therefore dominants may attack cheaters. Furthermore, it may pay to be aggressive towards an opponent who signals high RHP and acts submissively because being aggressive may ensure submissiveness in the next encounter. Opponents who signal similar or higher levels of RHP should be more threatening than opponents who signal lower RHP because opponents signaling similar or higher RHP should be more likely to win. Keys and Rothstein (1991) found that when the outcome of an interaction was least predictable, the cost of losing was higher. When competition among white crowned sparrows involved individuals from the same age-sex class or when competition resulted in an individual from a normally dominant group losing to an individual from a normally subordinate group, the loser was driven from the feeding area instead of just being displaced from the feeding spot. In addition, escalating aggression may reinforce the status of the dominant individual. There is evidence that losing experiences can reduce aggression in future interactions by elevating levels of serotonin in losers; and the loser effect suggests that reinforcing the losing experience will make reversals less likely in future interactions (reviewed in Oliveira 2004). Loser effects can last up to several days in some species, thus it may be beneficial for dominants to reinforce dominance even in the absence of a contested resource.

There is evidence that interacting with flock members is costly for cheaters; some Harris sparrows painted to appear as dominants were relegated to foraging on the periphery of the flock or foraging when the flock was absent (Rohwer 1977). The social control hypothesis predicts that cheaters will fight more often with dominants than honest subordinates will fight with dominants and fighting dominants will be more costly than

fighting subordinates. Support for the existence of the first prediction is mixed (Table 2.1). Subordinate Harris sparrows dyed to appear as dominants experienced an increase in frequency of attacks by dominants (Rohwer 1977) and house sparrows with enlarged bibs interacted more with opponents having larger bibs than did controls (Moller 1987a). However dominants were as aggressive to subordinate white crowned sparrows and female chaffinches painted to appear as dominants as they were to controls (Marler 1955, Fugle and Rothstein 1987b). There appears to be some fitness costs related to cheating. Survivorship of male house sparrows with bibs enlarged to a fixed size was positively related to their natural bib size (Nakagawa et al. 2008); the authors suggested that the differential cost for cheating was due to social control by large bib opponents and differences in discrepancy between signaled RHP and actual RHP. Thus far no studies have attempted to determine in what way fighting with dominants is more costly than fighting subordinates (e.g. injury rate). If fighting dominants is more costly, one would expect to find higher rates of injury among cheaters than among honest subordinates; however injury has not been reported in any studies of cheaters (Marler 1955, Rohwer 1977, Fugle and Rothstein 1987, Moller 1987a). Dominants may also impose cost on cheaters after status has been established. For example, subordinate paper wasps modified to appear as dominants receive more post contest mounts (where subordinate allows dominant to climb onto her head) than controls (Tibbetts and Dale 2004).

Aggression from intermediates and subordinates

It is possible that subordinates and intermediates may also identify cheating and adjust their behaviors to eliminate the benefits of cheating. Cheaters will likely behave submissively, rather than aggressively when confronted by a dominant and if flock members are attentive to interactions between other flock members, the incongruence between behavior and signal will reveal cheating and the identity of the cheater becomes public information. Additionally, if cheaters lose to subordinates, then cheating will also be revealed. Though the status signaling hypothesis predicts that it is beneficial for subordinates to avoid dominants, this may not apply in all situations. One example is when the contested resource is more valuable to the subordinate than to the dominant. When value asymmetry is large, status signals may not be as important in determining contest outcome and hungry individuals signaling low RHP may be more likely to win

than satiated individuals signaling high RHP. House sparrows that were deprived longer won more often regardless of RHP signaled (Andersson and Ahlund 1991). Hungry subordinates and intermediates may display some aggression (probe) to dominants to determine if dominants are motivated enough to defend the resource. Subordinate gold finches were more likely to initiate encounters against dominants when they had been starved (Popp 1987). Dominants that are probed by intermediates or subordinates will likely respond with some aggression to assert their dominant status, even if they are unmotivated to defend the resource. Repeated probing may then lead to the unmotivated dominant yielding the resource. Intermediates that probe cheaters will receive little aggression and the resource will be yielded quickly because cheaters perceive intermediates to be dominant. When cheaters behave submissively to intermediates, cheating may be revealed. Again, the identity of the cheater may become public information if flock members are observing. Once cheating is revealed, subordinates and intermediates should no longer defer to cheaters. Subordinates are predicted to initially avoid cheaters because they perceive cheaters to be dominant, but as opponents become familiar, and cheating is revealed, cheaters should no longer be avoided and subordinates should initiate more interactions against cheaters. Familiarity should not affect how often subordinates initiate interactions against controls (true dominants). Studies on cheating suggest that cheaters do fool intermediates and subordinates in the first few days after introduction (Fugle et al. 1984b, Rohwer 1985a) and may even fool them for longer (Fugle and Rothstein 1987b). Presently, there are no studies that have determined if subordinates that initially avoid cheaters continue to avoid cheaters in the long term.

Intermediates may persecute cheaters once cheating is revealed. Intermediates may be more aggressive to cheaters because intermediates may try to reinforce dominance over individuals that are known subordinates but are signaling dominance. If intermediates are more aggressive to cheaters than to honest subordinates, then costs resulting from increased aggression will make honest signaling more likely. Cheaters that have been in the flock for a long period will receive more aggression than honest subordinates if intermediates persecute cheaters. Observations of interactions between cheaters and subordinates suggest that subordinates are equally aggressive to cheaters and controls (Fugle and Rothstein 1987b). However it is possible that these observations were

done before cheating was revealed. Long-term studies are required to determine if there is social persecution of cheaters by subordinates.

Aggression related to mate choice

Cheaters may also incur costs due to interactions related to mate choice. Female house sparrows tend to direct more aggression at males that signal high RHP than to males that signal low RHP (Hein et al. 2003). The authors suggest that females may be using aggression to assess the quality of opponents as potential mates. Cheaters may receive more aggression from females than honest subordinates. Additionally, probing by females may also reveal cheating. When the opponent is female, males signaling high RHP are more aggressive than males signaling low RHP. When females initiate aggression against cheaters, cheaters will display less aggression than dominants and cheating will be revealed. Intersexual interactions that provide information about potential mates may also contribute to the evolutionary stability of honest signaling because females may display more aggression to cheaters than to honest subordinates and interactions with females may reveal cheating.

Social control of cheating in territorial species

The cost and benefits of signaling high RHP may be different in species that use status signals in territorial interactions than in species that use status signals for interactions within a flock. Resource value may differ in the two contexts. In flocking species, usually the resource contested is food and individuals likely engage in numerous contests per day with multiple opponents for access to food. In territorial species, the resource contested is territory, which includes the benefits of access to food and mate; and there are likely to be fewer contests and fewer opponents. Likely, the cost of fighting is the same in both contexts, but the ratio of cost to benefit will differ. These differences in the cost benefit ratio will change the cost and benefit of cheating and result in different mechanisms to maintain signal honesty. Though the status signaling hypothesis predicts that individuals signaling high RHP should receive less aggression, the results from intruder presentation experiments are mixed. Pryke et al. (2001)'s found that male red-collared widowbird territory owners approached models signaling low RHP closer than models signaling high RHP. However yellow warbler models signaling high RHP

solicited a higher response score (a composite of distance approached, rate of vocalization and number of movements) than yellow warbler models signaling low RHP (Studd and Robertson 1985). Additionally, in flocking species, there is the possibility that the identity of the cheater becomes public information and flock members can adjust their behavior to eliminate the benefits of cheating in future interactions and cheaters would need to leave the flock in order to find naïve opponents. In territorial species, there is no public information available, and once a cheater is discovered they can relocate to a territory with a naïve owner (Rohwer 1982). The cost of joining a new flock is likely more costly than finding naïve territory owners and therefore should contribute to the difference in cost and benefits of cheating in the different contexts.

Cheating and stress hormones

Cheating may be controlled through the negative effects of corticosterone, a stress hormone, on fitness. Corticosterone is a glucocorticoid, a class of stress hormones that are controlled by the Hypothalamus-Pituitary-Adrenal (HPA) (Sapolsky 1992b). Glucocorticoids are found in a variety of forms. Among primates, cortisol is the dominant form; and among rats and birds, corticosterone is the dominant form. The terms corticosterone, cortisol and glucocorticoids will be used interchangeably. In the presence of stressors, briefly elevated glucocorticoid levels are beneficial because it results in the mobilization of energy for immediate use, enabling the animal to respond to the stressor. However elevating glucocorticoid levels for prolonged periods can result in negative effects such as the inhibition of gonadal activities, suppression of the immune system, suppression of growth, severe protein loss, and impaired brain function (Sapolsky 1992b, Silverin 1998, McEwen and Wingfield 2003, Wingfield 2003). Fitness can also be negatively affected by high levels of glucocorticoids. Lower over winter survival was observed in house sparrows with high levels of glucocorticoids in feathers after post-nuptial molt (Koren et al. 2012). If cheaters receive additional aggression from flock members, they will likely experience more stress than honest subordinates. Animals exposed to stressors repeatedly will lose the ability to regulate glucocorticoid levels and start to secrete glucocorticoids in non-stressful circumstances (Sapolsky 1992b). Therefore glucocorticoids are likely to be higher in cheaters than in honest subordinates

and chronically elevated levels of glucocorticoids may reduce the fitness of cheaters in comparison to subordinates that are signaling appropriately, and this in turn may prevent cheating from spreading. However, Gonzalez et al (2002b) found no difference in the corticosterone level of subordinate house sparrows made to appear as dominants and the corticosterone level of controls.

The negative effects of glucocorticoids may also explain how individuals that signal a lower RHP than their actual RHP are controlled. These types of inappropriate signalers (Trojans) need to engage in frequent fights to maintain high status because they are signaling subordinate status and unfamiliar opponents will assume they are subordinate. Dominant Harris sparrows made to appear as subordinates increased the ratio of active to passive wins, indicating that they had to engage in more fights to win the same number of interactions (Rohwer 1977). However, the sample size for this study was low (n=3). Trojans will likely engage in more fights than dominants that are signaling appropriately, and thus have elevated levels of glucocorticoids. Inappropriate signalers will likely have depressed immune function, reduced muscle mass and depressed levels of testosterone in the mating season. The negative effects of chronically elevated levels of glucocorticoids will likely reduce the fitness of these inappropriate signalers. No studies have examined the long-term hormone profiles of inappropriate signalers. However, Lindstrom et al. (2005) suggests that there may be hormone-mediated costs to occupying a status that is inappropriate for an individual's RHP. Small house sparrows, which are subordinate, had higher levels of corticosterone when occupying a dominant position and large house sparrows, which are dominant, have higher levels of corticosterone when occupying a subordinate position. Additionally, small birds in dominant positions and large birds in subordinate positions had depressed cell-mediated immune response. However there was no correlation between signal level and status in the study, so it is unknown if individuals signaling low RHP in dominant positions and individuals signaling high RHP in subordinate positions have higher corticosterone than individuals occupying positions that corresponded with their signal. Additionally, for cheaters it is unknown if stress from increased exposure to aggression is larger than the reduction in stress due to increased access to food.

Signal Production

Signaling inappropriately will likely have negative fitness consequences; therefore selection would favor mechanisms that ensure a correspondence between the status of the individual and the signal the individual produces. Social experiences appear to be associated with signal production but the nature of the relationship is unclear. Male house sparrows that experience aggressive environments during molt have a greater change in bib size and grow larger bibs (McGraw et al. 2003b). However, it is unknown if bib development is related to the aggression received or aggression displayed; and if the relationship is correlative or causative. There are two general mechanisms which can match status to signal level. In the first mechanism, a hormone simultaneously affects status and signal production. In the second mechanism, status affects the release of a hormone that affects signal production. Two hormones that can potentially play a role in correlating status and signal are testosterone and corticosterone. Testosterone is thought to promote aggression and thus social dominance, and corticosterone is secreted in response to stress, which may be affected by social status.

Role of a possible status-affecting hormone in signal production

Testosterone may play a role in correlating status by simultaneously affecting status and signal production. Testosterone may affect status because testosterone can affect aggression (Leshner and Moyer 1975, Poiani et al. 2000), which is often correlated with dominance (e.g. Hegner and Wingfield 1987). Castrated individuals exhibit reduced levels of aggression and testosterone implants often restore aggression (Leshner and Moyer 1975). However testosterone does not cause aggression, it acts as a promoter of aggression, making it more likely to occur in the presence of stimuli (reviewed in Simon 2002a). For example, juvenile male satin bowerbirds with testosterone implants were more likely to initiate aggression, but they were selective at whom they direct aggression (Collis and Borgia 1992). The implanted juveniles initiated aggression more often against other juveniles and females but not against adult males, which are normally dominant. However, some species appear to be insensitive to increased levels of testosterone. Testosterone implants did not increase aggression in Gambel's white crowned sparrow in the late breeding period (Meddle et al. 2002) and no difference in aggression was

observed between testosterone implanted male rufous-collared sparrows and controls during the breeding season (Moore et al. 2004). However these studies used intact males, so androgen receptors may already have been saturated and no increase in response was possible. These and other studies (Wingfield and Hahn 1994, McDonald et al. 2001, Meddle et al. 2002, Moore et al. 2004) suggest that the relationship between aggression and testosterone is complex, and levels of circulating testosterone do not necessarily correspond with levels of aggression. Additionally, there is evidence that the relationship between testosterone and dominance is dependent on the level of glucocorticoids (Mehta and Josephs 2010).

The complexity of the relationship between testosterone and aggression is partially explained by the “Challenge Hypothesis” (Wingfield et al. 1990). The challenge hypothesis posits that aggression is correlated with testosterone only during periods of social instability. This correlation is seasonal, present only during the breeding period when males are engaged frequently in contest over breeding territory and mates. Once the period of social instability has passed, testosterone is suppressed to prevent interference with parental care behavior. Outside of the breeding period, testosterone levels are low though aggression can still be high (Wingfield and Hahn 1994). The challenge hypothesis is supported by studies using simulated territorial intrusions in the breeding period (e.g. Silverin 1993). Though the Challenge Hypothesis only predicts a correlation between testosterone and aggression during the breeding period, a similar phenomenon may occur in flocking species during flock formation. During flock formation, unfamiliar individuals interact frequently, similar to the territorial establishment phase of the breeding period. Social instability during flock formation is similar to the social instability during the breeding period, when the correlation between aggression and testosterone occurs. This suggests that a correlation between aggression and testosterone may also occur during flock formation, the period when plumage signals are produced. Of the small number of studies that have examined the relationship between aggression and testosterone in flock formation species, the results support the existence of a positive correlation. In the period before the flock hierarchy becomes stable, aggression and testosterone in house sparrows was positively correlated (Hegner and Wingfield 1987). In addition, aggression in white-throated sparrow was correlated with testosterone in

November, when flocks are forming, but not in January, after flocks have already formed (Schlinger 1987).

Though testosterone levels correlate with aggression, a component of dominance, testosterone levels do not necessarily affect status. Studies using testosterone implants in captive and free living birds show contradictory results. Testosterone implants increased dominance of captive white throated sparrows and house sparrows (Archawaranon and Wiley 1988, Poiani et al. 2000) but not of free living white throated sparrows (Archawaranon et al. 1991). Naturally circulating levels of testosterone during periods of social stability do not appear to predict status (Table 2.2); and it is not clear if elevated levels of testosterone result in elevated status.

Testosterone is correlated with signal level in natural populations (Gonzalez et al. 2001) and there is some evidence that testosterone can directly affect signal production. Development of non plumage status signals (e.g. combs) is typically under the control of testosterone (Owens and Short 1995). Comb growth in male jungle fowl is dependent on the amount of viscous intercellular mucoid and mucoid is produced by the fibroblasts of the connective tissue in the presence of testosterone (reviewed in Ligon et al. 1990). Additionally, testosterone injections result in comb growth (Stokkan 1979). However the relationship between testosterone and signal development in natural situations seem more complex. Testosterone of male jungle fowl is positively correlated with comb size when housed in flocks but not when housed in isolation (Parker et al. 2002). This suggests that the relationship between testosterone and comb development can be affected by social experience. Birds housed in isolation also experienced a larger increase in testosterone, suggesting that social interactions depressed testosterone levels. Perhaps testosterone levels in isolated birds were so high that maximum physiological response was achieved by most of the birds and variation in testosterone was unimportant for comb growth. The authors suggest that this is not the case because the range of testosterone levels for flock reared and isolated birds were the same. However comparing ranges does not provide information on the proportion of birds that have testosterone levels that result in maximum physiological response.

The relationship between testosterone and other types of status signals is also complex. For example, feathers of castrated house sparrows plucked from the upper

breast area (where the status signal is located) regenerate with normal melanin pigmentation (Keck 1934), suggesting that testosterone is not important in the development of melanin based signals. However male house sparrows implanted with high levels of testosterone molt into larger bibs than males implanted with low levels of testosterone or no testosterone (Evans et al. 2000) and chicks hatched from eggs injected with testosterone develop larger bibs than chicks hatched from eggs injected with just vehicle (control) (Strasser and Schwabl 2004). The results of these studies suggest that testosterone does affect development of melanin displays but the effect is not direct. In the testosterone implant and injection studies (Evan et al. 2000; Strasser & Schwabl 2004), individuals from different treatment groups were housed together so it is unclear if testosterone directly affected bib development or if testosterone resulted in behavior that affected the social experience of the birds assigned to different treatments. Birds with different social experiences will likely have different hormone profiles and this in turn may affect signal development. Individuals with low levels of testosterone may have more losing experiences, resulting in the down regulation of hormones that cause melanization. Castrated individuals are still able to produce melanin because the hormones that cause melanization are still functional, but testosterone in flock reared birds prevent those hormones from being down regulated in the presence of conspecifics. This hypothesis suggests that individuals reared in isolation will signal high RHP and the signal will not be correlated with status, and individuals reared in flocks will have larger variation in signal level and signal will be correlated with status. However, as discussed previously, testosterone does not affect status in a consistent manner, so testosterone is not likely to play a role in regulating the hormones that cause melanization. Furthermore, data from captive flocks of house sparrows show no correlation between testosterone levels in the fall and molted bib size (Laucht et al. 2010); but birds in the study had already been housed together for a long period prior to the hormone measure and therefore were not in the process of establishing a hierarchy. However, Laucht et al. (2011) study of day time and night time testosterone levels in free living house sparrow found a correlation between night time testosterone and bib size for birds sampled in the summer, but not for those sampled in the fall when birds were forming flocks.

Role of a possible status-responding hormones in signal production

It appears that social experience can play an important role in signal development. This is expected if social status and signal level are to be congruent. An individual's RHP may change between molts and the incongruence between the signaled RHP and the true RHP may result in social experiences that will produce an appropriate signal level at the next molt. Individuals whose RHP has increased from the previous molt will signal a lower RHP than they should. Because the individual is signaling a lower RHP than actual, they are likely to interact with subordinates that would avoid them if they were signaling appropriately. Since these opponents have lower RHP, the individual is likely to have many winning experiences. These winning experiences may result in the production of a trait that signals high RHP. An individual whose RHP has decreased since the previous molt will likely interact with opponents with higher RHP, and therefore will likely have many losing experiences. The losing experiences may result in the production of a trait that signals low RHP. Hormones that respond to social experience will likely be important in producing an appropriate signal.

Corticosterone is secreted in response to stress and therefore corticosterone levels may depend on social status. The relationship between status and glucocorticoid level is complex and likely differ between species. Initially, it was thought that status and glucocorticoids levels would be negatively correlated because subordinates were thought to experience more stress as a result of reduced access to food and mates, and increased harassment from dominants. This suggests that subordinates, who are thought to be exposed to more stressors than dominants, should have high baseline glucocorticoid levels. Negative correlations were observed between dominance and glucocorticoid levels in early studies (reviewed in Creel 2001); however, as Creel et al (1996) pointed out, those early studies were conducted on captive animals, and social dynamics in captivity may not reflect those in the wild. Creel et al (1996) suggested that among wild animals, dominants were the ones that were more stressed because subordinates can avoid aggressive interactions by avoiding dominants or by fleeing, while dominants initiate aggressive interactions to enforce social dominance. Creel et al (1996) found some support for this hypothesis; among African wild dogs and female dwarf mongooses, dominants did have higher baseline corticosterone concentrations than subordinates.

However, not all wild animals showed a positive correlation between glucocorticoids and dominance (Sapolsky 1990).

An important factor that can influence the relationship between status and glucocorticoid concentration is the stability of the dominance hierarchy (Sapolsky 1990). Psychological variables such as amount of control, amount of predictability and number of outlets for frustration can affect stress response (Sapolsky 1992b). Dominant and subordinate individuals vary in the ways in which they experience these psychological variables. For dominant individuals, the way they experience these psychological variables depend on the stability of the hierarchy. In stable hierarchies, dominants experience very little aggression, have large amount of control over outcomes of conspecific interactions, determine when conspecific interactions start and end, and have many subordinates on which to vent their frustration. By contrast, dominants in unstable hierarchies experience high levels of aggression, do not have a large amount of control over the outcome of interactions and have few subordinates that would tolerate bullying. Dominant individuals in stable hierarchies are predicted to have lower baseline glucocorticoids concentrations than subordinates and have as large a stress response as subordinates. Dominant individuals in unstable hierarchies are predicted to have the same or higher baseline glucocorticoids concentrations as subordinates and to have the same or smaller stress response as subordinates. These hormone profiles are observed in some species. Female Rhesus monkeys in recently formed groups show no correlation between baseline cortisol concentrations and dominance rank, but in long-term groups, subordinates have higher baseline cortisol concentrations (Gust et al. 1993b). However this relationship is not always observed. For example, dominant naked mole rats have higher cortisol concentrations than subordinates during periods of social stability and during periods of social instability there is no correlation between rank and cortisol (Clarke and Faulkes 1997). Additionally, wild male baboons showed a negative correlation between dominance and glucocorticoid level regardless of hierarchy stability (Gesquiere et al. 2011). These results suggest that hierarchy stability alone is not sufficient to explain the patterns of glucocorticoid secretion.

Within species that form flocks and use status signals, the status signaling hypothesis predicts that dominants should be less stressed since they are able to dominant

resources without fighting. Field studies of house sparrows and Harris sparrows, two flocking species that use melanin based signals, show no consistent positive or negative relationship between baseline corticosterone level and status (Table 2.3). Understanding the relationship between status, stress, and corticosterone level is important because pleiotropy in the melanocortin system suggests that positive correlations should exist between stress-resistance (in terms of increased glucocorticoid levels), darkness and aggressiveness (Ducrest et al. 2008). Melanocortins, which include melanin-stimulating hormones (MSH) and adrenocorticotropin hormone (ACTH), bind to G-protein-coupled melanocortin 1 receptor (MC1R) to produce black-brown eumelanin pigment instead of yellow-reddish pheomelanin, but also bind to MC5R to promote aggression and bind to MC4R to reduce oxidative stress. Stress stimulates the production of ACTH; and both ACTH and MSH increase the production of glucocorticoids, which activates the body's response to stress. There is evidence that darker individuals are more aggressive and more stress resistant. However, dominants are not necessarily darker despite the relationship between aggressiveness and dominance. Subordinate arctic charr had higher glucocorticoids and ACTH levels; and becoming subordinate increased the darkness of individuals (Hoglund et al. 2000). The relationship between stress and darkness is further complicated by the inhibitory effect of glucocorticoids on the production of melanocortins and on melanogenesis (Roulin et al. 2008). Furthermore, it appears that the dark individuals have reduced response to stress; barn owl nestlings of darker mothers had lower glucocorticoid levels after handling and cleared glucocorticoids more quickly than nestlings of lighter mothers (Almasi et al. 2010). Though stress and melanin production do appear to be related, the relationship is not a simple correlation and it is unclear how status is related to stress within flock forming species.

Another hormone that appears to be affected by status is testosterone. A strong correlation between androgen levels and status of male cichlids was observed after group formation but not before group formation (Oliveira et al. 1996). Studies on humans, non-human primates and mice also found correlations between status and post contest testosterone level (reviewed in Simon 2002a, Oyegbile and Marler 2005). During the contest, testosterone levels of participants became elevated; after the contest, testosterone levels of winners remain temporarily elevated and those of losers were temporarily

depressed (reviewed in Oliveira 2004). The changes in testosterone level lasted longer in losers than in winners (reviewed in Oliveira 2004). However status did not predict testosterone levels in all species. Post contest testosterone levels of winner and loser male tree lizards did not differ (Knapp and Moore 1995) and no difference was observed in the testosterone levels of male copperhead winners, losers and controls after a contest (Schuett et al. 1996). Furthermore a correlation between status and post contest testosterone levels is insufficient proof that social status affects testosterone. A correlation could also be observed if birds that secrete higher levels of testosterone during a contest are also more likely to become dominant. However there is some evidence that status affects testosterone level. A study in which winning experience was manipulated showed that mice that had 3 winning experiences have higher testosterone levels than mice with 0 or 1 winning experience (Oyegbile and Marler 2005).

Glucocorticoids do not seem to vary with status in flock forming species that use status signals and it is unclear if testosterone levels vary in response to status in flocking species. Since testosterone implants do affect signal production and testosterone levels do respond temporarily to status in some species, it is possible that the temporary differences in testosterone levels of winners and losers following a contest is sufficient to result in the production of different signal levels. Perhaps during flock formation individuals experience interactions frequently enough to produce a sustained change in testosterone levels. This change lasts until signals are developed. Following signal development, the number of encounters is reduced because subordinates recognize dominants by their signal and avoid them. This then results in fewer losing experiences and testosterone becomes uncoupled from status. This suggests that birds reared in isolation during molt will have signals that are incongruent with RHP while those reared in the presence of conspecifics will have signals that are congruent with RHP.

Conclusion

The costs that make status signaling evolutionarily stable are still unknown and these costs may differ for the different types of status signals. It appears that there are material tradeoffs between signal production and other components of fitness for carotenoid signals. However these tradeoffs do not appear to be condition dependent. At

least one melanin based ornaments is dependent on access to high quality food, but it is unclear if this is a general mechanism for all melanin based signals. The role of predation in controlling cheating is largely unexplored and support for the existence of social control of cheating is mixed. Though long-term costs, such as aggression following the revelation of cheating, are likely to be important in preventing cheating from spreading, long-term studies of the costs of cheating are lacking. Social interactions are likely to play an important role in matching status with signal level, however the mechanisms and role of the hormones testosterone and glucocorticoids are unclear.

Table 2.1 Studies examining the cost and benefit of cheating. Status signals in studies were modified to create cheaters.

Species	Social Environment	Signal	Increased aggression from dominants?	Rise in rank?	Notes	Source
House sparrow	Captive flock	Area of black on throat and chest	Yes-Higher number of aggressive encounters (from ?) Yes-Opponents have larger badge	No- 4 days		Moller 1987a
Paper wasp	Dyad	Number of facial spots	No-Threat rate and number of in contest mount attempts the same Yes-Number of post contest mounts higher	No		Tibbetts and Dale 2004
Harris sparrow	Free living Flock	Area of black on throat, breast and crown	Yes-Increase number of attacks by dominants	No	No shams	Rohwer 1977
Harris sparrow	Captive flock	Area of black on throat, breast and crown	?	Yes-among other juveniles,	no dominants present	Rohwer 1985
Chaffinch	Captive flock	Color of underparts	No-Number of attacks received from males the same	Yes with females No with males		Marler 1955
White crowned sparrow	Captive flock	Color of crown	No-Number of attacks received from adults the same	Yes with immatures, No with adults	Only 2 flocks tested	Fugle and Rothstein 1987
House sparrow	Captive flock	Area of black on throat and chest	No-Frequency of fights with large bib males the same as before manipulation	Yes -24 h	Introduced into familiar flock	Gonzalez et al 2002

Table 2.2 Studies examining the relationship between testosterone and social status.

Species	Period of T measurement	Correlation between T level and status?	Source
House sparrow	Before flock formation 1 week after flock formation 2 weeks after flock formation	No Yes, positive No	Hegner and Wingfield (1987)
Japanese Quail	150 days before dyad pairing 24 hours before dyad pairing 24 hours after dyad pairing 16 days after dyad pairing	No Yes Yes No	Ramenofsky (1984)
White throated sparrows	2 weeks after flock formation	No	Archawaranon et al 1991
Male Jungle fowl	6 weeks after flock formation	No	Ross et al 2004
Male Copperheads	1 hr after fight (5-15 min)	No	Schuett et al 1996
White throated sparrow	5 days after flock formation	No	Schwabl et al 1988
White throated Sparrows	1 week before dyad pairing	No	Schlinger 1987
Cichlid	Before group formation After group formation	No Yes	Oliveira et al 1996

Table 2.3 Studies examining the relationship between corticosterone and status in flock forming bird species.

Species	Social and physical environment	Corticosterone level	Source
Harris sparrow	Free living flock, bare ground Free living flock, snow covered ground	Dominant<Subordinate Dominant=Subordinate * Rank inferred from plumage	Rohwer and Wingfield 1981
House Sparrow	Unstable captive flock	Dominant=Subordinate	Hegner and Wingfield 1987

Chapter Three: The role of social control in maintaining honest status signals

Introduction

Status signals, morphological traits that signal the social status of the bearer, could benefit both signalers and receivers by reducing unnecessary aggression (Rohwer 1975). Status signals allow participants to assess the resource holding potential (RHP) of opponents without resorting to an all out fight, and this in turn allows receivers to evaluate the probability of winning a fight with the signaler. Receivers may then use this information to determine if they want to engage the receiver, avoid or defer to them. Status signals allow individuals to win encounters while also avoiding potential costs associated with fighting. Individuals signaling low status should defer to opponents signaling high status and only individuals with similar signals should fight. Individuals that are able to signal high status regardless of actual RHP may potentially benefit from exploiting the convention of the signal. If individuals all signal high status despite having different RHP, variation in the signal will be lost. If the signal becomes uncorrelated with dominance then individuals will stop attending to it, even if variation in the signal is retained. Since status signals are traits that do not contribute to fighting ability, it is unclear how they remain correlated with dominance despite the fitness benefits that could potentially arise by signaling dishonestly. Whether such traits can be stable depends on how they remain reliable indicators of true status.

Status signals are often found in birds (Moller 1987 b, Evans and Hatchwell 1992, Part and Qvarnstrom 1997, Senar and Camerino 1998a, Vedder et al. 2010), and are often based size on the size of a patch of feathers (Rohwer 1975, Moller 1987 b, Lemel and Wallin 1993). The patches often consist black feathers (Moller 1987 b, Lemel and Wallin 1993), indicating that melanization is linked with status through some unidentified mechanism. Studies in which amino acid precursors (Poston et al. 2005b) and other nutrients (Stewart and Westneat 2010) were reduced show no effect on the signaling aspect of the status signal , suggesting that signal honesty is not maintained by nutritional constraints. Since nutritional constraints are not important in maintaining the correspondence between the signal level and RHP, the honesty of status signaling must be maintained by alternative means. One such alternative is the existence of use costs, in

which the cost of having an inappropriate signal arises from the interaction between the state of the signaler and the reaction of the receiver to the signal (Johnstone 1998b). Signaling theory suggests that signals remain honest if signalers pay the full cost of the signal (Maynard Smith and Harper 1988). One way in which this may occur is if there is social control of cheating. If cheaters, signalers that signal high status when actual RHP is low, encounter more dominants than do honest signalers with low RHP, and if encountering dominants is more costly than encountering subordinates, then cheaters will pay the full cost of the signal. Frequent encounters with dominants could result in higher injury and stress for cheaters than controls; which may in turn result reduce the benefits of cheating and result in honest signaling.

In addition to cheaters, there is another other type of inappropriate signaler which can also reduce the information content of status signals, Trojans. Trojans, are the opposite of cheaters, they are individuals that signal a lower status than their actual RHP. Several models suggest that Trojans can be as successful as or more successful than individuals that employ an honest strategy (Owens and Hartley 1991a, Johnstone and Norris 1993, Szalai and Szamado 2009). Trojans may also experience some form of social control which can reduce their fitness in comparison to their counterparts that signal appropriately. Trojan sparrows may have high RHP but they must fight in order to obtain resources as their signal does not convey their true status. Though Trojans may win, they must expend time and energy that their appropriately signaling counterparts do not. This extra cost that Trojan sparrows must bear could contribute to honest signaling.

I propose to test if social control results in costs for inappropriate signalers in male house sparrow (*Passer domesticus*). House sparrows are sexually dimorphic and males have a black bib on the breast that is a signal of status and predicts dominance amongst both sexes (Moller 1987 b, Hein et al. 2003, Nakagawa et al. 2007). The bibs are renewed each year in the fall and the size of the bib is dependent on the number of feathers that are melanized. Melanin is deposited into the feathers as they emerge. Oddly, the bib feathers have a white tip when first molted in and the white tip conceals portions of the black bib. However the bib does become partially visible as birds move and when feathers are puffed out. The white tips gradually wear away, exposing a portion of the whole bib; this portion is called the visible bib. There is a positive correlation between

the size of the visible bib and the size of the whole bib (Jensen et al. 2006). The white tips gradually wear away until the whole bib becomes fully exposed, usually in mid-summer. House sparrows form large flocks in the fall and remain in flocks until the spring. The nonbreeding season provides many opportunities for birds to interact for access to food and perching spots, which in turn provide many opportunities for social control to affect the cost of signaling inappropriately and intimately the evolutionary stability of the status signal. I will manipulate the status signal of male house sparrows to create cheaters and Trojan sparrows, and determine if the response of the residents of a flock to the altered signals result in social control of inappropriate signalers, which in turn can contribute to honest signaling.

Method

House sparrows (*Passer domesticus*) were captured from various locations in Lexington, Kentucky between November 2003-February 2004 using mist nets and potter traps. Length of left tarsus, weight, length and width of whole bib (bib feathers with white tips) were measured. Bib measurements were taken with bird held upright and bill placed at 90° angle to the body and bib size was calculated using the formulae $(167+0.45*\text{length}*\text{width})$. The birds were banded with one metal band and three colored plastic bands for identification on videos. Birds were housed in same or mixed sex groups in outdoor aviaries (2.5m X 2.5m X 3.7m) prior to start of experiment. All birds were fed a mixture of 3 parts white millet to 1 part chicken starter feed. All birds were fed ad libitum prior to start of experiment.

Males were sorted into one of three groups based on bib size. Large bibbed males had a bib size that was at least 0.5 standard deviation above the mean, medium bibbed males had a bib size that was within 0.5 standard deviation of the mean, and small bibbed males had a bib size that was at least 0.5 standard deviation below the mean. Ten flocks were then formed, each consisting of three females and 1 medium and 1 small bibbed male in an outdoor aviary (2.5m X 2.5m X 3.7m). To determine the dominance ranks of residents within the flock, food was removed in the morning and interactions at the feeder, following the return of the food in the afternoon, were recorded with a Hi8 camera. Interactions were taped between Dec 2003 and February 2004. The winner of

each interaction was identified to determine the dominance relationship within a dyad. The winner was the individual that remained at the food while its opponent moved away from the food. The winner of more than 50% of the interactions in the dyad was the dominant individual in the dyad. Rank was assigned based on number of dyads dominated, with rank 1 being the most dominant and 6 the least. Ties were broken by assigning the higher rank to the individual that was dominant in a dyad consisting of the tied individuals.

At the start of the experiment, males that were not part of a flock were assigned to bib treatments. Males with large bibs were randomly assigned to a large control (LC) or large reduced (LR) treatment and males with small bibs were randomly assigned to small control (SC) or small enlarged (SE) treatment. The bib of SE males was enlarged to at least 0.5 standard deviation greater than the mean size by blackening the feathers adjacent to the edge of the natural bib using a black indelible marker (Marks-A-Lot). SC males received a sham treatment; the feathers adjacent to the natural bib were drawn over with a capped marker. The bib of LR males was reduced to at least 0.5 standard deviation smaller the mean size by bleaching the feathers at the edge of the natural bib. The bleach (Clairol Professional powder lightener mixed with Clairol Professional Clairoxide 40 volume developer until a creamy consistency) was applied to the feathers and remained on until dried (approximately 10 minutes). The bleach was rinsed away with water and feathers were allowed to air dry. LC males received a sham treatment; the feathers on the edge of the bib were wet with water and then allowed to air dry. Treatment males were housed in individual cages until the following morning, when they were introduced into unfamiliar flocks.

From Dec 2003 to March 2004, treatment males were introduced to unfamiliar flocks. On the morning of the introductions (8-9am), the food dish was removed from the aviary and one treatment male was introduced into the flock. At 3pm, food was placed in a feeding apparatus (figure 3.1) and all interactions at the feeding apparatus were videotaped for 2 hours. The feeding apparatus was designed to encourage only one bird to feed at a time, however sometimes birds feed from the sides instead of the front and multiple birds were able to feed in this manner. Five perching sticks radiated out of the platform where birds could land to feed and individuals on these perches interacted with

the bird on the platform and with other birds on the feeding apparatus. After the videotaping ended, the food dish was returned. Interactions at the feeding apparatus were taped for 2 more days; each time, the food was removed in the morning and returned in the late afternoon before videotaping. The treatment male was removed 1-2 days after the last videotaping. Each aviary received all 4 types of experimental males in a random order, with a minimum of three days between the removal of the one treatment male and the introduction of the next. Each treatment male was introduced into only 1 aviary.

If social control does result in a cost for cheaters, I expected to find higher ranked residents initiating more interactions with cheaters than their controls (SC). I also expected high ranked residents to express more aggression to cheaters (SE) than to controls (SC); including a higher probability of fighting when high ranked residents are interacting with cheaters than when interacting with controls. If social control also results in added cost for Trojans, I expected to find no difference in probability of winning between Trojans (LR) and their controls (LC), but I did expect a higher frequency of fighting for Trojans than for their controls.

From the videotapes, only interactions involving the treatment male were noted. The following information was extracted from the videotapes: the identity of the holder of the food, the identity of the intruder, the location of the intruder, behavior displayed by intruder when landing on food apparatus, behavior displayed by holder when intruder enters into area 1 of food apparatus (Figure 3.1), if fight occurred, identity of winner and loser. Behavior was scored on scale of 0-3, with 0 being least aggressive and 3 being most aggressive. 0- bird moves away when approached by opponent, 1-bird lands on feeding apparatus or turns body towards opponent 2-bird flutters wings or positions body horizontally, pecks opponent, or approaches 3-bird lunges at or fights with opponent.

Several measures of aggression were taken: behavior of intruder when it arrived on feeding apparatus, response of holder of food to intruder arriving in area 1 of the feeding apparatus (figure 3.1) and probability of fighting as an intruder and as a holder. Response of holder to intruder arriving at area 1 was chosen as the measure of aggression to standardize the approach of intruders. The probability of reaching area 1 after landing on the feeding apparatus and probability of winning were also measured. Rank of flock member and aggression scores are ordinal data and were tested using the GLIMMIX

procedure (SAS) for generalized linear mixed models (GLMM), with a Kenward-Roger degrees of freedom estimator, a multinomial distribution and cumlogit link. The probability of entering area 1, probability of fighting, and probability of winning are binomial data and were tested using the GLIMMIX procedure (SAS) for GLMM, with a Kenward-Roger degrees of freedom estimator, a binomial distribution and logit link. The GLMM included the following fixed effects: interaction number, bib treatment, resident rank and bib treatment by resident rank interaction. Interaction number is the sequence number of the interaction within a trial. Bib treatment indicates which treatment group the treatment male is in LC, LR, SC or SE. Resident rank is the rank of the resident bird, 1 being most dominant and 6 being least dominant. The following random factors were included in the model: aviary, resident id (nested within aviary), treatment male id (nested within resident id) and trial nested (within treatment male id).

Results

The mean bib size of all males combined was 354.2 mm^2 and standard deviation was 32.6 mm^2 . Most ranks were assigned based on a minimum of 10 interactions per dyad, except for 1 dyad where only 5 interactions were observed. There was 1 tie in 2 flocks and 2 ties in 7 flocks and 1 triangle in 1 flock. All members of the triangle received the same rank. Male and female residents were equally dominant (Proc GLIMMIX: $df_{1,27} F=0.04 p=0.84$) and bib size of males did not predict rank within flock (Proc GLIMMIX: $df_{1,60} F=0.26 p=0.62$). There were 10 flocks created but only 9 were used in the remaining analysis because one flock had 5 residents instead of 6 due to mortality at the beginning of the experiment. Additionally, any observations with less than 6 residents in the flock, due to mortality during the experiment, were excluded from the analysis. A total of 35 treatment males were introduced into aviaries, and a total of 87 trials were scored. Once 100 interactions were recorded for a treatment male, I stopped scoring additional trials.

The probability of the resident intruder entering area 1 was not affected by bib treatment or resident rank and the bib treatment by resident rank interaction was not significant (table 3.1). Aggression displayed by resident intruders when arriving at the feeding apparatus was affected by bib treatment but not affected by resident rank or the

bib treatment by resident rank interaction (table 3.2). Resident intruders were more aggressive to SC holders than to SE holders (SC-SE: odds ratio=0.54, S.E.=0.22, df=57, $t=2.43$, $p=0.02$). There is also a non significant tendency for resident rank to affect the aggression displayed by resident intruders when arriving at the feeding apparatus (table 3.2, figure 3.2). I was unable to test for the aggression displayed by resident holder in response to arrival of treatment males as the model failed to converge; therefore I examined the odds of resident holder fighting, an alternative measure of aggression. The odds of the resident holder fighting were not affected by bib treatment or resident rank, and the bib treatment by resident rank interaction was not significant (table 3.3). The odds of winning were not affected by bib treatment or resident rank and the bib treatment by resident rank interaction was not significant in the model when the resident was in the holder role (table 3.4). However the odds of winning were affected by resident rank when the resident was in the intruder role (table 3.5, figure 3.3).

To determine if bib reduction affected the ability of large bib males to win and the odds of fighting, I created reduced models with only interaction number and bib treatment as fixed effects and with the same random intercept terms as described for the other models. Bib reduction did not affect ability of large bib males to win interactions as holders (table 3.6) or intruders (table 3.7). LR males were equally dominant as LC males, but LR males may have to be more aggressive than LC males to achieve the same level of dominance. There was also no effect of bib treatment on the odds of treatment male fighting as holders (table 3.8) or intruders (table 3.9).

As the number of interactions increased, residents become less interested in approaching the food (odds of entering area 1: Estimate=-0.007, S.E.=0.002, df=1254, $t=-3.19$, $p<0.01$) but more likely to fight once they had possession of the food (odds of resident holder fighting: Estimate=0.010, S.E.=0.005, df=768, $t=2.10$, $p=0.04$). As the number of interactions increased, resident intruders lost more often (Estimate=-0.007, S.E.=0.003, df=1244, $t=-2.11$, $p=0.03$).

Discussion

There is no evidence for social control of cheaters, either by the general population or by dominants. Additionally, there is also no evidence for social control of Trojan sparrows. Instead the results show a benefit for cheating. However the chief benefit of cheating, increase in dominance was not observed.

To prevent the spread of cheating, cheaters must pay a cost appropriate for the signal (Maynard Smith and Harper 1988). However in house sparrows, there is no evidence that that cost occurs via social control. In the present study, cheaters received less aggression from residents than did the controls. The findings in this study are in contrast to those of Moller (1987a) and Gonzalez et al. (2002). Moller (1987a) observed an increase in aggressive encounters when he compared cheaters to controls, and Gonzalez et al (2002) observed no difference between cheaters and controls. The reduced aggression experienced by cheaters suggests that this is a benefit of cheating. There is no evidence for social control of cheaters by dominants as the rank of residents had no effect on aggression expressed to cheaters and dominants did not initiate against cheaters more than they did controls. These findings are in contrast to Moller (1987a) who observed that cheaters interacted with larger banded house sparrows than did the controls. However, similar to the findings of this study, Gonzalez et al. (2002) did not observe an increase in the frequency of fights with large bib house sparrows when comparing after bib enlargement to before bib enlargement.

Though cheaters received less aggression than controls, they were not able to completely deceive residents as they were not more dominant than controls. The results on dominance are similar to the results obtained in a Harris sparrows study (Rowher 1977) and a house sparrow study (Moller 1987 a). The inability to completely deceive conspecifics may be due to the incongruence between the signal and the behavior (Caryl 1982), though that would not explain why conspecifics expressed less aggression to cheaters than to controls. Trojan sparrows were also as dominant as their control counterparts but may have had to expended more effort to achieve the same level of dominance due to the lack of appropriate signal. Rohwer (1977) observed that Harris sparrows with a reduced signal had an increase in rate of active chase. I did not observe

an increase in aggression for Trojan sparrows in comparison to controls, suggesting that it was not more costly for Trojan sparrows than for controls to win.

The results of this study suggest that social control is not likely to impose costs on cheaters or on Trojans that would maintain the correspondence between dominance and signal. It is unclear what the mechanisms for ensuring signal integrity would be. It is possible that other types of use costs, such as probing, could impose cost for signaling inappropriately or alternatively. Unfortunately, there is no consensus on the existence or absence of social control, making it difficult to understand if it plays a role in the evolution of status signals.

Table 3.1 Test for fixed effects on the odds of the resident intruder entering area 1 of the feeding apparatus. Analysis of the generalized linear mixed model was performed with the GLIMMIX procedure (SAS) with a binomial distribution and logit link. The following random factors were included in the model: aviary, resident id (nested within aviary), treatment male id (nested within resident id) and trial (nested within treatment male id). Interaction number is the sequence number of the interaction within a trial. Bib treatment indicates the treatment male group: large control, large reduced, small control or small enlarged. Resident rank is the rank of the resident bird, 1 is most dominant and 6 is least dominant. The analysis is based on 9 aviaries, 35 treatment birds and 87 trials with 1969 interactions used.

Effects	Numerator df	Denominator df	F	p
Interaction number	1	1254	10.21	<0.01
Bib treatment	3	71	1.51	0.22
Resident rank	5	38	0.38	0.86
Bib treatment*Resident rank	15	71	1.16	0.33

Table 3.2 Test for fixed effects on the cumulative odds of the aggression displayed by resident intruder upon arrival on feeding apparatus. Analysis of the generalized linear mixed model was performed with the GLIMMIX procedure (SAS) with a multinomial distribution and cumlogit link. The following random factors were included in the model: aviary, resident id (nested within aviary), treatment male id (nested within resident id) and trial (nested within treatment male id). Aggression was score from 0-3, with 0 being least aggressive. Interaction number is the sequence number of the interaction within a trial. Bib treatment indicates the treatment male group: large control, large reduced, small control or small enlarged. Resident rank is the rank of the resident bird, 1 is most dominant and 6 is least dominant. The analysis is based on 9 aviaries, 35 treatment birds and 86 trials with 1201 interactions used.

Effects	Numerator df	Denominator df	F	p
Interaction number	1	778	1.12	0.29
Bib treatment	3	70	3.89	<0.01
Resident rank	5	37	2.33	0.06
Bib treatment*Resident rank	15	81	1.44	0.15

Table 3.3 Test for fixed effects on the odds of the resident holder fighting during an interaction. Analysis of the generalized linear mixed model was performed with the GLIMMIX procedure (SAS) with a binomial distribution and logit link. The following random factors were included in the model: aviary, resident id (nested within aviary), treatment male id (nested within resident id) and trial (nested within treatment male id). Interaction number is the sequence number of the interaction within a trial. Bib treatment indicates the treatment male group: large control, large reduced, small control or small enlarged. Resident rank is the rank of the resident bird, 1 is most dominant and 6 is least dominant. The analysis is based on 9 aviaries, 35 treatment birds and 86 trials with 1798 interactions used.

Effects	Numerator df	Denominator df	F	p
Interaction number	1	1773	5.99	0.01
Bib treatment	3	74	0.48	0.70
Resident rank	5	36	0.38	0.86
Bib treatment*Resident rank	15	96	0.64	0.84

Table 3.4 Test for fixed effects on the odds of the resident holder winning an interaction. Analysis of the generalized linear mixed model was performed with the GLIMMIX procedure (SAS) with a binomial distribution and logit link. The following random factors were included in the model: aviary, resident id (nested within aviary), treatment male id (nested within resident id) and trial (nested within treatment male id). Interaction number is the sequence number of the interaction within a trial. Bib treatment indicates the treatment male group: large control, large reduced, small control or small enlarged. Resident rank is the rank of the resident bird, 1 is most dominant and 6 is least dominant. The analysis is based on 9 aviaries, 35 treatment birds and 86 trials with 1149 interactions used.

Effects	Numerator df	Denominator df	F	p
Interaction number	1	1124	0.04	0.84
Bib treatment	3	77	0.38	0.77
Resident rank	5	43	0.64	0.67
Bib treatment*Resident rank	15	83	0.44	0.96

Table 3.5 Test for fixed effects on the odds of the resident intruder winning an interaction. Analysis of the generalized linear mixed model was performed with the GLIMMIX procedure (SAS) with a binomial distribution and logit link. The following random factors were included in the model: aviary, resident id (nested within aviary), treatment male id (nested within resident id) and trial (nested within treatment male id). Interaction number is the sequence number of the interaction within a trial. Bib treatment indicates the treatment male group: large control, large reduced, small control or small enlarged. Resident rank is the rank of the resident bird, 1 is most dominant and 6 is least dominant. The analysis is based on 9 aviaries, 35 treatment birds and 87 trials with 1269 interactions used.

Effects	Numerator df	Denominator df	F	p
Interaction number	1	1244	4.46	0.03
Bib treatment	3	80	1.55	0.21
Resident rank	5	35	3.55	0.01
Bib treatment*Resident rank	15	79	0.70	0.77

Table 3.6 Test for fixed effects on the odds of the treatment male holder winning an interaction. Analysis of the generalized linear mixed model was performed with the GLIMMIX procedure (SAS) with a binomial distribution and logit link. The following random factors were included in the model: aviary, resident id (nested within aviary), treatment male id (nested within resident id) and trial (nested within treatment male id). Interaction number is the sequence number of the interaction within a trial. Bib treatment indicates the treatment male group: large control, large reduced, small control or small enlarged. The analysis is based on 9 aviaries, 35 treatment birds and 87 trials with 1269 interactions used.

Effects	Numerator df	Denominator df	F	p
Interaction number	1	1264	4.61	0.03
Bib treatment	3	77	1.46	0.23

Table 3.7 Test for fixed effects on the odds of the treatment male intruder winning an interaction. Analysis of the generalized linear mixed model was performed with the GLIMMIX procedure (SAS) with a binomial distribution and logit link. The following random factors were included in the model: aviary, resident id (nested within aviary), treatment male id (nested within resident id) and trial (nested within treatment male id). Interaction number is the sequence number of the interaction within a trial. Bib treatment indicates the treatment male group: large control, large reduced, small control or small enlarged. The analysis is based on 9 aviaries, 35 treatment birds and 86 trials with 1149 interactions used.

Effects	Numerator df	Denominator df	F	p
Interaction number	1	1144	0.00	0.96
Bib treatment	3	72	0.40	0.75

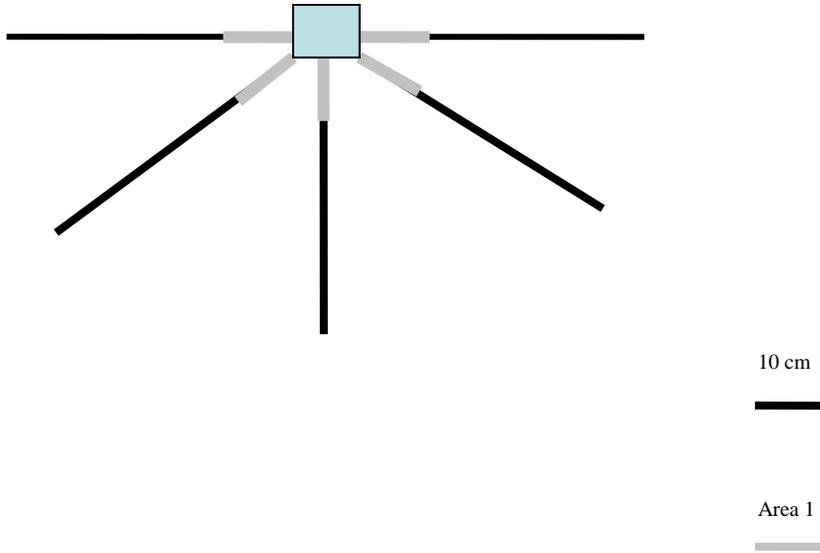
Table 3.8 Test for fixed effects on the odds of the treatment male holder fighting during an interaction. Analysis of the generalized linear mixed model was performed with the GLIMMIX procedure (SAS) with a binomial distribution and logit link. The following random factors were included in the model: aviary, resident id (nested within aviary), treatment male id (nested within resident id) and trial (nested within treatment male id). Interaction number is the sequence number of the interaction within a trial. Bib treatment indicates the treatment male group: large control, large reduced, small control or small enlarged. The analysis is based on 9 aviaries, 35 treatment birds and 87 trials with 1798 interactions used.

Effects	Numerator df	Denominator df	F	p
Interaction number	1	1288	0.00	0.96
Bib treatment	3	64	1.48	0.23

Table 3.9 Test for fixed effects on the odds of the treatment male intruder fighting during an interaction. Analysis of the generalized linear mixed model was performed with the GLIMMIX procedure (SAS) with a binomial distribution and logit link. The following random factors were included in the model: aviary, resident id (nested within aviary), treatment male id (nested within resident id) and trial (nested within treatment male id). Interaction number is the sequence number of the interaction within a trial. Bib treatment indicates the treatment male group: large control, large reduced, small control or small enlarged. The analysis is based on 9 aviaries, 35 treatment birds and 86 trials with 1798 interactions used.

Effects	Numerator df	Denominator df	F	p
Interaction number	1	1793	2.07	0.15
Bib treatment	3	60	0.46	0.71

Figure 3.1 Feeding apparatus viewed from above.



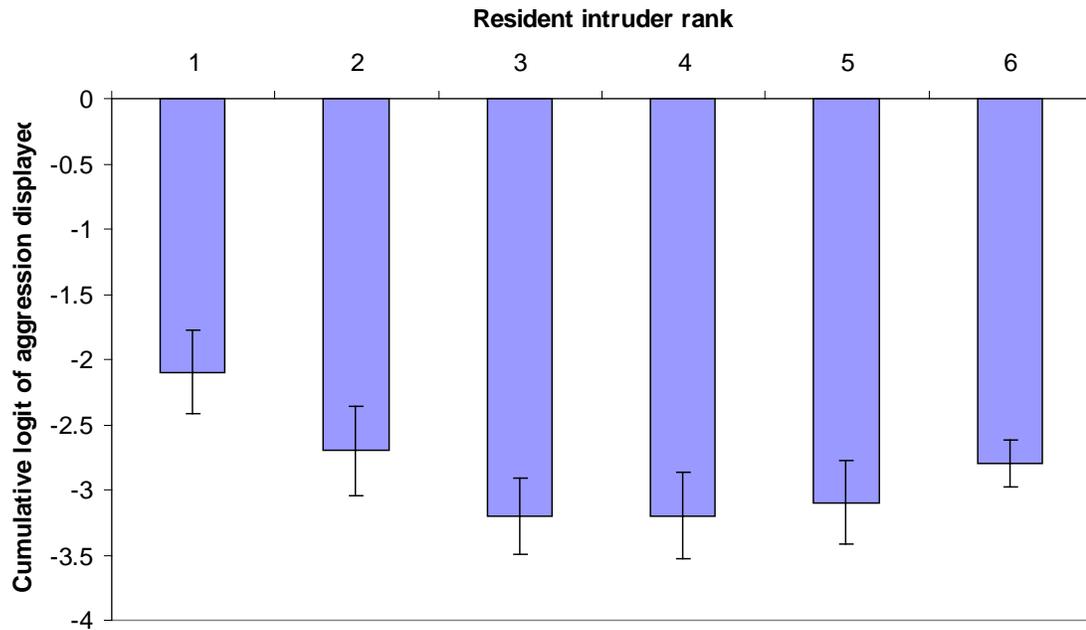


Figure 3.2 Effect of resident intruder rank on the cumulative logit of the aggression displayed by resident intruders upon arrival on the feeding apparatus. Standard errors shown. Aggression is scored on scale 0-3, 3 is most aggressive. Rank 1 is most dominant resident. Results are based on 9 aviaries, 48 residents, 86 trials and 1201 interactions.

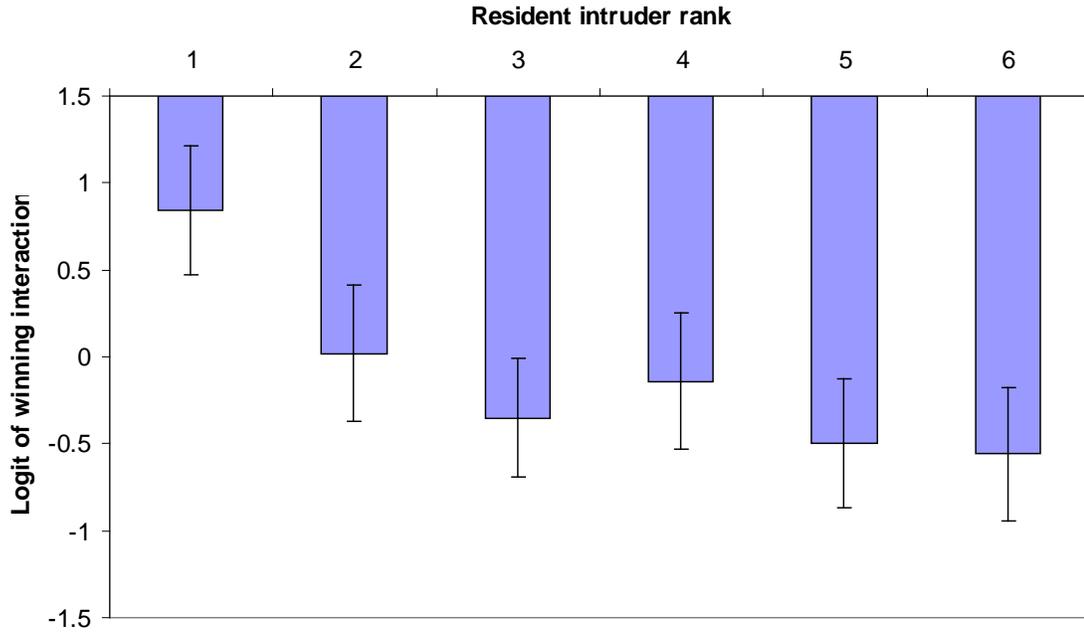


Figure 3.3 Effect of resident intruder rank on the odds of the resident intruder winning an interaction. Rank 1 is most dominant individual. Standard errors shown. Results are based on 9 aviaries, 48 residents, 87 trials and 1269 interactions.

Chapter Four: The role of probing in maintaining honest status signals

Introduction

Many species of animals live in groups and group members often compete for access to resources. The costs associated with these contests can be high, therefore evolution favors the development of traits that reduce the costs associated with these contests. Status signals, morphological traits that indicate the social status of the bearer, can reduce costs for contestants. Status signals allow contestants to evaluate the resource holding potential of their opponent without resorting to an all out fight. Contestants can then determine the likelihood that they will win a fight and either withdraw if they are likely to lose or escalate if they are likely to win and their opponent has not withdrawn. Fights should only occur when the contestants signal similar ranks and it is unclear who the likely winner would be.

A receiver's response to status signals should evolve due to the benefits of attending to the signals of opponents. However, it is the benefits of attending to status signals that make status signals vulnerable to exploitation by inappropriate signalers, which then make the receiver's response less favored. Seemingly, all individuals would benefit from signaling high status regardless of true status; however the presence of cheaters, individuals that signal high status when their resource holding potential is low, reduces the reliability of the signal. If cheaters are too numerous, there would be no net benefit to attending to the signal and the signaling aspect of the trait would disappear. Therefore, understanding the processes that curtail the spread of cheating is central to understanding the evolution of status signals.

Zahavi (1975) suggested that signals are honest because individuals of low quality pay a higher marginal cost to advertise at a given level than high quality individuals. For many status signals, the costs of advertising at a high level are unclear. This is especially true of signals that consist of white or black patches, as they do not appear to have high production costs (Poston et al. 2005, but see Veiga and Puerta 1996). An alternative to production costs are use costs, costs that arise from the interaction between the response of the receiver to the quality signaled and the signaler's quality (Rohwer 1977, Rohwer and Rohwer 1978, Maynard Smith and Harper 1988 and Owens and Harley 1991).

Maynard Smith and Harper's (1988) model of signals of aggression suggests that signaling remains honest when cheaters pay the full cost of the level signaled; which occurs when cheaters encounter true dominants. However it is unclear whether the costs arising from encounters with true dominants alone are sufficient to maintain signal honesty and if there are other costs associated with cheating that contribute to maintaining signal honesty.

Dawkins and Guilford (1991) suggest that cheating can persist because the cost of evaluating a signal is in proportion to the signal cost. Evaluating a signal would consist of an all out fight to determine the true resource holding potential of an opponent, which could be costly if the opponent is signaling high status and the signal is accurate. Therefore, few individuals, especially subordinates, would approach opponents for the purpose of evaluating the opponent's signal, and cheating may persist. However, evaluations may occur less directly through probing. Probing occurs when an individual displays some aggression to an opponent and uses the response of the opponent to determine the ability and motivation of the opponent to defending a resource. If an opponent signaling high status consistently withdraws when probed, that would suggest that the signal is not accurate. Though most models of status signaling suggest that probing should not occur because individuals signaling low status have a low probability of winning against opponents signaling high status, status signaling theory does not take into account the effects of asymmetry in resource value on the motivation to win. Deprived subordinates may probe opponents signaling high status to determine if opponents are motivated to defend the resource, because subordinates can increase the proportion of contests won or even reverse dominance order when they value the resource more than dominant individuals (Popp 1987, Lemel and Wallin 1993, Andersson and Ahlund 1991). During probing, individuals advertising subordinate status may display high aggression to opponents that advertise dominant status because subordinates might expect that a higher level of aggression may be needed to overcome an opponent signaling high resource holding potential. The higher aggression displayed to opponents signaling high status than to opponents signaling low status may result in subordinates imposing a cost for cheating.

The sex of opponents may also be an important factor affecting costs experienced by cheaters. Hein et al (2003) found that the sex of opponents affected the correlation between aggression received by male house sparrows and the bib size of male house sparrows. Aggression received from male opponents had a tendency to be negatively correlated with the bib size of the focal male; while aggression received from female opponents had a tendency to be positively correlated with the bib size of the focal male. The authors suggest that females were using interactions with males to evaluate potential mates; therefore the benefits of displaying high aggression differed for males and females. Thus female behavior may impose higher costs for cheating.

The black breast patch (bib) of male house sparrows (*Passer domesticus*) is a good trait for studying the costs of cheating. The bib is found only on males and the size of the bib predicts the proportion of opponents dominated (Moller 1987b, Liker and Barta 2001, Hein et al 2003, Nakagawa et al 2007). The bib is renewed each year in the fall when birds molt and when first molted in, the tips of the bib feathers are buff colored. The tips wear away during the winter and early spring until the bib becomes fully exposed in the summer. Older birds tend to have larger bibs (Nakagawa et al 2007, Morrison et al. 2010) and bib size appears to have low heritability (Griffith et al. 1999). The size of the bib is determined by the number of feathers that are melanized, and melanin is formed from amino acids that are found in the diet (Prota 1992). Studies in which access to nutrients were restricted showed no affect on bib size (Poston et al 2005) or showed no reduction in bib size (Stewart and Westneat 2010). This suggests that production costs of bibs are low and it is the use costs that are important in maintaining honesty in this status signaling system.

In this study, I will test if probing by subordinates imposes a cost for cheating. If probing does impose a cost for cheating, subordinates will be more aggressive to opponents signaling high status than to opponents signaling low status. I will also test for an interaction between signal level and resource value, and between signal level and sex as these factors may affect the costs and benefits of using aggression while probing. I predict that when resource value is low, subordinates will display a low level of aggression to both types of opponents; however when resource value increases, I predict that subordinates will display higher aggression to opponents signaling high status than to

opponents signaling low status due to the increase in motivation to win and the expectation that more aggression is needed to overcome opponents signaling high status. If the aggression displayed by subordinates to opponents signaling high status depends on the value of the resource, then cheating becomes more costly and less likely to spread when resources are scarce. I also predict that females will display higher aggression to opponents signaling high status than to opponents signaling low status and males will display less aggression to opponents signaling low status than to opponents signaling high status.

Methods

Male and female house sparrows (*Passer domesticus*) were captured from various locations in Lexington, Kentucky from November 3, 2006 to January 12, 2007 using mist nets and potter traps. Length and width of the black bib was measured using dial calipers with the bird held upright and bill placed at 90° angle to the body. Black bib size was calculated using the formulae $(167+0.45*\text{length}*\text{width})$ (Moller 1987b). Mean bib size was 352 mm² and standard deviation was 31mm². Birds were banded with one metal and three plastic color bands. Males and females were housed together in same or mixed sex flocks in outdoor aviaries (2.5m X 2.5m X 3.7m), with a maximum of 15 birds in each aviary. Birds were fed a 3:1 mix of white millet: chicken feed (Southern states) *ad libitum* from multiple food dishes placed within the aviaries. A water dish, 2 trees, and a roost box were also placed in each aviary.

The experiment started on November 21 2006 and finished on January 24 2007. Birds were separated into 6 blocks and placed in individual cages (metal 25cm width X 25cm height X 40cm length). The cages were hung on brackets and three rows of three adjoining cages were hung on each panel. Each row contained a subject in a cage on one side and an opponent in a cage on the other. Panels dividing the cages were removable and there was a single removable panel in the middle cage. The panel in the middle cage was mounted on a platform (10 cm wide) that extended from the front of the cage to the back and divided the cage in half. Within each end cage there was a roost tube, perching sticks, a water dish and a food dish. The birds were fed the same diet as in the aviary *ad libitum*. The birds were placed in the cages 7-11 days before the start of the tournaments.

Males with bib sizes within 1 standard deviation of the mean were randomly assigned to the subject or opponent group, and opponents were randomly assigned to a control (C) or enlarged treatment (E). Opponents in the enlarged treatment had their natural bibs enlarged by the application of Rodol A dye (1g/25ml H₂O) and peroxide to the feathers on the edge of the natural whole bib using a cotton swab. Some feathers at the center of the bib were also dyed in the same manner. The feathers were then allowed to air dry. Opponents in the control treatment were held in the same position and for the same amount of time as the opponents in the enlarged treatment. A dry cotton swab was used to touch the edge of the natural bib while the bird was held. Near the end of the handling period, some dye and peroxide was applied to the feathers in the center of the bib. The feathers were then allowed to air dry. Dye was applied to the center of the bib of control treatment opponents to control for the presence of dye on the feathers of the enlarged treatment opponents, and dye was applied to the center of the bib of enlarged treatment opponents to control for presence of a dark patch on the control treatment opponents.

Subjects and opponents unfamiliar to the subjects were assigned to blocks. Each block consisted of 6 male opponents, 3 male subjects and 3 female subjects. Each block had 36 possible dyads (Figure 4.1). The blocks were started at different times due to the space constraints. Block 1-11/2006; block 2 and 3-12/5/2006, block 4-12/14/2006, block 5 & 6-1/11/2007. Tournaments were started 4-11 days after birds were placed in cages. On day one of the tournament, the cages were moved so that each subject was placed in the same row as their assigned opponent. The divider separating the left and right cages from the middle cage was removed and the birds were allowed to access half of the space in the middle cage. To familiarize the birds with feeding in the middle cage, the food in both the left cage and right cage was placed next to the panel in the middle cage. At 12 pm on day two of the tournament, the food of birds in the high deprivation treatment (4hr) was removed and the dummy cameras were replaced by real cameras. At 3:30 pm, the food of birds in the low deprivation treatment (0.5hr) was removed. At 4 pm the divider in the middle cage was removed and a single food dish was placed into the center of the middle cage, near the front of the cage. The video camera mounted in front of the middle cage was turned on and all interactions were recorded for approximately 1 hour.

At the end of the recording period, the food dish was removed, the center partition was reinserted, food was placed in each cage and the real camera was replaced with a dummy camera. The opponents were then moved to be adjacent to another subject. Day 1 and 2 of the tournament were repeated until all the subjects met all the opponents within the block. The first tournament for each subject was repeated at the end to control for the behavior related to exploration of new space (middle cage). The birds were returned to their capture sites at the end of the tournaments.

Only the first 15 minutes of the videos was scored to ensure that the deprivation treatment remained effective. Events, the period when one bird was on screen until when one bird leaves the screen, were divided into an intrusion, approach and arrival stage for analysis. The intrusion stage starts when a bird arrives on screen and ends when a second bird arrives or when the first bird leaves the screen. The approach stage starts when a second bird arrives on screen and ends when the second bird arrives at the food. The arrival stage occurs after the second bird arrives at the food. Each stage represents a distinct opportunity for subjects to choose a level of aggression to display. At the intrusion stage, intrusion time, time from arrival of opponent on screen until arrival of subject on screen, was used as a measure of aggression. At the approach stage, approach time, time from arrival of subject on screen until arrival of subject at the food, was used as a measure of aggression. At the arrival stage, the aggression of the arrival behavior, first behavior displayed by a bird after arriving at the food, was scored. The arrival behavior was scored on a scale ranging from 1-5, with 5 being the most aggressive. Approach food without any overt aggression =1; turn towards =2; approaches other bird, horizontal posture, wing flutter =3; peck=4; lunge, fight =5. The behavior of intruders were given a score from 1-5 and the behavior of holders were given a score from 2-5. All behavior displayed prior to a supplant or holdoff was scored on the same scale as the arrival behavior.

Of 36 subjects, 34 met all 6 opponents, 1 met 5 opponents and 1 met 3 opponents, producing 212 dyads. All measurements were averaged for all events within a dyad unless noted otherwise. Most of the dependent variables tested did not meet the assumptions necessary for analysis using parametric tests, therefore nonparametric tests were performed when appropriate. There are no nonparametric tests that allow me to test

for statistical interactions between variables, therefore I evaluated the main effects and the interactions with a repeated measures ANOVA and then performed nonparametric tests to confirm any significant results from the repeated measures ANOVA. In the analysis on aggression displayed by probing subjects, I only included the trials in which the opponent deprivation was low and subject deprivation was varied. In addition, I restricted the analysis to interactions in which the opponent was the holder of the food and the subject was the potential prober. In this restricted data set, a total of 142 possible dyads were analyzed; 34 subjects met 4 opponents and 2 subjects met 3 opponents.

Results

Behavior of opponents

I assumed that the bib treatment did not affect the behavior and dominance of the treated males; to test this I analyzed the dyads in which both the subject and opponent were in the high deprivation treatment. Bib treatment had no effect on intrusion time (Wilcoxon signed ranks test, $N=31$, $S=-79.5$, $p=0.12$), approach time (Wilcoxon signed ranks test, $N=27$, $S=26$, $p=0.54$), arrival behavior (Wilcoxon signed ranks test, $N=27$, $S=-8$, $p=0.55$), the total aggression displayed by the opponent in the holder role (Wilcoxon signed rank test, $N=33$, $S=-11$, $p=0.77$) or in the intruder role (Wilcoxon signed rank test, $N=31$, $S=-20.5$, $p=0.46$). Bib treatment also had no effect on the proportion of total interactions won by the opponent (Wilcoxon signed rank test, $N=35$, $S=104$, $p=0.07$).

Novelty

It is possible that the behavior of the subject in the first trial could differ from those of subsequent trials due to the novelty of being in a larger cage and the novelty of the presence of another bird in the cage. I tested for the effect of novelty by comparing the behavior of the subject in the first trial to its behavior in a subsequent trial repeated 12 days later, after it had already met all or nearly all the opponents in its block. In the first and repeated trial, subjects were paired with the same opponent and experienced the same deprivation treatment. Though birds approached food sooner after food was placed in the cage in the repeated trial than in the first trial (paired t-test, $df=32$, $t=5.5$, $p<0.01$), there was no difference in intrusion time (Wilcoxon signed rank test, $N=25$, $S=17.5$, $p=0.65$),

approach time (Wilcoxon signed rank test, $N=18$, $S=-13$, $p=0.59$), arrival behavior (Wilcoxon signed rank test, $N=18$, $S=-5$, $p=0.59$), total aggression displayed as holder (Wilcoxon signed rank test, $N=16$, $S=2.5$, $p=0.82$) and total aggression displayed as intruder (Wilcoxon signed rank test, $N=18$, $S=-8.5$, $p=0.61$). Since there was no difference in the measures of aggression between the first trial and the repeated trial, I used only the first trial in the analysis.

Dyad order and block

I also tested for the effects of dyad order and block on the different measures of aggression as these may have had an effect on the subject's behavior. I omitted the 2 subjects that did not meet all 6 opponents. Dyad order had no effect on intrusion time (log transformed data, Repeated Measures ANOVA, $F=0.8$, $df=5,151$, $p=0.58$), approach time (Friedman's test, Row mean scores differ =5.2, $df=5$, $p=0.40$), and arrival behavior (Friedman's test, Row mean scores differ =5.9, $df=5$, $p=0.32$). Block had no effect on intrusion time (log transformed data, Repeated Measures ANOVA, $F=0.4$, $df=5,30$, $p=0.86$). To analyze the effect of block on approach time and arrival behavior, I summed the values from the 6 dyads for each subject and used the summed value in the analysis. There was no effect of block on approach time (Kruskal-Wallis test, $X^2 = 5.0$, $df=5$, $p=0.42$) or arrival behavior (Kruskal-Wallis test, $X^2 = 1.7$, $df=5$, $p=0.88$).

Resource Value

To confirm that the deprivation treatment was effective, I examined the time it took for subjects to approach the food after it was placed in the cage. The deprivation treatment was highly effective in producing a difference in motivation to access food; after the food was placed in the cage, subjects in the high deprivation treatment approached the food sooner than subjects in the low deprivation treatment (log transformed, Repeated Measures ANOVA, $F=26.4$, $df=1,106$, $p<0.01$, Figure 4.2). Nonparametric analysis of time to approach food using summed scores also showed a significant effect of deprivation treatment (Wilcoxon signed ranks test, $N=34$, $S=192.5$, $p<0.01$).

Measures of aggression displayed by subject

Intrusion stage

The probability of at least one intrusion occurring was not affected by sex (Repeated measures logistic regression, $N=142$, $Z=0.6$, $p=0.54$), bib treatment (Repeated measures logistic regression, $N=142$, $Z=0.5$, $p=0.64$) or deprivation treatment (Repeated measures logistic regression, $N=142$, $Z=-1.9$, $p=0.06$). Intrusion time was log transformed to create a normal distribution. The sex by bib treatment interaction was not significant for intrusion time or any of the other measures of aggression displayed by the subject, therefore the interaction was removed from all the remaining analysis presented. None of the main effects or interaction affected intrusion time (Table 4.1)

Approach stage

At the approach stage, subjects must decide if they will approach the food; being in close proximity to the food increases the probability of obtaining food but can be costly as it can place the subject within striking distance of the opponent and can trigger an attack by the opponent. Of 126 dyads in which at least one intrusion occurred, subjects did not approach in 21 dyads. The probability of at least one approach occurring was not affected by deprivation treatment (Repeated measures logistic regression, $N=126$, $Z=0.8$, $p=0.42$), sex (Repeated measures logistic regression, $N=126$, $Z=-1$, $p=0.33$) or bib treatment (Repeated measures logistic regression, $N=126$, $Z=-0.7$, $p=0.48$).

I expected aggressive subjects to approach the food quickly, the most extreme case being if the subject lunged at the opponent from off-screen; and less aggressive subjects to hop around and take longer to approach the food. The bib treatment and the deprivation treatment by bib treatment interaction term were not significant; but the sex and deprivation treatment term were (Table 4.2). Females and highly deprived subjects approached food sooner (Figure 4.3 a,b). For the nonparametric analysis of the effect of sex, I summed the values of subjects competing against all bib treatments and all deprivation treatments. Subjects that competed against fewer than 4 opponents were omitted. Sex did not have a significant effect on approach time (Mann-Whitney test, 5 females and 6 males, $T=31$, $p=0.92$). For the nonparametric analysis of deprivation treatment, I summed the values of subjects competing against opponents with enlarged

and control bibs within each deprivation treatment. Subjects that did not compete against opponents with both enlarged and control bibs in both the low and high deprivation treatment were omitted. The deprivation treatment did not have a significant effect on approach time (Wilcoxon signed ranks test, $N=11$, $S=8$, $p=0.52$).

Arrival Stage

Analysis of the arrival behavior revealed that subjects in the high deprivation treatment were more aggressive at the food than those in the low deprivation treatment (Table 4.3, Figure 4.4 a). Sex and bib treatment had no effect on arrival behavior (Table 4.3). The interaction between deprivation treatment and bib treatment was significant (Table 4.3). Subjects in the low deprivation treatment were equally aggressive to E opponents and C opponents; but subjects in the high deprivation treatment were more aggressive to E opponents than to C opponents (Figure 4.4 b).

I attempted to confirm the results of the parametric analysis on arrival behavior using nonparametric tests. For the analysis of the effect of deprivation treatment, I summed the aggression score of both bib treatments for each subject within each deprivation treatment and used the summed score in the analysis. Birds in the high deprivation treatment were more aggressive than those in the low deprivation treatment (Wilcoxon signed ranks test, $N=11$, $S=14$, $p=0.02$). I evaluated the deprivation treatment by bib treatment interaction in three ways. First, I tested for the effect of bib treatment separately in the low deprivation group and the high deprivation group. I found no evidence that birds in the low deprivation group behaved differently to E opponents compared to C opponents (Wilcoxon signed ranks test, $N=22$, $S=2.5$, $p=0.69$). However, birds in the high deprivation group were more aggressive to E opponents than to C opponents (Wilcoxon signed ranks test, $N=18$, $S=-16.5$, $p=0.05$). Second, I tested for the effect of deprivation treatment separately for the C opponents and E opponents. When the opponents had enlarged bibs, subjects in high deprivation were more aggressive than subjects in low deprivation (Wilcoxon signed ranks test, $N=18$, $S=18$, $p<0.01$); but deprivation treatment did not affect aggression displayed by subjects when the opponent had an unmodified bib (Wilcoxon signed ranks test, $N=20$, $S=-0.5$, $p=0.95$). Third, I tested for the deprivation treatment X bib treatment interaction by taking the difference in

aggression at food when competing against E opponents and when competing against C opponents within each deprivation treatment and then testing for an effect of deprivation treatment on those differences. No interaction between deprivation treatment and bib treatment was detected using this method (Wilcoxon signed ranks test, $N=11$, $S=-10.5$, $p=0.09$) though the difference was in the pattern that matched the results of the repeated measures ANOVA; the difference in aggression displayed by subjects to C opponents and E opponents was larger in the high deprivation group than in the low deprivation group (high deprivation C-E median =-2, low deprivation C-E median=0).

To better understand the nature of the difference in aggression experienced by E opponents and C opponents during periods of high deprivation, I tested several aspects of the aggression displayed by the subjects. Bib treatment did not affect the probability of the subject displaying the highest level of aggression (fight or lunge) at least once in the arrival behavior (Repeated measures logistic regression, $N=51$ (no=40, yes=11), $Z=0.4$, $p=0.67$); and did not affect total aggression, aggression of all behavior displayed by the subject between the time the subject arrives on screen until a bird leaves or is supplanted (Wilcoxon signed ranks test, $N=24$, $S=-15$, $p=0.53$). The arrival behavior did not correlate with the proportion of interactions won when competing against C opponents (Spearman's rank correlation, $N=26$, $r=0.02$, $p=0.91$) or E opponents (Spearman's rank correlation, $N=25$, $r=0.1$, $p=0.70$). However there was a trend for subjects to win more frequently when competing against E opponents than when competing against C (arcsine transformed data, Paired t-test, $df=31$, $t=-2.0$, $p=0.06$, Figure 4.5). This trend was not observed in the low deprivation treatment (arcsine transformed data, Paired t-test, $df=32$, $t=-0.8$, $p=0.41$).

Aggression displayed by opponents in high deprivation treatment

Subjects may be more aggressive to E opponents than to C opponents during periods of high deprivation because E opponents display more aggression than C opponents and the subjects are matching the aggression they receive. To evaluate this hypothesis, I compared the aggression displayed by E opponents to aggression displayed by C opponents during periods of high deprivation. When the opponent was the holder, bib treatment had no effect on aggression displayed when the subject approached the food (Wilcoxon signed ranks test, $N=18$, $S=32$, $p=0.17$), on total aggression displayed

(Wilcoxon signed ranks test, $N=24$, $S=24.5$, $p=0.13$) and proportion of behaviors with high aggression (Wilcoxon signed ranks test, $N=24$, $S=7$, $p=0.56$). When the opponent was the intruder, bib treatment had no effect on aggression displayed at the food (Wilcoxon signed ranks test, $N=30$, $S=-28.5$, $p=0.15$), on total aggression displayed (Wilcoxon signed ranks test, $N=31$, $S=-19.5$, $p=0.54$) and proportion of behaviors with high aggression (Wilcoxon signed ranks test, $N=31$, $S=-22$, $p=0.35$).

Discussion

A cost for cheating did not occur in the intrusion or approach stage, but did occur in the arrival stage of probing. Cheaters received more aggression than controls when resource value was high but not when resource value was low. Sex of the focal may affect some aspects of probing, but there is no evidence that sex of the focal affects how the focal responds to the signal level of the opponent during probing. Deprivation also affects some aspects of probing but does not increase the likelihood of probing.

Though mixed, the results suggest that individuals displayed more aggression to opponents signaling high status when resource value was high but not when resource value was low. The repeated measures ANOVA and the nonparametric analysis on the separate deprivation groups showed that the aggression displayed at the food was dependent on both the status signal of the opponent and the deprivation experienced. However, the deprivation treatment by bib treatment interaction was not significant when the deprivation groups were analyzed together in a nonparametric test. The difference in the results of the two nonparametric tests may be due to a reduced sample size in the later test. The difference in aggression displayed to enlarged opponents and controls when resource value is high may be due to individuals being more motivated to win and individuals expecting that a higher level of aggression would be needed to overcome an opponent signaling superior fighting ability. This is similar to Lemel and Wallin (1993)'s observation that the intensity of interactions was high when a low ranking great tit challenged a high ranking great tit. The absence of an effect of status signal on aggression, when resource value is low, may be due to the relatively low value of the resource in comparison to the high cost of displaying high aggression to opponents, regardless of the status signaled.

I found no effect of bib treatment on the proportion of interactions won at low deprivation, when resource value is presumed to be low, but did find a non significant tendency for subjects to win more often against enlarged opponents than against controls at high deprivation, when resource value is presumed to be high. Maynard Smith and Harper (1988) observed a different relationship between the proportion of interactions won, status signal and resource value. The authors found a negative correlation between the feeding rate of free living great tits, greenfinches and corn buntings and the proportion of interactions won by the individual signaling higher status. Maynard Smith and Harper (1988) interpreted the correlation to mean that as the value of the resource increased, the less important the signal became in determining the outcome of contests. This interpretation is supported in part by Gonzalez et al (2002) who found that enlarging the bibs of house sparrows increased the proportion of interactions won in non food deprived flocks, and Andersson and Ahlund (1991) who found that bib size had no effect on dominance under high deprivation in unmanipulated house sparrows. However the authors in the latter study admitted that sample size was small and unlike this study, the bird with the smaller bib was not always the more deprived bird in the asymmetrical deprivation treatments. In this study, I did not observe an effect of status signal on the proportion of interactions won when resource value was low, possibly due to the design of the experiment. It is possible the clumped nature of the food in this study resulted in too high a value for the food; displaced birds could not find alternative food sources. The birds in this study were forced to be scroungers whereas the birds in Maynard Smith and Harper's (1988) study could choose to be producers if they failed in the scrounger role. The decision to continue fighting or give up depends partly on the probability of obtaining food through alternative tactics and in this study there were no alternative tactics available, but in Maynard Smith and Harper's (1988) study there were. Alternatively, subjects may have recognized the incongruence between the status signaled and behavior of the opponents and "believed" the information that was the least advantageous for the signaler (Caryl 1982). It is possible the incongruence between the signal and behavior indicated that the opponent was an individual that would normally be dominant but was currently ill, and therefore would be easier for others to dominate. However, if behavior can not be faked, then why attend to status signals at all? Perhaps

status signals are used for assessing opponents from long distances since, they are easily viewed, whereas behavior is used for assessing opponents from short distances. The distances in which status signals might be used are likely larger than the area recorded in this study since bib treatment had no effect on probability of intrusion or intrusion time.

The status signaling hypothesis suggests that individuals should avoid opponents that signal high status. This is supported by studies showing that subjects preferred to feed next to individuals signaling low quality rather than individuals signaling high quality (Senar and Camerino 1998, Tibbetts and Lindsay 2008), though the preference may only be observed when resource value is low (Tibbetts 2008). Since individuals should avoid opponents signaling high status, I predicted that subjects would take longer to approach enlarged opponents than controls. The results from the analysis of the intrusion and approach stage do not support my prediction. Bib treatment, and the bib treatment by deprivation treatment interaction had no effect on any of the variables measured at the intrusion or approach stage. However, the variables measured at the intrusion stage may have failed to capture the motivations of the subjects. For example, though deprivation treatment was effective in increasing motivation to access food, deprivation treatment had no effect on the variables in the intrusion stage. Probably the subjects do not perceive some of the space on screen to be different from the space off screen in terms of proximity to the opponent and or food. Sex and deprivation treatment were significant variables in the analysis on approach time suggesting that approach time was successful in capturing some aspect of motivation. Therefore, the absence of an effect of bib treatment and a bib treatment by deprivation treatment interaction on approach time was not due to the inadequacy of the response variable but due to subjects approaching high and low ranking opponents indiscriminately. The lack of effect of bib treatment does seem to negate a chief benefit of signaling high rank and is difficult to explain.

The absence of an effect of bib treatment on aggression displayed in the arrival stage is in contrast to the findings of Moller (1987a), who found that enlarged house sparrows introduced into unfamiliar flocks received more aggression than their unmodified counterparts. However the results are consistent with Hein et al (2003), who found no effect of bib size on aggression received by unmodified house sparrows and

with Tibbetts and Shorter (2009), who found no effect of the number of facial spots on the challenger wasp or owner wasp on the intensity of conflict over a nest. The difference in the results of this study and Moller's (1987a) study may be due to the difference in the constitution of the subject group. The enlarged males in this study only encountered subjects with medium bibs, whereas enlarged males in Moller's (1987a) study encountered subjects with a range of bib sizes and therefore a range of dominance ranks. Moller (1987a) noted that enlarged males were involved with aggression with opponents with larger bibs than those involved with the control males. The absence of subjects with large bibs in this study may have resulted in results that differed from Moller's (1987a).

There is some evidence that some aspects of aggression displayed were affected by the sex of the subject. The results of the repeated measures ANOVA suggest that female subjects approached opponents quicker, though the nonparametric results show no effect of sex. If females do approach opponents quicker, it is not clear why female subjects would do so. In this study, male and female subjects were equally dominant so would have equal access to food. Additionally, their activity levels appear to be similar (personal observation) so would have similar energy demands. Furthermore, the weights of male and female subjects were similar at capture (male-27.9g, female-27.8g) and at the end of the study (male-30.2g, female-30.3g). Once at the food, male and female subjects displayed similar levels of aggression, consistent with the findings of Hein et al (2003) (but see Jawor 2000). However, in contrast to Hein et al (2003), I did not find a sex by bib size interaction on aggression displayed.

The effect of deprivation on probing is complex. Though increasing deprivation did not make probing more likely to occur, it did change the aggression used during probing. Increasing deprivation shortened the time it took for subjects to approach the food and increased the amount of aggression displayed at the food. Similar results were obtained by Andersson and Ahlund (1991) on house sparrows and predicted by theories on the evolution of fighting behavior and resource value (Bishop et al 1978; Enquist and Leimar 1987).

It is not clear if subjects that displayed higher aggression to enlarged opponents in high deprivation would also display higher aggression when probing honest dominants or if the subjects detected the incongruity between behavior and signal, and displayed

increase aggression to reverse a signaled dominance order (Rohwer 1977). Tibbetts and Izzo (2010) found that paper wasp queens with enhanced signals received a higher number of aggressive acts than their unaltered counterparts and counterparts that had both enhanced signal and altered behavior. However the subjects in this study were only more aggressive in the high deprivation treatment, suggesting that resource value played a larger role than dominance reversal in determining the amount of aggression to display.

The benefits of probing may vary with the degree of cheating in the population. The correlation between the status signaled and actual resource holding potential may become weaker as time progresses because the resource holding potential for an individual may change though the signal remains fixed. Indeed, some theory suggests that cheaters can comprise a significant portion of the population in a stable signaling system Szamado (2000). It might be beneficial for subordinates to probe more frequently as time since the last molt increases because the signal becomes a less reliable indicator of status as time progresses. The benefits of probing are inversely proportional to the degree of cheating in the population, therefore probing should occur more frequently as time since last molt increases.

The results of this study suggest that probing may result in a cost for cheating in the natural environment. In the natural environment, the availability of resources will fluctuate over time. During periods when resources are scarce, probing is the most beneficial because the reward is highest. The results of this study suggest that during these periods, the probability of probing does not increase but instead, the aggression used does. It is also during this period that probing would produce a cost for cheating. For house sparrows, the season of low food availability is probably the winter; therefore probing during the winter may be especially costly for cheaters. The increased aggression experienced during the winter may reduce over winter survival of cheaters compared to honest signalers and may contribute to honest signaling.

In conclusion, probing may contribute to honest signaling when resource value is high but not when resource value is low. Of the different stages of probing, the costs for cheating occur at the arrival stage, when opponents are within striking distance. Probing by females does not appear to be more costly for cheaters than probing by males and increasing the resource value does not make probing more likely. An aggression cost for

cheating due to probing has been demonstrated and this cost may contribute to the evolutionary stability of status signaling.

Table 4.1 Factors influencing subject intrusion time. Repeated measures ANOVA of log transformed intrusion time (second). Deprivation treatment are low (0.5hrs) and high (4hrs) subject deprivation time. Sex is subject sex. Bib treatments are control and enlarged opponent bib treatment.

Effect	df	F	p
Deprivation treatment	1,97	0.03	0.87
Sex	1,34	0.00	0.97
Bib treatment	1,96	0.01	0.92
Deprivation treatment X Bib treatment	1,96	0.02	0.90

Table 4.2 Factors influencing subject approach time. Repeated measures ANOVA of log transformed approach time (second). Deprivation treatments are low (0.5hrs) and high (4hrs) subject deprivation time. Sex is subject sex. Bib treatments are control and enlarged opponent bib treatment.

Effect	df	F	p
Deprivation treatment	1,74	3.86	0.05
Sex	1,30	4.05	0.05
Bib treatment	1,72	0.08	0.78
Deprivation treatment X Bib treatment	1,72	3.17	0.08

Table 4.3 Factors influencing aggression displayed by subject arriving at the food. Repeated measures ANOVA of arrival behavior. Deprivation treatments are low (0.5hrs) and high (4hrs) subject deprivation time. Sex is subject sex. Bib treatments are control and enlarged opponent bib treatment.

Effect	df	F	p
Deprivation treatment	1,83	6.72	0.01
Sex	1,36	0.04	0.85
Bib treatment	1,81	1.37	0.25
Deprivation treatment X Bib treatment	1,82	5.56	0.02

		Opponent						
								
Subject	♀	0.5/0.5	4/0.5	4/4	0.5/0.5	4/0.5	4/4	
	♀	4/0.5	4/4	0.5/0.5	4/0.5	4/4	0.5/0.5	
	♀	4/4	0.5/0.5	4/0.5	4/4	0.5/0.5	4/0.5	
	♂	0.5/0.5	4/0.5	4/4	0.5/0.5	4/0.5	4/4	
	♂	4/0.5	4/4	0.5/0.5	4/0.5	4/4	0.5/0.5	
	♂	4/4	0.5/0.5	4/0.5	4/4	0.5/0.5	4/0.5	

Figure 4.1 Experimental set up within a block. Subjects are females or males. Opponents are males assigned to enlarged or control bib treatment. Numbers shown are subject and opponent deprivation times (hr) respectively.

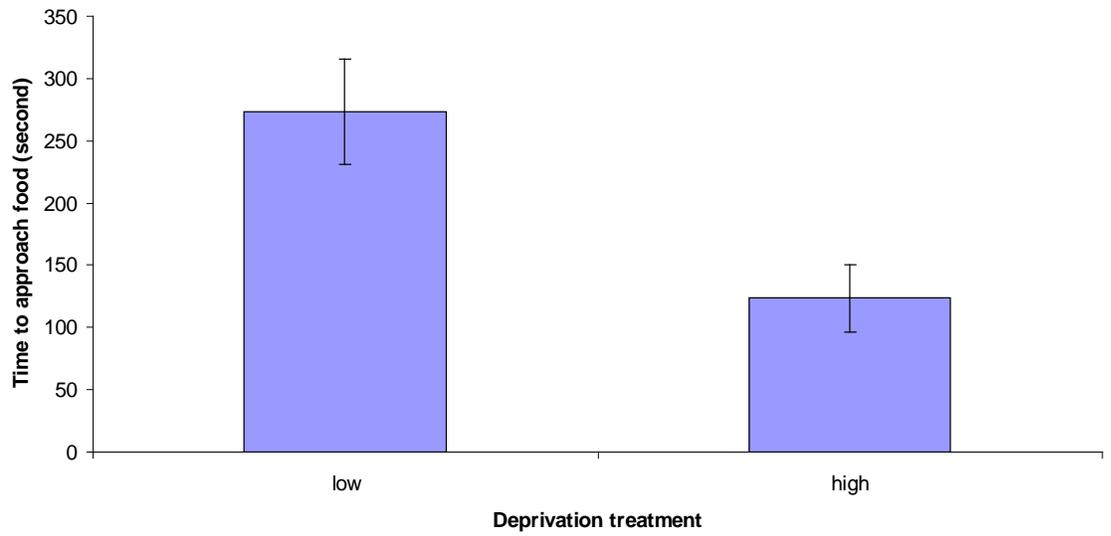
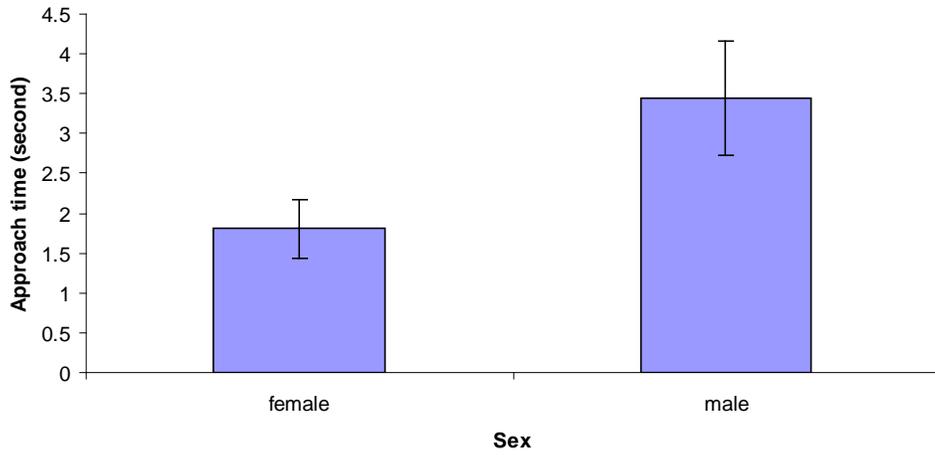
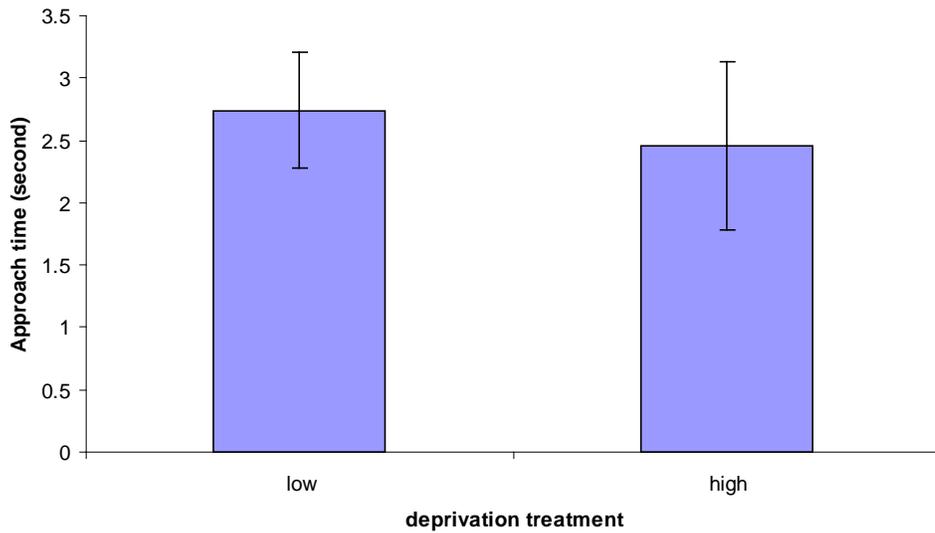


Figure 4.2 Time for birds to approach food in the low (0.5 hr) and high (4 hr) deprivation treatment. The means and standard errors are shown. Low deprivation n=68, high deprivation n=68.

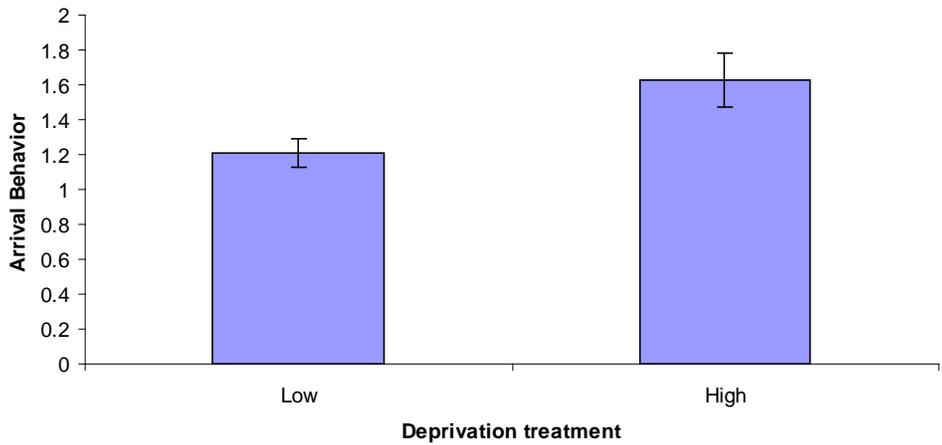


a)

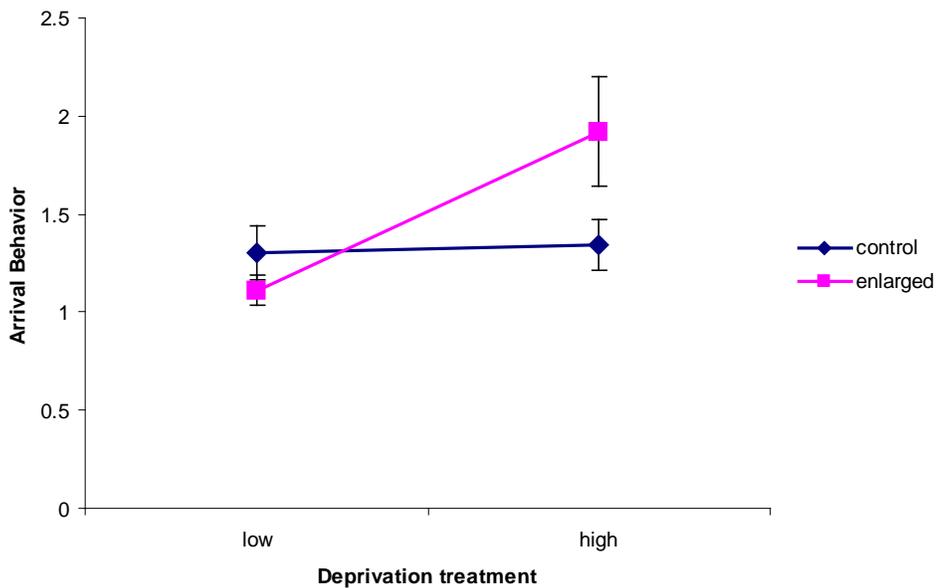


b)

Figure 4.3 Time for subject to approach food. The means and standard errors are shown.
 a) Effect of subject sex, females n=54, males n=51 b) Effect of subject deprivation treatment, low (0.5 hr) n=54, high (4 hr) n=51.



a)



b)

Figure 4.4 Aggression displayed by subject arriving at the food. The means and standard errors are shown. a) Effect of subject deprivation treatment, low (0.5 hr) n=54, high (4 hr) n=51 b) Interaction between subject deprivation treatment and opponent bib treatment. Deprivation treatments are low (0.5 hr) and high (4 hr) deprivation. Bib treatments are control and enlarged bib. low/control n=28, low/enlarged n=26, high/control n=26, high/enlarged n=25

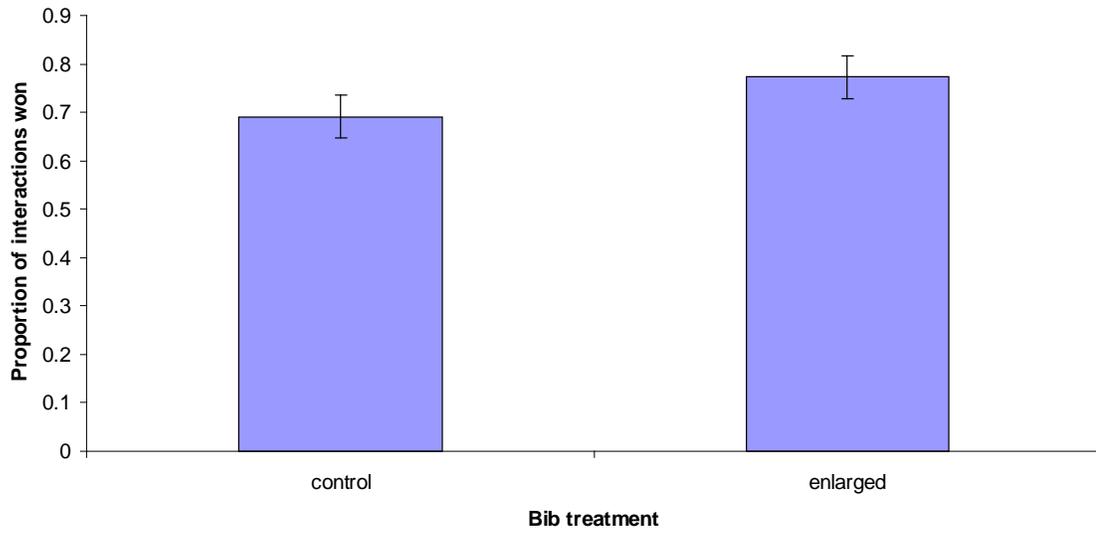


Figure 4.5 Proportion of interactions won by subjects against opponents with control or enlarged bib treatment. The means and standard errors are shown, control n=32, enlarged n=32.

Chapter Five: The role of familiarity in maintaining honest status signals

Introduction

Status signals, morphological traits that are correlated with dominance (Rohwer 1975), were identified more than three decades ago but still remarkably little is known about how status signals remain evolutionarily stable. Status signals have been identified in many species from a diverse set of taxa (Fox et al. 1990b, Senar 1999, Tibbetts and Lindsay 2008). Most of these signals consist of black (Rohwer 1975, Moller 1987 b, Senar and Camerino 1998a) or white patches (Fugle et al. 1984a) or black spots (Tibbetts and Lindsay 2008) and therefore do not directly contribute to the resource holding potential (RHP) of the bearer. Status signals are believed to be most useful in animals that encounter unfamiliar opponents frequently (Rohwer 1975) and are not able to assess RHP of opponents easily by observing body size or other morphological traits that would affect fighting ability. Amongst birds, status signals should be most likely to evolve in species that form large flocks during the nonbreeding period. There is some support for this as the evolution of patches for old and new world sparrows is related to winter sociality (Tibbetts and Safran 2009).

Status signals allow subordinates to assess the RHP of potential opponents, thereby allowing individuals to avoid costly fights with opponents that they have little prospect of dominating. Subordinates should avoid individuals that signal high status or retreat when confronted by individuals that signal high status. Thus individuals signaling high status can dominate group mates whilst still avoiding the costs associated with fighting. Since individuals with such signals could win contests without having to display proof of advertised RHP, it appears that it would be beneficial for everyone to signal high status regardless of their true RHP. Widespread adoption of this strategy would result in a loss of variability and information; and the signal would fall into disuse. The existence of status signals suggest that there must be mechanisms that prevent individuals from cheating, signaling high status when their true RHP is low.

Status signals which consist of patches of white or black do not appear to have high production costs (Poston et al. 2005b, Stewart and Westneat 2010) (but see Veiga, J. and Puerta 1996) suggesting that it is possible for all individuals to signal high status if it

benefits them to do so. This suggests that the honesty of status signaling is maintained by other types of costs. One type of cost that may be important in honest signaling is use costs; costs that result from interactions between the receiver's response to the signal and the performer's state (Johnstone 1998a).

Most models of signaling describe the costs and benefits to individuals that interact only a single time with unfamiliar opponents to gain access to a resource (Enquist 1985, Maynard Smith and Harper 1988, Dawkins and Guilford 1991, Owens and Hartley 1991a); the exception being Szamado's (2011a) model studying the effect of requiring individuals to interact multiple times to gain access to a resource. These models assume that opponents are always unfamiliar and individuals never gain any information about opponents RHP aside from the information conveyed in the signal. This follows from the expectation that status signals are most useful when opponents are unfamiliar (Rohwer 1975); however some social structures provide opportunities for opponents to learn about one another either directly by interacting with the same opponent multiple times or indirectly by observing opponents interacting with others. If individuals reside in small groups or if subgroups exist within larger groups, there may be opportunities to gain additional information about the RHP of opponents. Familiarity may provide opportunities for cheaters to be revealed. Once cheating is revealed, individuals can adjust their behavior according to what they perceive the true RHP of the cheater to be. Familiarity can reduce the benefits of cheating or even impose cost on cheaters if there is any form of retaliation for cheating (Tibbetts and Dale 2004). Therefore the effects of familiarity may be important in limiting inappropriate status signaling.

The benefits and costs of cheating could depend on the status signal of the receiver, whom I will call the subject. Subjects signaling low status are predicted to avoid opponents that signal high status, including cheaters. However, subjects signaling high status are predicted to fight cheaters if cheaters do not flee. The cheaters, who are aware of their true RHP, may avoid subjects that signal high status because cheaters will likely lose to them in a fight. Since cheaters can win against subjects signaling low status without fighting and cheaters can only win against subjects signaling high status by fighting, the benefits of cheating are greatest when subjects signal low status and smallest when subjects signal high status. In some studies, enhanced birds dominate controls

(Fugle et al. 1984a, Rohwer 1985b) or become dominant following enhancement of the status signal (Grasso et al. 1996), but none have determined if the change in dominance is due to a change in dominance of the enhanced individual with opponents that signal low status or with all opponents. The fitness loss for subjects due to the presence of cheaters may depend on the subject's status signal. Subjects signaling low status should withdraw and avoid cheaters so they may lose resources to cheaters that they would otherwise not have, but subjects signaling high status should not withdraw or avoid cheaters so would not lose resources to cheaters. Since the presence of cheaters may reduce the fitness of subjects signaling low status more than the fitness of subjects signaling high status, subjects signaling low status may be more likely than subjects signaling high status to "punish" cheaters by display more aggression to cheaters than to honest controls and to other individuals signaling high status. If subjects signaling low status can detect cheating, they may change their behavior to reduce the fitness of cheaters.

I tested for the effects of familiarity and subject rank on the benefit and cost of cheating in house sparrows (*Passer domesticus*). House sparrows form mixed sex flocks during the fall and remain in flocks until the spring. Status signals are thought to be most useful during the fall and winter when birds interact frequently over access to food and perching sites. Male house sparrows have a black bib on the breast and the size of the bib has been shown to act as a status signal against both sexes (Moller 1987 b, Liker and Barta 2001, Hein et al. 2003, Nakagawa et al. 2007). Males renew their bib in the fall during their annual molt and the size of the bib is determined by the number of melanized feathers. Initially, the molted feathers have buff colored tips but as the season progresses, the tips are worn away to reveal the black bib. The signaling component of the bib does not appear to be affected by the reduction of key nutrients during the molt period (Poston et al. 2005b, Stewart and Westneat 2010). This suggests that use costs rather than production costs are important in maintaining signal honesty. Some evidence exists in house sparrows for costs to large-bibbed individuals of interacting with true dominants (Rohwer 1977, Moller 1987 a, Tibbetts and Dale 2004), females (Hein et al. 2003), or especially motivated opponents (Chapter 4). The potential effect of familiarity and rank on the cost and benefits of signaling inappropriately in house sparrows has not been studied.

Methods

Male house sparrows (*Passer domesticus*) were captured from various locations in Lexington Kentucky from November 2007 to January 2008 using mist nets and potter traps. The birds were weighed; and tarsi, wing chord, length and width of whole bib (composed of black feathers with white tips) were measured using dial calipers. Bib measurements were taken with the bird held upright and bill placed at 90° angle to the body. Bib size was calculated using the formulae $(167+0.45*\text{length}*\text{width})$ (Moller 1987 b). Mean bib size was 352 mm² and standard deviation was 31mm². The birds were banded with one metal and three plastic color bands for identification. The birds were housed in same or mixed sex flocks in outdoor aviaries (2.5m X 2.5m X 3.7m), with a maximum of 15 birds in each aviary. The birds were fed a mixture of white millet and poultry feed ad libitum and each aviary contained multiple food dishes, one water dish, one roost box and 2 trees for perching.

The males were categorized as having a small, medium or large bib. Small bibs were those that measured at least 1 standard deviation below the mean, medium bibs those that measured within 1 standard deviation of the mean, and large bibs were those that measured at least 1 standard deviation above the mean. Males were then assigned to blocks and each block consisted of 4 subjects and 3 unfamiliar opponents. Subjects within each block consisted of two medium bib males and two large bib males. Opponent birds were males having either a large or small bib, and assigned to a large bib control (LC), small bib control (SC) and small bib enlarged (SE) treatment. There were 12 possible dyads in each block and 8 blocks total. The blocks were staggered in time due to space constraints.

The experiment started on January, 2007 and finished March, 2007. At the start of the experiment, subject birds were placed into individual cages and opponent birds were subjected to either a control or enlargement treatment before being placed into individual cages (metal 25cm width X 25cm height X 40cm length). The cages were hung on brackets and 4 rows of three adjoining cages were hung on a wall. Each row contained a subject in a cage on one side and either an opponent in a cage or an empty cage on the other side. Panels dividing the cages were removable and there was a single removable panel in the middle cage. The panel in the middle cage was mounted on a platform (10

cm wide) that extended from the front of the cage to the back and divided the cage in half. The panel in the middle cage allowed the birds to have audio contact but not visual contact. In each cage there was a roost tube, 2 perching sticks, a water dish and a food dish. Food and water were replenished daily.

Small bib males in the enlarged bib treatment (SE) had their bibs enlarged by the application of Rodol A dye (1g/25ml H₂O) and peroxide to the feathers on the edge of the natural bib using a cotton swab. Bibs were enlarged to at least 1 standard deviation above the mean bib size. Some feathers at the center of the bib were also dyed in the same manner to control for the dye in the center of the bib in LC and SC males. The feathers were then allowed to air dry and the males were then placed inside cages. Males in the LC and SC treatment were handled in a similar manner as the SE males. The LC and SC males were held in the same position as the SE males and had the edge of their natural bibs touched with a dry cotton swab for the same amount of time as used for SE males. Near the end of the handling period, some dye and peroxide was applied to the feathers in the center of the bib to control for the presence of dye on SE males. The feathers were then allowed to air dry and the males were then placed inside cages.

Tournaments were started 6-7 days after the birds were placed in cages. On day 0, the cages were moved so that subjects were placed in the same row as their assigned opponents. The panels separating the left and right cages from the middle cages were removed and the birds were allowed access to half of the space in the middle cages. To familiarize birds with feeding in the middle cage, the food in both the left and right cages were placed next to the middle panel. At 12 pm on day 1 of the tournament, the food was removed and the dummy cameras were replaced by real cameras. At 4 pm, the panels in the middle cages were removed and a single food dish with food was placed in each middle cage. All interactions in the middle cage were then recorded for approximately 1 hour. At the end of the recording period, the single food dishes were removed, 2 new food dishes filled with food were placed in each middle cage and the real cameras were replaced with dummy cameras. The birds then remain together for day 2, 3 and 4 of the tournament. On day 4 of the tournament, the food was again removed at 12 pm, a single food dish with food was returned at 4 pm, and interactions in the middle cage were recorded for 1 hour. The tournaments were repeated with new opponents until all the

subjects had met all the opponents in the block. At the end of the tournaments, the birds were returned to their capture site.

The videos were scored in random order, with the viewer blind to the tournament day and bib treatment. Subjects and opponents were able to occupy the holder role, the role of the bird that is at the food at the start of the interaction, or the intruder role, the role of the bird that arrives second on screen, and measurements of aggression were taken for both roles. Measures of aggression taken include the approach time, and the aggression displayed when an intruder arrived at the food, either in the holder or intruder role. Approach time is the time between the arrival of the intruder on screen and time for the intruder to arrive the food. Aggression displayed by the holder when the intruder approached the food was scored on a scale from 0-5, with 5 being the most aggressive (Table 5.1). Aggression displayed by the intruder was scored from 1-4 with 4 being the most aggressive (Table 5.2). Aggression displayed as holder and intruder were scored on different scales because some behaviors displayed by the holders could not be displayed by intruders (e.g. leaving) and or was rarely displayed by intruders (e.g. pecking).

Analysis

To test for the effects of familiarity, I compared the behavior of subjects when initially introduced to opponents with their behavior after being housed with opponents for 4 days. The opponents were one of three treatments: small bib control (SC), large bib control (LC) or small bib enlarged (SE). I predicted that if familiarity reduces the benefits of cheating, then SE opponents would win at a higher rate than SC opponents on day 1 but SE opponents would win at the same rate as SC opponents on day 4. Additionally, SE opponents would be approached less frequently than SC opponents on day 1 but at the same rate on day 4. If familiarity produces a cost for cheating, then SE opponents would receive less aggression than SC opponents on day 1 but SE opponents would receive more aggression than SC opponents on the day 4. If a cost of cheating is observed, then a comparison between aggression displayed to SE and LC opponents would indicate if the difference qualifies as punishment.

I also tested for the effect of subject status signal on benefits and cost of cheating. If the status signal of subjects affects benefits of cheating I expected medium bibbed subjects to win less frequently than large bib subjects against SE opponents on day 1. Additionally, medium bibbed subjects should approach SE opponents less frequently than large bib subjects will approach SE opponents on day 1. If the benefits of retaliatory behavior affect the cost of cheating, then I expected medium bib subjects to display more aggression than large bib subjects to SE opponents on day 4.

Aggression scores are ordinal data and were tested using the GLIMMIX procedure (SAS) for generalized linear mixed models (GLMM), with a Kenward-Roger degrees of freedom estimator, a multinomial distribution and cumlogit link. The probability of approach and probability of winning are binomial data and were also tested using the GLIMMIX procedure (SAS) for GLMM, with a Kenward-Roger degrees of freedom estimator, a binomial distribution and logit link. The model for the analysis of opponent behavior included the following fixed effects: opponent bib, day, subject bib, block, observation time and day by opponent bib interaction; and the following random effects to account for the repeated measures design of the study: subject id and trial nested within subject id. Block was included in the models to account for effects of location, date and opponent group on dependent variables. Observation time was included in the model to account for satiation as time from return of food elapsed. The model for the analysis of subject behavior included all the same effects plus a day by subject bib interaction, an opponent bib by subject bib interaction and a day by opponent bib by subject bib interaction.

Though approach time was not normally distributed and remained so despite log transformation, approach time was analyzed using generalized linear mixed models, with a normal distribution and identity link. The GLMM allowed me to test for a day by opponent bib interaction. Any significant effects from the GLMM were then confirmed with non-parametric tests.

There were 32 subjects, 16 large bib and 16 medium bib subjects. Not all subjects met 3 opponents, 24 subjects met 3 opponents, 6 subjects met 2 opponents and 2 subjects met 1 opponent. Three subjects met with an opponent on day 2 but not day 5. There were

a total of 171 trials, with 2443 subject intruder observations and 2180 subject holder observations.

Results

Effect of bib treatment on opponent behavior

I assumed that the bib enlargement did not affect the behavior of SE opponents; to test this I constructed a GLMM with only the main effects and no interactions. Bib treatment had no effect on aggression displayed as holder at the food ($df=1,124$, $F=0.03$, $p=0.97$) and as intruder at the food ($df=1,101$, $F=1.48$, $p=0.23$).

Effect of familiarity

Familiarity had no effect on aggression displayed by subjects at the food as holders or as intruders (Table 5.3) and did not affect the probability of approach (Table 5.4) or approach time (Table 5.4). Familiarity did affect the probability of subject winning; subject holders and intruders had a higher probability of winning on day 4 than on day 1 (subject holders, Table 5.5, day1-day4: odds ratio=-0.54, S.E.=0.20, $df=99$, $t=-2.64$, $p=0.01$; subject intruders, Table 5.5, day1-day4: odds ratio=-0.49, S.E.=0.22, $df=107$, $t=-2.23$, $p=0.03$).

Effect of observation time

Observation time, time from start of trial to time of event, affected some measures of aggression and dominance. As observation time increased, subject intruders were less likely to approach (Table 5.4, estimate= -0.0004, S.E.=0.00006, $df=1325$, $t=-6.48$, $p<0.0001$) and took longer to approach (Table 5.4, estimate= 0.0029, S.E.=0.00038, $df=823$, $t=7.56$, $p<0.0001$). However once an approach occurred, subject intruders displayed more aggression at the food as observation time increased (Table 5.3, estimate=0.0004, S.E.=0.00012, $df=860$, $t=3.62$, $p<0.001$). Interestingly, opponents also displayed more aggression at the food as observation time increased, in both the holder (Table 5.6, estimate=0.0002, S.E.=0.00009, $df=853$, $t=2.19$, $p<0.03$) and intruder role (Table 5.6, estimate=0.0005, S.E.=0.00011, $df=866$, $t=4.18$, $p<0.0001$). The effect of observation time on dominance was dependent on the role of the subject. The probability of the subject holder winning decreased as the observation time increased (Table 5.5, estimate=-0.0003, S.E.=0.00008, $df=793$, $t=-4.31$, $p<0.0001$) but the probability of the

subject intruder winning increased as observation time increased (Table 5.5, estimate=0.0002, S.E.=0.00008, df=792, t=2.77, p<0.01).

Effects of bib size

Bib size had no effect on any of the measurements of aggression or dominance. There was no main effect of opponent bib or focal bib on aggression displayed at the food (Table 5.3), probability of approaching (Table 5.4), approach time (Table 5.4) or probability of winning (Table 5.5) by subjects.

Effect of familiarity on benefit and cost of cheating

There was no evidence that familiarity reduced the benefits of cheating because there were no benefits of cheating detected. There was no significant day by opponent bib interaction for the probability of approach (Table 5.4), and subjects were not more likely to approach SC opponents than SE opponents on day 1, instead the opposite pattern occurred. There was a trend for subjects to approach SE opponents more frequently than SC opponents on day 1 (SC-SE opponent: odds ratio=-0.56, S.E.=0.30, df=98, t=-1.86, p=0.07). This difference in tendency to approach disappears by day 4 (SC-SE opponent: odds ratio=-0.04, S.E.=0.36, df=154, t=-0.10, p=0.92). The tests on approach time also revealed no effects of familiarity on the benefits of cheating. Though the day by opponent bib interaction for approach time was close to significant (Table 5.4), there was no significant difference in approach time for SC and SE opponents on either day (day 1 SC-SE opponent: odds ratio=-1.95, S.E.=1.98, df=74, t=-0.98, p=0.33; day 4 SC-SE opponent: odds ratio=1.95, S.E.=2.22, df=103, t=0.88, p=0.38). Additionally, familiarity appeared to have no effect on the probability of winning, the predicted benefit of cheating. There was no day by opponent bib interaction on the probability of subject winning (Table 5.5) and there was no significant difference in probability of winning on either day against SC and SE opponents for both subject holders (day 1 SC-SE opponent: odds ratio=-0.07, S.E.=0.34, df=99, t=-0.19, p=0.85; day 4 SC-SE opponent: odds ratio=-0.07, S.E.=0.37, df=115, t=-0.19, p=0.85) and subject intruders (day 1 SC-SE opponent: odds ratio=0.06, S.E.=0.34, df=78, t=0.16, p=0.87; day 4 SC-SE opponent: odds ratio=0.35, S.E.=0.40, df=118, t=0.87, p=0.38).

The evidence that familiarity produced a cost for cheating is mixed. The day by opponent bib interaction was not significant for aggression displayed at the food by subjects (Table 5.3); but there was a non-significant trend for subject holders to display more aggression at the food to SC opponents than SE opponents on day 1 (SC-SE opponents: odds ratio=0.57, S.E.=0.38, df=104, t=1.49, p=0.14). However there was no difference in aggression displayed at food for SC and SE opponents on day 4 (SC-SE opponents: odds ratio=-0.46, S.E.=0.42, df=120, t=-1.09, p=0.28). Though the effects were non significant, the pattern of change in aggression displayed by subject holders at the food was similar to that predicted if there was a cost for cheating (Figure 5.1).

Effect of bib size of signal receiver on benefit of cheating and receiver retaliatory behavior

There is no evidence that bib size of the receiver affected the predicted benefits of cheating. The day by opponent bib by subject bib interaction did not significantly affect the probability of subject winning (Table 5.7) or the probability of approach (Table 5.8). There was no effect of subject bib size on the probability of subject winning against SE opponents on day 1 in the intruder role (large bib -medium bib subject: odds ratio=0.18, S.E.=0.48, df=87, t=0.38, p=0.70) but there was a trend for large bibbed subjects to win more than medium bibbed subjects against SE opponents in the holder role on day 1 (large bib subject-medium bib subject: odds ratio=0.69, S.E.=0.48, df=98, t=1.42, p=0.16). Though there is a trend for large bib subjects to win more than medium bib subjects, SE opponents do not avoid large bib subjects more than medium bib subjects (probability of SE opponent approaching subject, large bib subject-medium bib subject: odds ratio=0.01, S.E.=0.36, df=127, t=0.01, p=0.99). There was no effect of subject bib on probability of subject approaching SE opponents on day 1 (large bib subject-medium bib subject: odds ratio=0.38, S.E.=0.48, df=96, t=0.79, p=0.43).

There is also no evidence that the bib size of the receiver affected retaliatory behavior. The day by opponent bib by subject bib interaction was not significant for aggression displayed by subject at the food (Table 5.9) and there was also no effect of subject bib size on aggression displayed by subject at food to SE opponents on day 4 in holder role (large bib subject-medium bib subject: odds ratio=0.19, S.E.=0.58, df=129,

$t=0.32$, $p=0.75$) or intruder role (large bib subject-medium bib subject: odds ratio=0.36, S.E.=1.03, $df=102$, $t=0.35$, $p=0.73$).

Discussion

There are trends which suggest that familiarity did have some effects on the costs and benefits of cheating but not always in the patterns initially predicted. Familiarity had no effect on dominance as cheaters and controls were equally dominant when unfamiliar and when familiar. There was a tendency for subjects to approach unfamiliar cheaters more frequently than unfamiliar controls, which is opposite of that predicted by the status signaling hypothesis (Rohwer 1975) and familiarity eliminates this cost of cheating. There was also a tendency for familiarity to affect the aggression displayed at the food in a pattern that produced a cost for cheating. Controls tended to receive more aggression at the food than cheaters when unfamiliar, but the opposite was observed when birds were familiar, therefore familiarity seemed to eliminate this benefit of cheating. These results suggest that the role of familiarity in the evolutionary stability of status signals is complicated because it both eliminates the cost and the benefit of cheating.

The lack of effect of bib enlargement on winning when unfamiliar contradicts the predictions of the status signaling hypothesis (Rohwer 1975), which states that opponents should be more likely to yield to individuals signaling high status. Surprisingly, there are few studies in which dominance amongst enhanced individuals and unfamiliar conspecifics were tested. Our results are in agreement with those obtained by Tibbetts and Dale (2004), who found no effect of signal enhancement on dominance amongst unfamiliar paper wasps. However our results do contradict those of Vedder et al. (2010), who observed a negative effect on dominance when the UV reflectance of the crown on male blue tits was reduced. One possible explanation for the lack of effect in our study is that the resource value was sufficiently high such that dominance was determined by actual RHP (fighting) rather than by signals, as suggested by Maynard Smith and Harper (1988) and observed by Tibbetts (2008). An alternative explanation is that the combination of high status behavior and high status signal are needed to convince a competitor of a high RHP; this skeptical recipient hypothesis (Caryl 1982) has some support from experiments in which both signal and behavior were altered (Rohwer and

Rohwer 1978). Rohwer and Rohwer (1978) found that enhancing the signal alone was insufficient to produce an increase in dominance, but a combination of signal enhancement and testosterone implants to increase aggression was. In this experiment the bib enlargement treatment did not affect the behavior of the opponents; therefore the cheaters would have continued to behave as subordinates. The incongruence between low status behavior and high status signal could have resulted in opponents believing in the information that conveyed the lowest status. The incongruence between signal and behavior may indicate that a normally dominant individual is ill and therefore the observer may be more likely to win. If the skeptical recipient hypothesis is true, it does beg the question of why the status signal exists since if the observer can use the information in the behavior (a signal that is always reliable since it cannot be faked) instead of the information in the status signal (a signal that may or may not be reliable).

Familiarity did not affect dominance, the main benefit of cheating. This is not surprising since cheating had no effect on winning against unfamiliar opponents. It follows then that bib treatment in general had no effect on dominance. Moller (1987 a) also observed no difference in proportion of interactions won between house sparrows with enlarged bibs and controls; and Gonzalez et al. (2002b) observed no increase in proportion of fights won after enlarging the bib of house sparrows. This suggests that it is difficult to produce cheaters simply by altering the bib in house sparrows and that house sparrows may use multiple indicators of status and incongruence between the indicators would result in unsuccessful cheaters. Relying on multiple indicators of status rather than just one may be a more effective method of guarding against cheating.

The status signaling hypothesis predicts that one of the benefits of signaling high status is the reduced probability of being challenged (Rohwer 1975), however the results suggest that it is actually a cost of signaling high status. It is unclear why subjects had a tendency to approach unfamiliar opponents signaling high status more than unfamiliar opponents signaling low status. One possible explanation is that cheaters monopolized the food more than the controls and therefore the resource value and motivation to approach is higher when the opponent is a cheater. If cheaters are able to monopolize the food more than controls then the difference in approach rate may actually hint at a benefit of cheating. However, there was no difference in probability of subjects winning against

unfamiliar cheaters and controls, suggesting that cheaters did not monopolize the food more than controls; but I do not have data on how long subjects were at the food when paired with cheaters and when paired with controls so I cannot reject this explanation. The results obtained on tendency to approach are inconsistent with previous studies on the effects of status signals on avoidance as those studies showed that subjects avoided opponents that signaled high status (Senar and Camerino 1998a, Tibbetts and Lindsay 2008). Those studies were choice experiments in which subjects could choose which of two opponents with different advertised status to approach; whereas in the present study, subjects could decide only whether to approach or not an opponent with a particular status advertised. Both types of designs are a test of the status signaling theory but differ subtly in what is measured. The decision to approach may be influenced by factors other than the signal of the opponent, such as resource value (Tibbetts 2008), whereas the decision of which opponent to approach is likely only influenced by the signal of the opponents. Familiarity eliminated the difference in probability of approach, therefore reducing what appears to be a cost of cheating. However, without knowing why subjects approached cheaters more than controls initially, it is not clear if what is being reduced is a cost or benefit of cheating.

I observed no difference in aggression received by cheaters and by controls; however there were nonsignificant trends supporting the theory that familiarity produces a cost for cheating. The pattern shows cheaters receiving less aggression than small controls when birds are unfamiliar; but when birds are familiar, the opposite relationship occurs, with cheaters receiving more aggression than controls. In contrast to our results for unfamiliar opponents, cheaters in Moller (1987 a) and Tibbetts and Izzo (2010) studies experienced more aggression than controls. The status signaling hypothesis predicts that one of the benefits of signaling high status among unfamiliar opponents is receiving less aggression; therefore Moller (1987a) and Tibbetts and Izzo (2010) study did not support this prediction of the status signaling hypothesis. Though the aggression received by cheaters and unfamiliar controls in this study is in the direction predicted by the status signaling hypothesis, it is not particularly convincing.

Cheating does not appear to be more costly to individuals signaling medium rank than to individuals signaling high rank. The lack of effect of signal enhancement on

dominance and avoidance suggests that the make up of the group does not affect the benefit of cheating, which seems at odds with the fact that the status signaling hypothesis predicts that the benefit of signaling high rank is dependent on the proportion of opponents that signal a lower rank. There was also no evidence that the cost of cheating was dependent on the status signal of the subject, suggesting that make up of the group did not affect the cost of cheating. These results suggest that group make up has little effect on the evolution of honest signaling in house sparrows.

The negative relationship between probability of approach and observation time probably resulted from a reduction in subjective resource value as time spent in the presence of food increased. This is supported by the increase in approach time as observation time increased. However I do not have data on the quantity of food consumed by each competitor and therefore can not conclude that subjective resource value was reduced as observation time increased, though it seems a reasonable assumption. The positive relationship between aggression displayed at the food and observation time is similar to the pattern between aggression and order of interaction observed by Lemel and Wallin (1993). Lemel and Wallin (1993) suggested that the positive correlation between intensity of interaction and order of interaction was in accordance to that predicted by the war of attrition model (Parker and Rubenstein 1981). The sequential assessment model also predicts a positive correlation between intensity of interaction and order of interaction (Enquist and Jakobsson 1986). If contestants have opportunities to interact multiple times, such as when flocks are small or when subgroups exist within a larger flock, then actual RHP are more likely to be assessed and cheating more likely to be revealed since the intensity of interaction increases as time spent interacting increases.

Though there were no significant effects observed, there is a trend that suggests that the bib size of receiver may affect the cost of cheating to the receiver. Subjects with large bibs had a nonsignificant tendency to win more often than medium bib subjects against cheaters. This is in agreement with the hypothesis that natural bib size does reflect some aspect of RHP in house sparrows (Nakagawa et al. 2007). High status group members may be more likely to reveal cheating since they are more aggressive. Though there are some hints that the cost of cheating for the receiver is dependent on the

receiver's own status, there is no evidence that receivers display retaliatory behavior based on potential cost of cheating to them.

It is not clear why subject holders and subject intruders show opposite directions in the relationship between probability of subject winning and observation time. It is possible that birds identified as 'holders' have by definition an opportunity to feed and therefore the value of food is decreasing for them as observation time increases. Thus, when challenged by increasingly aggressive opponents, the holders are more willing to relinquish the food. This hypothesis would explain why subject intruders win more frequently as time increases. Once an intruder supplants a holder, it becomes the new holder and has the opportunity to feed, lower the value of food for the new holder. The difference in effect for subject holders and subject intruders does suggest that depending on the question, it may be important to consider the role of the individual when analyzing its behavior.

In summary, I found no significant effects of familiarity though there are trends that hint that familiarity may affect both the both the cost and benefit of cheating, therefore it difficult to determine if familiarity promotes or discourages honest signaling. Due to the ambiguity of the effects of familiarity on the stability of status signals, it is seems unlikely that familiarity will have a strong effect on honest signaling. Costs in other forms are likely to be more important in the stability of honest signaling.

Table 5.1 Aggression of behavior displayed by subject as the holder at food.

Aggression score	Behavior
0	leave, move away
1	ignore
2	turn toward opponent
3	horizontal body, approach opponent, wing flutter
4	peck
5	fight, lunge, grapple

Table 5.2 Aggression of behavior displayed by subject as the intruder at food.

Aggression score	Behavior
1	approach food without overt aggression
2	turn toward opponent
3	horizontal body, approach opponent, wing flutter
4	fight, lunge, grapple

Table 5.3 Test for fixed effects on the cumulative odds of the aggression displayed by subject at food. Analysis of the generalized linear mixed model was performed with the GLIMMIX procedure (SAS) with a multinomial distribution and cumlogit link. Subject id and trial (nested within subject id) were included as random effects in the model. Day is unfamiliar (day 1) or familiar (day 4) treatment. Observation time is time from return of food. Opponent bib is large bib control, small bib control or small bib enlarged treatment. Subject bib is medium bib or large bib. The block effect was removed from the analysis of aggression expressed by subject intruder to allow the model to converge.

Effects	Subject as holder			Subject as intruder		
	df	F	p	df	F	p
Day	1,110	0.78	0.38	1,92	0.34	0.56
Block	7,21	2.63	0.04			
Observation time	1,862	2.27	0.13	1,860	13.10	<0.001
Opponent bib	2,116	0.18	0.83	2,84	0.28	0.76
Subject bib	1,20	1.33	0.26	1,26	0.76	0.39
Day X Opponent bib	2,111	2.16	0.12	2,83	0.08	0.93

Table 5.4 Tests for fixed effects on approach behavior of subject intruder. Generalized linear mixed model was constructed for the analysis of the odds of subject approaching and approach time. Analysis of the odds of subject approaching food was performed with the GLIMMIX procedure (SAS) with a multinomial distribution and cumlogit link. Analysis of approach time was performed with the GLIMMIX procedure (SAS) with a normal distribution. Subject id and trial (nested within subject id) were included as random effects in the model. Day is unfamiliar (day 1) or familiar (day 4) treatment. Observation time is time from return of food. Opponent bib is large bib control, small bib control or small bib enlarged treatment. Subject bib is medium bib or large bib.

Effects	Odds of subject approaching food			Approach time (sec)		
	df	F	p	df	F	p
Day	1,136	2.06	0.15	1,92	0.58	0.45
Block	7,23	1.45	0.23	7,19	2.39	0.06
Observation time	1,1325	42.04	<0.0001	1,823	57.21	<0.0001
Opponent bib	2,134	1.03	0.36	2,90	1.01	0.37
Subject bib	1,23	0.04	0.84	1,20	1.94	0.18
Day X Opponent bib	2,133	0.79	0.43	2,90	2.78	0.07

Table 5.5 Test for fixed effects on odds of subject winning an interaction. Analysis of the generalized linear mixed model was performed with the GLIMMIX procedure (SAS) with a binomial distribution and logit link. Subject id and trial (nested within subject id) were included as random effects in the model. Day is unfamiliar (day 1) or familiar (day 4) treatment. Observation time is time from return of food. Opponent bib is large bib control, small bib control or small bib enlarged treatment. Subject bib is medium bib or large bib. The block effect was removed from the analysis of aggression expressed by subject intruder to allow the model to converge.

Effects	Subject as holder			Subject as intruder		
	df	F	p	df	F	p
Day	1,99	6.98	0.01	1,107	4.98	0.03
Block	7,21	2.52	0.05	7,24	0.89	0.53
Observation time	1,793	18.58	<0.0001	1,792	7.65	<0.01
Opponent bib	2,108	0.29	0.75	2,99	0.32	0.73
Subject bib	1,20	1.21	0.29	1,25	0.35	0.56
Day X Opponent bib	2,103	0.2	0.82	2,98	0.99	0.37

Table 5.6 Test for fixed effects on the cumulative odds of the aggression displayed by opponent at food. Analysis of the generalized linear mixed model was performed with the GLIMMIX procedure (SAS) with a multinomial distribution and cumlogit link. Subject id and trial (nested within subject id) were included as random effects in the model. Day is unfamiliar (day 1) or familiar (day 4) treatment. Observation time is time from return of food. Opponent bib is large bib control, small bib control or small bib enlarged treatment. Subject bib is medium bib or large bib.

Effects	Opponent as holder			Opponent as intruder		
	df	F	p	df	F	p
Day	1,131	1.26	0.26	1,112	1.43	0.23
Block	7,14	4.35	0.01	7,13	0.75	0.64
Observation time	1,853	4.78	0.03	1,866	18	<0.0001
Opponent bib	2,14	0.57	0.58	2,13	0.34	0.72
Subject bib	1,124	0.03	0.87	1,101	1.48	0.23

Table 5.7 Test for an interaction between familiarity, opponent bib treatment and subject bib on odds of subject winning an interaction. Analysis of the generalized linear mixed model was performed with the GLIMMIX procedure (SAS) with a binomial distribution and logit link. Subject id and trial (nested within subject id) were included as random effects in the model. Day is unfamiliar (day 1) or familiar (day 4) treatment. Observation time is time from return of food. Opponent bib is large bib control, small bib control or small bib enlarged treatment. Subject bib is medium bib or large bib.

Effects	Subject as holder			Subject as intruder		
	df	F	p	df	F	p
Day	1,98	6.50	0.01	1,105	4.15	0.04
Block	7,21	2.59	0.04	7,24	0.94	0.50
Observation time	1,788	18.41	<0.0001	1,787	7.57	<0.01
Opponent bib	2,108	0.27	0.76	2,97	0.46	0.63
Subject bib	1,20	1.04	0.32	1,25	0.33	0.57
Day X Opponent bib	2,102	0.24	0.79	2,96	0.85	0.43
Day X Subject bib	1,98	1.06	0.31	1,103	1.04	0.31
Opponent bib X Subject bib	2,108	0.23	0.79	2,99	1.23	0.30
Day X Opponent bib X Subject bib	2,101	0.20	0.82	2,96	0.67	0.51

Table 5.8 Test for an interaction between familiarity, opponent bib treatment and subject bib on odds of subject intruder approaching food. Analysis of the generalized linear mixed model was performed with the GLIMMIX procedure (SAS) with a binomial distribution and logit link. Subject id and trial (nested within subject id) were included as random effects in the model. Day is unfamiliar (day 1) or familiar (day 4) treatment. Observation time is time from return of food. Opponent bib is large bib control, small bib control or small bib enlarged treatment. Subject bib is medium bib or large bib.

Effects	df	F	p
Day	1,125	2.17	0.14
Block	7,23	1.47	0.23
Observation time	1,1320	41.48	<0.0001
Opponent bib	2,125	0.90	0.41
Subject bib	1,24	0.06	0.81
Day X Opponent bib	2,123	0.87	0.42
Day X Subject bib	1,123	0.02	0.88
Opponent bib X Subject bib	2,127	0.06	0.94
Day X Opponent bib X Subject bib	2,124	1.98	0.14

Table 5.9 Test for an interaction between familiarity, opponent bib treatment and subject bib on the cumulative odds of the aggression displayed by subject at food. Analysis of the generalized linear mixed model was performed with the GLIMMIX procedure (SAS) with a multinomial distribution and cumlogit link. Subject id and trial (nested within subject id) were included as random effects in the model. Day is unfamiliar (day 1) or familiar (day 4) treatment. Observation time is time from return of food. Opponent bib is large bib control, small bib control or small bib enlarged treatment. Subject bib is medium bib or large bib. The block effect was removed from the analysis of aggression expressed by subject intruder to allow the model to converge.

Effects	Subject as holder			Subject as intruder		
	df	F	p	df	F	p
Day	1,105	0.81	0.37	1,94	0.29	0.59
Block	7,21	2.50	0.05			
Observation time	1,857	2.42	0.12	1,855	12.27	<0.001
Opponent bib	2,111	0.17	0.84	2,87	0.40	0.67
Subject bib	1,20	1.20	0.29	1,26	0.68	0.42
Day X Opponent bib	2,106	2.13	0.12	2,90	0.15	0.86
Day X Subject bib	1,104	0.00	0.95	1,95	0.00	0.95
Opponent bib X Subject bib	2,113	0.26	0.77	2,85	0.04	0.96
Day X Opponent bib X Subject bib	2,106	0.56	0.57	2,91	1.72	0.19

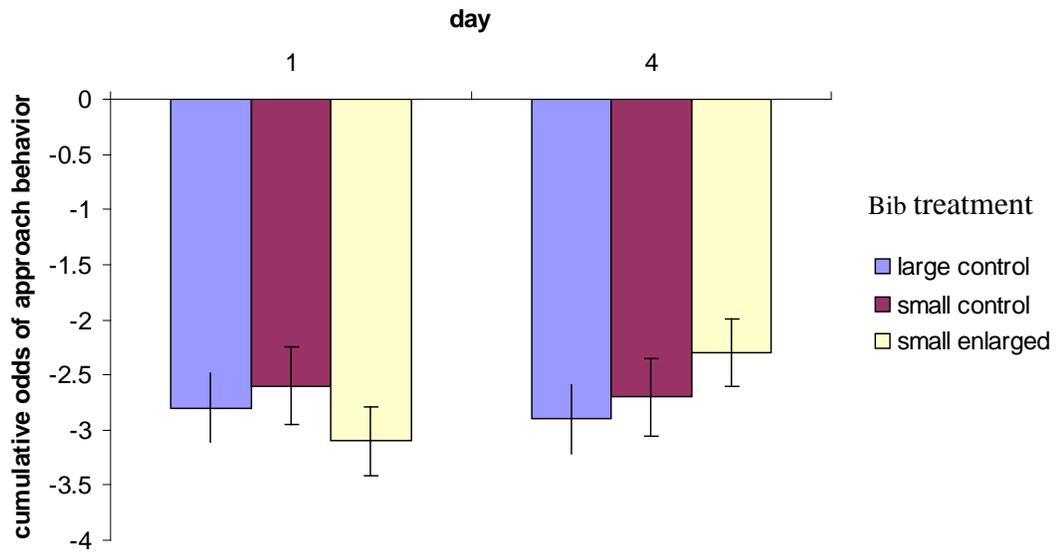


Figure 5.1 Effect of familiarity by opponent bib treatment interaction on aggression displayed by subject holders as opponent approaches food. Cumulative odds and standard error shown.

Chapter Six: The role of social experience in the development of a status signal

Introduction

Many species have evolved traits which facilitate communication with conspecifics. Status signals are morphological traits which evolved to convey information about the resource holding potential (RHP) of the bearer to the receiver (Rohwer 1975). This information is valuable to the receiver because it allows the receiver to more accurately predict the outcome of a contest with the opponent. The receiver of the signal can incorporate this information into their decision to engage or retreat. Theoretically, individuals should flee from potential opponents that signal a higher RHP than their own RHP and engage those that do not. By attending to the status of conspecifics, individuals can avoid potential injury and energetic costs from contests they are unlikely to win. Correlations between the magnitude of morphological traits that have no other obvious utility in contests have been observed in a number of species (Rohwer 1975, Balph et al. 1979, Solberg and Ringsby 1997, Liker and Barta 2001, Kraaijeveld et al. 2004) and manipulation of these morphological traits can alter the behavior of opponents (Fugle et al. 1984a, Rohwer 1985b, Fugle and Rothstein 1987a, Moller 1987 a, Senar and Camerino 1998a, Gonzalez et al. 2002b, Tibbetts and Dale 2004). These results suggest that the traits do function as status signals. Status signals have been most commonly studied and found in birds (Rohwer 1975, Moller 1987b, Senar and Camino 1998, Fugle et al 1984) though they have been observed in a variety of taxa (Fox et al. 1990b, Senar 1999, Tibbetts and Lindsay 2008).

For status signals to remain evolutionarily stable, they must remain honest otherwise they would fall into disuse. To ensure honesty, inaccurate signaling must result in costs that reduce the fitness of signalers. Most status signals consist of black (Rohwer 1975, Moller 1987b, Senar and Camerino 1998, Tibbetts and Lindsay 2008) or white patches (Fugle et al. 1984) that do not appear to directly contribute to the resource holding potential (RHP) of the bearer. Patches of white or black do not appear to have high production costs (Poston et al. 2005b, Stewart and Westneat 2010) but see (Veiga and Puerta 1996), suggesting that it is possible for all individuals to signal high status if it benefits them to do so. Other costs must ensure honesty. One type of cost that appears to

be important for signal honesty is use costs. These arise from an interaction between the response of the receiver to the information signaled and the RHP of the bearer.

Individuals that signal high RHP but have low RHP may incur costs that are avoided by signaling low RHP (e.g. chased by dominants). Use costs should favor the evolution of precise and accurate signals to minimize use costs that arise from errors between what the receiver perceives the signal to mean about the state of the signaler and the actual state of the signaler (Lachmann et al. 2001).

To understand how signals remain honest we must understand how status signals are matched to the bearer's status during the process of signal development. One possibility is that social experience influences the size of the signal. House sparrows (*Passer domesticus*) which happened to be housed in more aggressive groups grew larger bibs (McGraw et al. 2003b), suggesting that the aggression may have affected bib development. However, it is unknown if the birds in more aggressive groups developed larger bibs because experiencing aggression affected the development of the bib or if individuals who happened to be aggressive also happened to produce larger bibs.

To test if bib development is sensitive to social experience, I manipulated the dominance rank of the social partners of subject house sparrows. House sparrows are an ideal species to study the role of social experience on production of status signals. House sparrows are sexually dimorphic and males have a black patch (bib) on the breast. The size of the bib is correlated with dominance against both sexes of House sparrows (Moller 1987 b, Liker and Barta 2001, Hein et al. 2003, Nakagawa et al. 2007). The bib is molted in every year during the fall. Older birds tend to have larger bibs (Nakagawa et al. 2007) and bib size has low heritability (Griffith et al. 1999a). The size of the bib is determined by the number of feathers that are melanized during molt. The melanin granules are deposited by melanocytes into the feathers as the feathers are grown (Ralph 1969). The size of the bib does not appear to be affected by dietary restriction of the precursor, tyrosine and phenylalanine (Poston et al. 2005b) nor by restriction of calcium, a dietary mineral that is thought to be important for melanin production (Stewart and Westneat 2010). These studies suggest that production of the signaling component of the bib is probably not limited by dietary components. Aggression experienced has been shown to affect bib production (McGraw et al 2003) and the molt period coincides or

follows the period when the birds form winter flocks. Membership in flocks allows birds to interact with a large number of partners and it is possible that those interactions will affect the development of the bird.

There are many types of social experience which could affect signal development. For example, expressing aggression may have a different effect than receiving it. I tested for the different effects of expressing aggression and receiving aggression on status signal production. The most direct method of correlating status signals with status is for winning experience to positively affect status signal production, therefore I also tested for the effects of the frequency of winning on status signal production. Larger bodied individuals have larger body parts and therefore may have larger status signals; therefore I will also test for the role of body morphology on status signal production.

Methods

Male and female house sparrows were captured between late winter 2004 and early spring 2005 to form 13 mixed sex flocks, with 5-8 birds in each flock. Each flock was housed in an outdoor aviary (2.5m X 2.5m X 3.7m) and fed a mixture of white millet and southern state poultry feed ad libitum. The dominance hierarchy was determined for each flock by observing interactions at the feeder after birds were deprived overnight or during the day. Multiple observations were made for each flock from start of 2005 until summer 2005 to determine dominance hierarchy. Dominance was determined for each bird within a flock by calculating proportion of flock mates dominated (win more than 50% of interactions). Birds occupying ranks at the extremes in the dominance hierarchy were used as opponents in the dominant and subordinate treatments. Individuals from the middle of the hierarchy were used as opponents in the random treatment.

To obtain subjects with known social history, 45 nestlings were sexed using PCR of the CHD genes (Griffiths et al. 1996) at 4-5 days old. Males were removed from their nest at 6-8 days old from 6/3/05-8/13/05. Nestlings were handfed rehydrated cat food every 15 minutes from 8 am - 5 pm until they were able to feed themselves. Nestlings were housed in plastic cups lined with paper towel at an indoor facility. Subjects remained indoors until 12-15 days old, at which point they were moved to outdoor cages. Each outdoor cage contained only one subject and was either a wall mounted cage

(25cm X 25cm X 40cm) or a freestanding cage (16cm X 23.5cm X 14cm). The subjects had audio but not visual or tactile contact. The birds remained on the cat food diet until they started to consume millet.

At the start of the experiment subjects were randomly assigned to a social rank treatment (random, subordinate and dominant). 14 subjects had been killed by avian pox prior to this point, so I assigned 11 nestlings in the dominant treatment, 12 in the subordinate treatment and 8 in the random treatment. Subjects assigned to the subordinate treatment were housed with opponents that had been subordinate in their flock. Subjects assigned to the dominant treatment were housed with opponents that had been dominant in their flock. Subjects assigned to the random treatment were housed with opponents that were randomly chosen from the mid level ranks. Subjects (38-64 days old) were placed with their first opponent between July 30/2005-Sept 25/2005. After 28-47 days, the first opponent was removed and another opponent of the same treatment category was placed into the cage. Opponents were changed to create an environment that more closely mimic the situation in the wild, where an individual meets multiple opponents.

Birds were deprived the morning of videotaping (8-9am). After food was returned in the afternoon (3-5pm), interactions at the feeder were videotaped for 15 minutes. If possible, dyads were videotaped over multiple days to ensure an adequate number of interactions were captured. In November 2005 the experiment was ended and subjects were measured, weighed and released. Bib measurements were taken with the subject held upright and bill placed at 90° angle to the body. Bib size was calculated using the formulae $(167+0.45*\text{length}*\text{width})$ (Moller 1987 b). The length of the left tarsus was also measured.

Each subject was housed sequentially with two opponents of the same social rank. To determine if the aggression expressed to and received from each opponent should be averaged together, I tested for correlations between behaviors seen during trials with opponent 1 and with opponent 2. There was no significant correlation between the rate of aggression expressed by subjects when housed with opponent 1 and when housed with opponent 2 (Spearman rank correlation, $N=30$, $r=-0.07$, $P=0.72$). I also found no correlation between the rate of aggression received from opponent 1 and from opponent 2 (Spearman rank correlation, $N=30$, $r=-0.02$, $P=0.92$). Additionally, I also tested for a

correlation in proportion of interactions dominated when competing against opponent 1 and when competing against opponent 2 and found no evidence of one (arcsine transformed, Pearson correlation, $N=30$, $r=0.28$, $P=0.13$). Therefore I included the effects from opponent 1 and from opponent 2 as separate independent variables in the model.

Aggression expressed by subjects and aggression received from opponents was measured as number of fights/min. I also calculated the ratio of aggression expressed to aggression received by subjects. Win rate and lose rate was also calculated as win/min and lose/min for the subject. The winner is defined the individual who retained access to the resource after the interaction. Only outcomes with clear winners were included. I also calculated the ratio of win rate to lose rate for the subject to examine the effect of dominance on bib development.

Results

To determine if the treatment was effective in manipulating social experience, I tested for the effect of treatment on proportion of interactions won by the partner and found no effect (arcsine transformed, ANOVA, $N=30$, $df=2$, $F=1.22$, $P=0.31$).

I tested for the effect of treatment on the aggression displayed by partners (aggression received) and found no effect of treatment (Nonparametric ANOVA, $N=30$, $df=2$, $X^2=2.27$, $P=0.32$). Therefore social rank treatment was not included in the models and instead aggression experienced and dominance was used to examine the effect of social experience on bib development.

The subjects gained an average of 6.62g and had a mean weight of 26.28g by the end of the study. There was no difference in the tarsus length of subjects and opponents by the end of the study ($df=31.57$, $t=-1.57$, $P=0.13$). Measures of body morphology at end of study and capture date had no effect on bib size produced (table 6.1).

There was no evidence that aggression expressed by subjects or received by subjects when with partner 1 or partner 2 affected the size of the bib produced (table 6.2). Unexpectedly, there was a trend for aggression expressed to partner 1 to be negatively associated with bib size produced. There was also no effect of the ratio of aggression expressed to aggression received when with partner 1 or partner 2 on the size of the bib produced (table 6.2). Rate of aggression expressed did not differ when with partner 1 and

partner 2 (log transformed, paired t-test: $t=-0.94$, $df=29$, $P=0.36$) and aggression received rate also did not differ when with partner 1 and partner 2 (log transformed, paired t-test: $t=-1.12$, $df=29$, $P=0.27$).

Dominance did have some effect on bib development. The rate of losing interactions had no effect on bib size, however the rate of winning and the ratio of win rate to lose rate had opposite effects on size of bib developed (table 6.3). Win rate against partner 1 was negatively associated with bib size but win rate against partner 2 had no effect on bib size. Though the effect of win rate on bib size was only observed for partner 1, there was no difference in win rate when with partner 1 and when with partner 2 (log transformed, paired t-test: $t=-0.62$, $df=29$, $P=0.54$). There was also no difference in lose rate when with partner 1 and when with partner 2 (log transformed, paired t-test: $t=-1.59$, $df=29$, $P=0.12$). The rate of expressed aggression was predictive of win rate but aggression received was not (table 6.4). Body morphology had no affect on win rate against partner 1 (table 6.5) but did have an effect with partner 2 (table 6.6). Heavier birds won frequently than lighter birds and there was a nonsignificant tendency for shorter birds to win more frequently against partner 2.

The ratio of win rate to lose rate was positively associated with bib size when with partner 2 but not partner 2 (table 6.3) but there was no difference between ratio of win rate to lose rate against partner 1 and against partner 2 (log transformed, paired t-test: $t=-1.59$, $df=29$, $P=0.12$). The ratio of win rate to lose rate was affected by body morphology in when with both partner 1 (table 6.7) and partner 2 (table 6.8). With both partners, shorter and heavier birds had higher ratios of win rate to lose rate and there is a trend for younger birds to have higher ratio of win rate to lose rate.

Discussion

I found little evidence that social experience influenced bib development. Aggression expressed and received was not predictive of bib size. Measures of winning experience did seem to have an effect on bib development but the different measures produced conflicting conclusions. Additionally, there were some issues that made it difficult to conclude if social experience had an effect on bib development. The social

status treatment was not effective; therefore I am unable to determine if any effects on bib development were causal or merely correlated.

I found no correlation between body morphology and bib size but this was not surprising as (Nakagawa et al. 2007) only found a weak association between body condition and bib size in their meta-analysis. This suggests that the development of the signaling aspect of the bib was probably not directly affected by nutrient intake. However body morphology did seem to affect bib size indirectly by affecting measures of dominance, with shorter and heavier birds being more dominant. Therefore social experiences, such as expressing aggression or having frequent winning experience, likely played a role in correlating dominance with bib size.

There was no evidence that aggression experienced had an effect on the development of the bib in House sparrows. These results are in contrast to those found in (McGraw et al. 2003b) study which found a positive relationship between aggression experienced and size of bib molted. House sparrows in more aggressive groups grew larger bibs in captivity than those from less aggressive groups and aggressive interaction rate during molt was predictive of bib size post molt. (McGraw et al. 2003b) did not consider the effects of expressing aggression separately from the effects of receiving aggression making their results difficult to interpret in terms of the evolution of status signals. Theoretically, subordinates would receive more aggression and dominants would express more aggression, but it is unclear if a higher aggressive interaction rate, would be associated with subordinate or dominant status. Expressing aggression and receiving aggression should be associated with different hormone profiles and therefore may have different and possibly opposing effects on bib development. Expressing aggression is related to higher ratio of testosterone to corticosterone (T:CORT) (reviewed in Montoya et al. 2012) whereas receiving aggression is related to higher levels of the stress hormones corticosterone (Sapolsky 1992a). It is not clear how experiencing a high aggressive interaction rate would affect the hormone profile and in turn affect bib development.

In the present study, the ratio of the rate of aggression expressed to the rate of aggression received was not important in predicting bib size. I expected that higher ratios would reflect higher dominance and therefore be associated with larger bibs. The lack of

effect of the ratio of aggression expressed rate to aggression received rate, combined with the lack of effect of aggression rates suggests that hormones that are associated with aggression are not important in regulating melanin production. This is puzzling as the literature suggests that hormones associated with aggression and stress are also associated with melanin production. (Gonzalez et al. 2001) and (Evans et al. 2000) found that male house sparrows with high androgen levels molted in larger bibs and (Roulin et al. 2008) found that corticosterone implants reduced the amount of melanin produced in barn owls. It is possible that aggression experienced had no effect because the magnitude experienced by captive birds was lower than that experienced by birds in the free living population and was insufficient to affect bib size. The captive birds in this study had access to food ad libitum from 2 separate feeders, and therefore may not have had enough interactions outside of the video period to affect bib development. Likely, the interaction rate measured after the deprivation was higher than what the birds normally experience in the cage. Additionally, the variance in aggression rates observed on the videos was likely higher than when the birds were not on the video because when the birds were off video, the birds did not have to compete for access to food and therefore had less incentive to fight. Unfortunately, I do not have measures of aggression rate when birds were not deprived.

The lose rates have no effect on bib development but win rate and ratio of win rate to lose rate does, suggesting it is likely that winning experience affects the hormones that affect bib production. Hormones that may be involved in translating winning experience into bib development include testosterone (reviewed in Simon 2002b, Oyegbile and Marler 2005) and corticosterone (Gust et al. 1993a, Oyegbile and Marler 2006). Individuals with higher ratios of win rate to lose rate are more dominant than those with low ratios of win rate to lose rate and therefore the positive association of ratio of win rate to lose rate with bib development is in the correct direction for dominance to affect bib development. The effect of ratio of win rate to lose rate was only observed in partner 2 but not partner 1, suggesting that there is a critical time window in which social experience can affect bib development instead of it being a gradual cumulative effect.

The direction of the effect of win rate is opposite of that predicted if the frequency of winning is an indicator of dominance and bib size is positively correlated with

dominance. This unexpected relationship may have resulted from exposure to avian pox early on in the study. All birds in the study could have potentially been exposed. It is possible that mounting an immune response to avian pox affected the relationship between win rate and bib size as the effect was only significant in partner 1, when exposure to the avian pox was more recent. It is not clear which hormones would be affected by mounting an immune response, though both testosterone and corticosterone have been shown to be linked to immunocompetence (Evans et al. 2000, Buchanan et al. 2003a). However, this explanation seems unlikely as (McGraw and Hill 2000a) found no effect of endoparasite load on development of a melanin based ornament.

The effects of dominance in this study are somewhat different from that of (McGraw et al. 2003a) study, in which medium rank male house sparrows grew larger bibs than the least dominant males but there was no difference in bib size between the most dominant males and least dominant males. In that study it is not clear if dominance rank was associated with bib size in a linear relationship. In this study, win rate and ratio of win rate to lose rate have opposing effects on bib size, therefore it is difficult to conclude from this study if our measures of dominance do translate to an appropriate bib size.

This study has revealed that social experience does have an effect on bib development, but it is still unclear why one indicator of dominance would have the opposite effect on bib size as another indicator of dominance. These conflicting results suggest that the mechanisms that allow social experience to affect bib production are complicated. Likely, the final bib size depends on a mix of hormones that respond to multiple indicators of dominance and act antagonistically to affect bib production. The fine tuning of this mix of hormones occurs with every opponent the subject interacts with and ultimately allows birds to produce signals that reflect their average dominance rank. It is possible that the greater the number of interactions, the more accurately the signal reflects the dominance rank. The social environment in the late summer, in the premolt period, does seem to provide abundant opportunities for social interactions as birds switch from the breeding activities to flocking activities. During that time, birds are likely meeting many unfamiliar opponents, and juveniles are likely fighting more frequently than adults, as they lack a status signal. It is likely that in the late summer juveniles

experience very high win and lose rates and it is the interactions which determine the size of the bib.

Table 6.1 Effects of body morphology and date of capture on size of bib produced in house sparrows. Analysis performed with proc GLM (SAS). Date of capture is mean centered. N=28.

Effect	Coefficient	S.E.	t	p
Intercept	438.01	125.50	3.49	0.01
Date of capture	0.13	0.37	0.37	0.72
Tarsus length	-7.88	7.39	-1.07	0.30
Weight	2.87	3.08	0.93	0.36

Table 6.2 Effects of aggression experienced on size of bib produced in house sparrows. Analysis performed with proc GLM (SAS). Aggression rates are fights/min N=30.

Effect	Coefficient	S.E.	t	p
Intercept	354.85	17.32	20.48	<0.0001
Partner 1 aggression expressed rate	-48.11	27.64	-1.74	0.10
Partner 2 aggression expressed rate	-1.93	29.04	-0.07	0.95
Partner 1 aggression received rate	41.60	36.93	1.13	0.27
Partner 2 aggression received rate	-8.26	37.38	-0.22	0.83
Partner 1 ratio aggression expressed rate to aggression received rate	3.82	8.18	0.47	0.64
Partner 2 ratio aggression expressed rate to aggression received rate	12.83	10.42	1.23	0.23

Table 6.3 Effects of dominance on size of bib produced in house sparrows. Analysis performed with proc GLM (SAS). Win rates are win/min and lose rates are lose/min. N=30.

Effect	Coefficient	S.E.	t	p
Intercept	369.39	9.87	37.43	<0.0001
Partner 1 win rate	-18.45	7.38	-2.50	0.02
Partner 2 win rate	2.31	7.58	0.30	0.76
Partner 1 lose rate	6.64	9.36	0.71	0.49
Partner 2 lose rate	6.90	41.02	0.17	0.87
Partner 1 ratio win rate to lose rate	-0.16	0.15	-1.08	0.29
Partner 2 ratio win rate to lose rate	0.09	0.03	3.28	<0.001

Table 6.4 Effects of aggression on log transformed win rate. Analysis performed with proc GLM (SAS). Aggression rates are fights/min and win rates are win/min N=60.

Effect	Coefficient	S.E.	t	p
Intercept	0.28	0.05	5.56	<0.0001
aggression expressed rate	0.55	0.11	4.78	<0.0001
aggression received rate	-0.22	0.15	-1.51	0.14

Table 6.5 Effects of body morphology and date of capture on win rate when with first partner. Analysis performed with proc GLM (SAS). Date of capture is mean centered. N=28.

Effect	Coefficient	S.E.	t	p
Intercept	0.83	1.39	0.60	0.55
Date of capture	0.01	0.01	1.32	0.20
Tarsus length	-0.02	0.08	-0.30	0.77
Weight	0.01	0.03	0.11	0.91

Table 6.6 Effects of body morphology and date of capture on win rate when with second partner. Analysis performed with proc GLM (SAS). Date of capture is mean centered. N=28.

Effect	Coefficient	S.E.	t	p
Intercept	1.08	1.36	0.79	0.44
Date of capture	-0.01	0.01	-0.98	0.33
Tarsus length	-0.13	0.08	-1.62	0.11
Weight	0.07	0.03	2.14	0.04

Table 6.7 Effects of body morphology and date of capture on ratio of win rate to lose rate when with first partner. Analysis performed with proc GLM (SAS). Date of capture is mean centered, tarsus length is mm and weight is g. N=28.

Effect	Coefficient	S.E.	t	p
Intercept	9.36	4.52	2.07	0.05
Date of capture	-0.03	0.01	-1.90	0.07
Tarsus length	-0.68	0.27	-2.55	0.02
Weight	0.23	0.11	2.07	0.05

Table 6.8 Effects of body morphology and date of capture on ratio of win rate to lose rate when with second partner. Analysis performed with proc GLM (SAS). Date of capture is mean centered, tarsus length is mm and weight is g. N=28.

Effect	Coefficient	S.E.	t	p
Intercept	10.32	5.78	1.79	0.09
Date of capture	0.01	0.02	0.21	0.84
Tarsus length	-0.94	0.34	-2.76	0.01
Weight	0.40	0.14	2.80	0.01

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