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Minimizing the cost of competition in the black-crested titmouse: status signaling, dominance, and foraging behavior

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MINIMIZING THE COST OF COMPETITION IN THE BLACK-CRESTED TITMOUSE:
STATUS SIGNALING, DOMINANCE, AND FORAGING BEHAVIOR
PHILIP STRASSMANN QUELLER

A DEPARTMENT HONORS THESIS SUBMITTED TO THE
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Minimizing the cost of competition in the black-crested titmouse:
status signaling, dominance, and foraging behavior

by
Philip Strassmann Queller

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Table of contents

Acknowledgments.....	4
Table of contents.....	5
Abstract.....	6
Chapter 1: A Review of Status Signaling in Birds	7
Correlational evidence of status signaling	8
Experimental evidence of status signals	9
Sexual or social selection?.....	11
Modeling of the evolutionary stability status signaling systems	13
Empirical evidence of signal honesty	16
Handicap enforcement of honesty	16
Socially-enforced costs	19
Dietary production costs	20
Future work.....	21
Dynamic signaling in dynamic social environments	21
Multiple status signals.....	22
Conclusions.....	23
Chapter 2: Minimizing the cost of competition in the black-crested titmouse: status signaling, foraging behavior, and resource availability.....	25
Introduction.....	25
Methods:	28
Study species.....	28
General.....	28
Recording foraging data with radio-frequency identification (RFID).....	30
Does crest size related to access to resources during the post-breeding season?	31
Does both crest size and dominance relate to access to limited resources during the pre-breeding season?	31
Statistics	33
Results.....	33
Does crest size related to access to resources during the post-breeding season?	33
Does both crest size and dominance relate to access to limited resources during the pre-breeding season?	34
Discussion:.....	36
Chapter 1 References	48
Chapter 2 References	52

Abstract

Status signals allow senders and receivers to minimize the costs of competition by minimizing the need for costly physical fights. While much research has focused on demonstrating that individuals respond to status signals in both breeding and non-breeding contexts, less is known about how the function of status signals may change as resource availability changes seasonally. In this thesis, I provide a basic review of status signaling in birds and report the results of an investigation on status signaling in the black-crested titmouse during different environmental conditions. The black-crested titmouse is a socially monogamous passerine that defends territories throughout the year. This species forms small family groups during the breeding and post-breeding season, which dissolve into mated pairs during the non-breeding and pre-breeding seasons. Using an array of supplemental seed-feeders outfitted with RFID technology, I investigated the relationship between the crest size of adult male titmice and their foraging behavior during the post- and pre-breeding seasons. I also investigated the effect of both crest size and dominance on an individual's ability to maintain baseline foraging behavior after approximately half of the feeders were removed. I found that birds with larger crests had greater access and monopolization of feeders during the post-breeding season, but not the pre-breeding season. When the number of available feeders were reduced during the pre-breeding season, males that monopolized their most-used feeder the most during baseline, and males that had longer crests, reduced their access to the feeders relatively less than other birds. Taken together, these findings indicate that the crest is used to signal status, particularly during times of increased competition (i.e. due to seasonal fluctuation in resources or increased competition between family groups).

Chapter 1: A Review of Status Signaling in Birds

The acquisition and defense of limited resources is a vital aspect of survival and reproduction for animals. Competition is costly in terms of time, energy, and risk of injury, and many animals have evolved signals that preemptively display their ability to invest in a fight (Rowher 1975). The ability to predict the fighting ability or aggression of a competitor reduces the likelihood of an aggressive encounter escalating to physical contact and can therefore minimize the cost of competition. Less attention has been paid to ornamental signals that function to mediate competitive interactions (i.e., status signals) compared to those signals that function to attract mates; however there is great interest in understanding the evolutionary processes that select for signal used to convey fighting status. Status signals are unique because they require both the sender and receiver to assess one another simultaneously while both individuals also signal their strength. This dynamic interaction between signaler and receiver requires that, on average, both parties honestly convey an accurate assessment of their fighting abilities, otherwise the interactions would not be evolutionarily beneficial to both parties (i.e., would be selected against). Decades of research has shown that status signals mediate conflict over breeding and non-breeding resources, and both theoretical modeling and empirical evidence demonstrate that status signaling systems are generally honest and can be evolutionarily stable.

Status signaling is intriguing because cooperative signaling between competitors invites deception, yet deception appears to occur at low frequency in most communication systems. Given that there can be a high high benefit to a subordinate by simply cheating a signal, one might expect a dishonest strategy to evolve. If such a cheating mutant invaded an honestly signaling population, the stability of the signaling system would be reduced. Loss of stability

would occur when receivers cease to benefit from assessing status signals and are selected to disregard them, and this loss of response is expected in populations where cheaters become prevalent (Maynard Smith & Harper 2003, Hurd 1997). But the observation that these status signaling systems persist over time demonstrates that both senders and receivers do benefit from these signals.

In this review, I will show that receivers respond to status signals in ways that suggest that they accurately represent fighting ability, and I will show how these signals are used in both breeding and non-breeding contexts. I will provide evidence for the honesty of status signals from theoretical models and empirical evidence that tests predictions of these models. I will demonstrate that status signals are reliable indicators of competitiveness and that signal reliability is enforced by production costs such as T-induced immunosuppression and socially enforced costs and risk of injury, such that only individuals in top condition can express the most dominant signals.

Correlational evidence of status signaling

Correlative studies provide important support for status signaling systems. These studies show a link between ornamentation and fighting ability, which supports the hypothesis that ornamentation is actively used to assess competitive differences. Such correlative evidence provides important preliminary evidence for status signaling by showing that receivers can benefit by responding to differences in ornamentation and by indicating which morphological traits likely encode the signal. For example, black-capped chickadees vary in the degree of achromatic black and white head coloration, both between the sexes and within males. Males with darker achromatic plumage on their heads are of higher rank than those with lighter

plumage, and have faster feather growth rates (Mennill et al. 2003). Another correlative example comes from male house sparrows, which possess dark melanin coloration on the bill and throat, breast that varies between individuals. In captive flocks of males, individuals with larger throat and breast melanin patches (Gonzalez 2002, Evans 2001), and darker bills (Laucht et al. 2010) dominate those with smaller patches.

There is also correlative evidence that males use status signals during territorial competition. Male scarlet-tufted malachite sunbirds display red pectoral plumage tufts during competition over territories—whose quality is predominately determined by the number of nectar providing inflorescences that can be defended by a male. Males with naturally wider tufts defend an area with more inflorescences and produced more fledglings than males with narrower tufts (Evans & Hatchwell 1992).

Experimental evidence of status signals

There is compelling experimental evidence that birds use status signals to assess the fighting ability of competitors. Experimental evidence is an essential compliment to correlational studies, which cannot demonstrate that specific morphological traits are directly being assessed during competition. For example, one might argue that birds might settle contests physically, without signaling, despite a correlation between coloration and dominance. Research has therefore focused on experimental manipulation of plumage and bare-part coloration and its effect on social status.

Experimental manipulation of ornaments has demonstrated that status signals directly mediate competition for food resources in a variety of contexts. Plumage manipulations in a variety of avian taxa has experimentally demonstrated that status signals are used to settle

contests over food resources (Evans and Hatchwell 1992, Lemel and Wallin 1993, Laucht et al. 2010, Pryke and Andersson 2003, Jones and Hunter 1999). For example, when the melanin throat and breast patch of adult male house sparrows are manipulated, birds with experimentally enlarged patches become dominant over control birds independently of the signaler's size (Gonzalez et al. 2001), indicating that adult males use this melanin plumage to obtain information on fighting ability that cannot be obtained by observing differences in size. In adult female American goldfinch, females with more carotenoid-based coloration in their bills are dominant over less-colored females during the breeding season, which indicates that females, and not just males, signal dominance to one other as well. As another example, among first-year male blue tits, experimental reduction of the ultraviolet (UV) crown coloration caused these birds to lose dyadic contests against un-manipulated controls (Vedder et al. 2010). This finding demonstrates that status signals can function within a specific age class (here, first-year males), which indicates that status signals can contain information on fighting ability that is not age-related.

Manipulation of plumage ornaments has also shown that status signals are used during territorial competition. In red-shouldered widowbirds, birds that had experimentally enlarged and brightened shoulder epaulets were more likely to obtain a breeding territory than those that had their epaulets reduced or blackened, which indicates that epaulet size signals an individual's ability to acquire a territory. Within males that did obtain territories, those that had larger manipulations also had larger territories and spent more time defending boundaries, which indicates that the epaulets also signal an individual's ability to maintain and expand territory boundaries (Pryke and Andersson 2003). The authors also showed that territory owners respond most aggressively towards intruders with large epaulets, indicating that the territory owner

perceives intruders with large epaulets as more threatening to their territorial tenure.(Pryke and Andersson 2003). Similar findings have been reported in the scarlet-tufted malachite sunbird, where a male's territory quality is largely dependent on the number of nectar-rich flowers, which they do vigorously defend, often while displaying their red pectoral plumage tufts. When these tufts are experimentally enlarged or reduced, males with larger tufts were able to defend more flowers than males whose crests were reduced, which indicates that status signals are used not only in defense of territory boundaries, but also in defense of specific breeding resources. The difference in the number of flowers defended as a result of the manipulation had a direct affect on reproductive success: males with enlarged tufts that defended more flowers had higher reproductive success than males with reduced tufts that defended fewer flowers. These findings demonstrate that status signals are used to signal dominance during defense of both territorial boundaries and key breeding resources within a territory.

Sexual or social selection?

Experimental evidence shows that status signals can mediate the cost of competition over both non mate-based and mate based resources, and as such, are selected for by both social (West-Eberhard 1983, Lyon and Montgomerie 2012) and sexual (Darwin 1871, Andersson 1994) selection. Social selection is a broad category of selection that is defined by selection that acts on traits or behaviors that mediate social interactions. Sexual selection is a more narrow type of selection that is defined by selection that acts on traits or behaviors that mediate sexual interactions, and therefore directly affect reproductive success. Therefore, status signals that mediate conflict over non mate-based resources are socially selected, whereas status signals that mediate conflict over mate-based resources are sexually selected. Because sexual behavior is a

type of social behavior, sexual selection is considered a form of social selection (Lyon and Montgomerie 2012).

Status signals can arise through both social and sexual selection, and the behaviors associated with status signals are strongly determined by ecological context. Competition over non mate-based and mate-based resources often occurs in different ecological contexts that demand different types of social behavior. For example, during the winter, birds often join flocks that help individuals to maximize their foraging success and predator awareness. As such, maintaining flock stability is important to all individuals, but each individual might further maximize its fitness by acquiring more food than its flockmates. Therefore, the role of status signals in wintering flocks is often to display an individual's place in a social hierarchy, which allows contests over food (i.e. non mate-based resource) to be settled without completely repelling the loser from the flock. This method of settling contests with minimal conflict highlights the trade-off between the benefits of flocking and the costs of sharing resources with flock-mates. Because this trade-off does not directly influence reproduction this method of conflict resolution is socially selected. Indeed, a recent comparative analysis suggests that melanin throat and breast status-signaling plumage co-evolved with winter sociality (Tibbetts and Safran 2010), which suggests that mediating conflict during competition within social flocks has important fitness effects.

Competition over mate-based resources, on the other hand, is intense and unhindered by a social tradeoff: individuals generally maximize their fitness by completely warding off all potential competitors from a breeding territory. As such, these contests can be prolonged and potentially dangerous. Status signals that mediate conflict over mates or mate-based resources (i.e., territories that a mate will seek) therefore signal information about an individual's resource

holding potential, not their place in a social hierarchy, and are sexually selected (Laubach and Blumstein 2013). However, because food is used as a resource during the breeding and non-breeding season, it can be difficult to say exactly when selection that occurs during competition for food changes from social selection to sexual selection. It is also difficult to separate sexual and social selection for species that defend territories year round, like the black-crested titmouse, because an individual's ability to defend a feeding territory during the non-breeding season (social selection) likely affects their ability to maintain that same territory during the breeding season (sexual selection). Despite these difficulties, it is important to understand how selection works differently in different social contexts.

Modeling of the evolutionary stability status signaling systems

The stability of any communication system is dependent on honesty, and when the benefits of deception are high, as they are in competitive signaling contexts, it is crucial to show that the system is honest to be evolutionarily stable. Modeling of status signaling systems provides important ideas as to how signal honesty can be maintained. Most of these models propose that in order for selection for a signaling system to persist, signals must be costly and thus prevent deception. These models make two assumptions: 1) individuals that honestly signal their status and thus minimize the amount of time and energy spent fighting would have higher fitness than they would in a non-signaling system, and 2) all else being equal, every individual could further maximize its fitness by signaling high competitiveness despite their actual fighting ability. Despite the benefit associated with cheating (reducing the costs of competition), if many individuals adopt the cheating strategy, the signaling system would be selected against because there would no longer be a benefit for receivers to respond to these dishonest signals.

A number of theoretical models have attempted to answer resolve how status signaling systems persist despite the possible benefit of cheating. One such model by Zahavi (1975) hypothesized that signaling systems are honest because signals handicap their bearers, and importantly, that bearing a signal of a certain signal strength is differentially costly to individuals in different condition, such that high-quality individuals suffer lower costs. Signals can handicap their bearers in a number of ways. They can impair mobility, and thus decrease an individual's ability to escape from predators, as is the case with the extravagant tail of the long-tailed widowbird (Andersson 1982; note that this is not a signal of status, but provides a compelling example of this type of honesty-enforcing mechanism). By maintaining long tails, males display their ability to effectively buffer the cost of the handicap (i.e. pay reduced costs) compared to the costs that would be imposed on an individual of poorer condition. The 'handicap principle' has been supported with mathematical modeling (Grafen 1990) and is now widely accepted to enforce honesty in a variety of signal types.

While the honesty of status signals can be maintained if they differentially confer handicap costs to individuals of different quality, many status signals do not appear to be fall under the purview of a handicap signal (i.e., the signals are expressed with minimal costs), and so different models address how honesty is maintained when status signals are cheap to produce. Maynard Smith and Harper (1998) modeled honesty in this context, using the idea that honesty is not enforced by difference in individual quality, and the authors termed this honesty enforcing mechanism 'conventional signaling'. To assess the honesty of such a signaling system, the authors modeled the fitness of a 'cheating' mutant who signals a level of aggressiveness (or fighting ability) that is higher than what it can actually invest. A finding of this model is that the costs to an individual in poor condition (i.e. a subordinate bird) of fighting a dominant bird are

greater than those costs to fighting a subordinate bird (because dominant birds will invest more in fighting). As such, signal honesty can be maintained by the differential costs of fighting birds of different fighting ability. Under these conditions, the cost to a subordinate of constantly fighting dominant birds would outweigh the benefits of increased access to resources.

One hypothesis, termed “social control” hypothesis (Rohwer 1977) predicts that the cost of fighting an individual of greater strength is more costly than the cost of fighting an individual of equal strength. Thus, the cost of fighting a dominant individual is predicted to be greater for a subordinate than for another dominant. The prediction that cheaters face extra aggression from dominants is dependent on the assumption of “like versus like” aggression, in which individuals of similar badge size fight more often than individuals of different badge sizes. This is a fair assumption, although not always true (Slotow et al. 1993b, Senar 2006), because if status signals reduce the need for fights between individuals of different fighting abilities, it follows that when signal strengths are equal, minute differences in fighting ability can only be determined with physical aggression. In such cases, if the cost of the increased aggression from dominant individuals a cheating subordinate faces outweighs the benefits of dominance, cheating would be prevented because an honest signaling strategy would yield greater net benefits.

Rohwer (1977) proposed another hypothesis based on costly behavioral responses faced by cheating individuals. He hypothesized that, because individuals should be attentive to both signaling and behavior during competitive interactions, incongruence between these two modes of communication would make the receiver skeptical of the most impressive signal such that it would likely socially probe the sender in order to ascertain its true dominance status. If individuals whose behavior is incongruent with their signal suffer more costs from increased social probing than they do from displaying a large badge, an honest signaling strategy would

yield higher fitness. Indeed, there is evidence that deception in dominance rank in Harris' sparrows requires both testosterone-induced behavioral changes coupled with enlargement of the badge of status; either manipulation done in the absence of the other fails to cause a change in dominance rank, and results in increased social costs for the cheater (Rohwer 1978). Some authors have suggested that social control of status signaling is more likely to account for signal honesty in species that exhibit like vs. like aggression, like the Harris' sparrow, than in species that do not, such as the white-crowned sparrow (Searcy and Nowicki 2005). For species that do not exhibit like vs. like aggression, other costs are thought to maintain signal honesty.

Empirical evidence of signal honesty

There is much empirical evidence that demonstrates that many status signals are indeed costly. Researchers have found that the honesty of status signals are maintained by social or physiological costs that trade-off signal quality with other factors (e.g. immune stress) that affect fitness, such that only individuals in good condition can achieve maximal signal expression. Status signals whose honesty is maintained by physiological costs are handicap signals, whereas status signals whose honesty is maintained by social costs are conventional signals. There is also evidence that dietary limitations mediate signal honesty as well.

Handicap enforcement of honesty

Physiological costs associated with T levels have the potential to mediate signal honesty. T has been shown to correlate with the expression of several status signals, such as the melanin big of the house sparrow (Alonso-Alvarez 2007) and I have shown a similar relationship in the carotenoid-based bill coloration of female American goldfinch (Pham et al. 2013). Several

studies on house sparrows have shown that naturally varying testosterone levels during the molt correlate with post-molt badge sizes (Evans et al. 2000, Gonzalez et al. 2001). Furthermore, experimental studies confirm this correlation: males treated with testosterone implants during the molt developed larger signals than control males (Evans et al. 2000, Buchanan 2001)

To show that testosterone does indeed mediate signal honesty, the hormone should not only influence signal production, but should also confer costs such that only individuals in top condition can display an intense signal. Two hypotheses predict that testosterone related costs might mediate signal honesty. The “immunocompetence handicap hypothesis” (ICHH) posits that the immunosuppressive affect of testosterone maintains signal honesty in testosterone-dependent signals (Folstad and Karter 1992), while the “oxidative stress hypothesis” predicts that testosterone-dependent signals are honest because they are tied to increased oxidative stress (Alonso-Alvarez et al. 2007).

I: T-induced immunological costs

In support of the ICHH, Poiani (2000) found that male house sparrows treated with testosterone had significantly higher ectoparasite loads than controls, which suggests that testosterone may affect their ability to repel these parasites. Experimentally increasing circulating testosterone in house sparrows has also been shown to suppress antibody production (Evans et al. 2000, Buchanan et al. 2003a), but had no effect on cell-mediated responses (Buchanan et al. 2003a). However, these researchers had to use high levels of testosterone that are only present during the breeding season to achieve these results. Because testosterone levels are much lower during the non-breeding season (Hegner and Wingfield 1986) when badges are developed (molted) (Evans et al. 2000, Gonzalez et al 2001), studies must show that these low,

non-breeding testosterone levels are costly enough to maintain signal honesty. Alternatively, studies could support the ICHH if they could demonstrate that testosterone levels were tightly correlated between the seasons such that individuals with relatively high non-breeding T levels have proportionally high T levels during the breeding season. If this were the case, the immunosuppressive costs of badge development could still maintain signal honesty even if they are not felt at the same time as badge production. Also, testosterone has been shown to mediate badge size after the molt is complete. Gonzalez et al. (2001) report that testosterone is positively related to the rate of abrasion of the white tips of badge feathers that erode away during the breeding season to reveal the full badge. More evidence is needed to understand how testosterone might enforce signal honesty, particularly on how and when the costs of badge development are conferred.

II: T-induced oxidative stress

There is also evidence that T-dependent ornaments are made honest by T-induced oxidative stress. The bill of the zebra finch, which signals status (Ardia et al. 2010), varies from orange to red, and is regulated by T (McGraw et al. 2006). Alonso-Alvarez et al. (2007) hypothesized that male zebra finch exposed to high T levels will suffer from increased oxidative damage to red blood cells than birds with lower T levels. They manipulated T levels in three groups of zebra finch to see how resistance to oxidative damage to red blood cells varies with T treatment. One group received subcutaneous T implants; another received subcutaneous implants filled with flutamide, an androgen receptor antagonist; and the last group received empty implants. Birds that were given flutamide (and so had less testosterone activity) had the highest resistance to oxidative damage to red blood cells, while the control group had moderate

resistance, and the T-implanted group had the weakest resistance to oxidative stress. This same pattern was also observed when looking at how the treatment groups varied in their ability to mount a T-cell mediated immune response.

Socially-enforced costs

There is mixed support from empirical data that status signals are honest due to socially enforced costs. For example, Rohwer and Ewald (1981) found correlational evidence for the social control hypothesis. Free-living, small-badged Harris's sparrows were more likely to behave aggressively towards individuals of similar badge size. This finding provide evidence for like vs. like aggression and indicates that, if the costs of fighting stronger individuals are greater than fighting opponents of equal strength, the honesty of badges of status could be enforced through social control. In contrast, Gonzalez et al. (2002) reported no evidence for the social control hypothesis in house sparrows. The badge size of low ranking males was manipulated to resemble adult badges, and the birds were then re-introduced into captive flocks. These cheating males were neither involved in more fights overall, nor in more fights with actual dominant individuals, but they did win more fights than they did prior to the manipulation, indicating that low-ranking males manipulated to have large badges are able to rise in dominance rank. Also, cheaters did not have elevated corticosterone levels, which are associated with stress, which indicates cheaters were not suffering from more stress than honest individuals. Together, these results indicate that cheaters do not suffer from increased aggression or increased stress levels. Thus, social costs fail to explain the honesty of House sparrows' melanin badge (but see Moller 1987b, where house sparrow cheaters were found to have increased aggression from dominants).

Dietary production costs

A variety of studies have tested the hypothesis that status signals can be associated with production costs that only high quality individuals are able to sustain. If status signals carry significant production costs, subordinates would be prevented from cheating because the costs associated with a dominant signal outweigh its benefits. Veiga and Puerta (1996) hypothesized that melanin badges could be limited by diet. They found that juvenile house sparrows held in aviaries with unlimited access to food developed larger badges than free-living juveniles with no diet supplementation. These results must be interpreted with caution because other factors, like stress, are likely to be different between captive and free-living populations. In a similar study, McGraw et al. (2002) nutritionally stressed juvenile house sparrows during their autumn molt by limiting access to food during unpredictable periods and found no difference in badge size or color compared to controls. Also calling into question the relationship between nutrition and the honesty of (melanin based) status signal, Gonzalez et al. (1999) manipulated access to protein during juvenile house sparrows' autumn molt and found no difference in badge size or color between experimental groups and controls. However, more recent studies provide evidence that specific aspects of diet, such as amino acid content, affect signal expression. There is an expected link between access to essential amino acids and melanin coloration because amino acids serve as the building blocks for melanin pigments. Poston et al. (2005) showed that restricting phenylalanine and tyrosine content in the diet of male house sparrows reduced the darkness, but not the size, of their melanin badges. However, it is badge size, not darkness, that correlates most strongly with status in this species, so this evidence must be taken with caution. Taken together, these studies suggest that differences in diet do not account for large differences in melanin badge expression.

There is also evidence that mineral availability may limit coloration. Minerals such as calcium, zinc, iron, copper, and magnesium are often limited in the diets of wild animals (McDowell 2003). Studies on eagles show that some of these elements are more common in melanized feathers than in feathers lacking melanin (Niecke et al. 2003). Roulin et al. (2006) found that calcium concentrations in bones of barn owls was positively correlated with the extent of black spotting on the breast plumage, which is an honest signal of quality (Roulin and Altwegg 2007). The most convincing study on the relationship between minerals and coloration in birds was conducted by McGraw (2007). He manipulated melanin content in male zebra finch and found that birds that had more calcium in their diet developed larger melanin patches on their breast than controls. These findings demonstrate that minerals may be the main player when considering the effect of dietary access on the limitation of badge production.

Future work

Dynamic signaling in dynamic social environments

The plethora of evidence that status signals reveal the fighting ability of competitors has led to new and fascinating questions that merit further study. There is evidence that status signals can change rapidly (Ardia et al. 2010, Rosenthal et al. 2012) and that they themselves are influenced by an individual's recent social context, which suggests that the directionality of signal strength to social outcomes is not as linear as previously thought (Dey et al. 2013). These dynamic signals provide receivers crucial information about an individual's recent competitive environment in ways that static signals cannot.

Recent evidence on carotenoid-based ornamentation on bare-parts indicates that status signals can dynamically reflect phenotypic condition in real-time. For example, the carotenoid-based frontal shield of pukekos is T-dependent (Eens et al. 2000), and can change color rapidly in dynamic social environments (Dey et al. 2013). Research in zebra finch show that T can mobilize carotenoids from storage tissues into the blood stream, which allows for rapid changes in carotenoid-colored ornaments (Ardia et al. 2010). Dey et al. (2013) showed that when the size of the shield is artificially enlarged, individuals not only rise in dominance rank, but also increase the natural size of their shield after the artificial manipulations are removed, which indicates that dynamic signals can reflect an individual's immediate social environment. The bill of female American goldfinch is also carotenoid-based, can change color rapidly with changes in condition (Rosenthal et al. 2012), and is potentially T-dependent (Pham et al. 2013), which suggests it might function in dynamic contexts as well. These findings demonstrate that the directionality of cause and effect that determine the intensity of a signal is not necessarily linear: dynamic signals can both determine dominance and be affected by dominance interactions.

Multiple status signals

Recent research has suggested that multiple ornaments in a single individual can signal different aspects of fighting ability. Because different colors are produced via different mechanisms, different colors can reflect different aspects of condition that reflect fighting ability in different ways (Bokony et al 2006, Hegyi et al. 2007). Until recently, most studies on status signaling have focused on how single plumage or bare-part traits signal status, but there has been recent interest in how multiple ornaments in a single individual can signal different aspects of status. This is particularly interesting because many different qualities affect fighting ability, so a

signaling system in which different traits signal different aspects of fighting ability would allow competitors to make more informed assessments about each other's fighting ability. Chaine et al. (2013) found that golden crowned sparrows use both the black and gold crown coloration to signal status. This study measured dominance interactions after manipulating both color patches (one at a time) to show that individuals respond to both colors in competitive contexts.

Furthermore, these authors found that when there was a greater differences between competitors in the size of the gold patch, this led to an increase in aggression, and that that the difference in the size of competitors' black patch size did not have as strong of an effect on increased aggression. These findings suggest that birds can not only use multiple ornaments to signal status, but that each color may signal a different aspect of fighting ability (e.g. energy available to invest into aggression, or the probability of increasing aggression during a fight). These findings are consistent with other studies that show that different colors are maintained by different mechanisms and are therefore linked to different aspects of condition. In this manner, status signals of different colors may encode different information about the sender's fighting ability.

Conclusions

The ability for individuals to preemptively signal their fighting ability during competition for resources reduces the costs of competition for both senders and receivers, and winners and losers. By signaling status, dominant birds can gain access to resources without physically competing for them, and subordinate birds can avoid investing in a fight they would likely lose anyway. Correlational and experimental evidence demonstrates that status signals are used by a variety of birds, and that males, females, adults, and juveniles respond to them. However, the

potential benefit of displaying a dominant signal regardless of an individual's actual fighting ability has led theoretical modelers to conclude that, unless signals are kept honest by costs, deception would be favored and the signaling system would be evolutionarily unstable. Subsequent research has shown that many status signals are indeed costly. The expression of many status signals has been shown to be influenced by testosterone, which is immunologically costly and increases risk of predation by increasing risky behavior, such that only high-condition birds that can withstand the costs of T can afford to express dominant status signals. There is also some evidence that social probing of honesty can be costly, such that only birds who can withstand the costs of behaviorally demonstrating that their signal is honest can express dominant signals. The recent findings that show that status signals can rapidly change in their intensity and that individuals can express multiple status signals have set the framework for future research. Future studies should focus on what type of information on fighting ability different signals have, and how an individual's social environment can affect signal expression in dynamic signals. Another avenue of future research could look at how signals are used differently throughout the year as environmental conditions fluctuate.

Chapter 2: Minimizing the cost of competition in the black-crested titmouse: status signaling, dominance, and foraging behavior

Introduction

The ability to minimize conflict during competition for resources is an important adaptation for many animals. Individuals that evolve to honestly signal their status are able to minimize the time and energy spent competing, and both dominants and subordinates benefit by minimizing the costs associated with fighting (Rowher 1975). While status signals have been shown to settle disputes over territories (Pryke et al. 2002) or food (Murphy 2009), less is known about how they are used to communicate over seasonal and temporal shifts in resource availability when defense in changing environments may require dynamic shifts of allocation towards defense.

When there is competition for resources, dominant individuals often garner prioritized access (Hahn and Bauer 2008, Mennill et al. 2003). However, establishing dominance relationships can be costly, especially when contests are settled with physical fights (Maynard Smith and Harper 1988). Consequently, many animals have evolved conspicuous traits that minimize the need for costly fights by relaying encoded information that communicates the sender's fighting ability. Traits that signal information about individual fighting are called status signals (Rohwer 1975), and these types of signals have been shown to mediate conflict in birds, lizards, fish, and primates (Whiting et al. 2003). Signaling status allows winners to gain access to key resources without paying the high costs of physical contests. It also allows losers to avoid wasting time and energy fighting over resources that they would lose anyway. For example, Red-

shouldered widowbirds use the conspicuous coloration of their epaulets to signal dominance in territorial contests (Pryke et al. 2003), and scarlet-tufted malachite sunbirds use their pectoral tufts to signal status during competition over key food resources at territory boundaries (Evans and Hatchwell 1992a, b). These signals allow dominant individuals to maintain territories with higher quality resources, which can lead to increased reproductive success (Evans and Hatchwell 1992a, b).

A change in resource availability (e.g. due to drought, seasonal fluctuations) can lead to changes in competition (Dearbor 1998, Golabek et al. 2012, Dunk and Cooper 1994). Due to the importance of food for reproduction and survival, there are generally large benefits associated with an individual's ability to maintain and access to food resources during food-limited periods and during periods of increased competition. If quality resources cannot be defended, animals often alternate from a resource defense strategy to an opportunistic and sporadic foraging strategy (Davies 1978). Brown (1964) argued that the size of a territory is determined by optimizing the difference between the benefits gained from having a territory of certain size and the costs of maintaining such a territory, such that the amount of net benefits gained are maximized. He termed this optimum the "economic defensibility" of territories (modeled in Figure 1). Because the size of a territory is determined by an individual's ability to invest in its defense, the aforementioned optimization of benefits and costs applies to investment in resource defense in general, not just breeding territories. It is expected that changes in the degree of competition in the population will alter an individual's net benefits of territoriality and that the costs of resource defense should increase with competition (Brown 1964). Because dominant and subordinate birds generally have different fighting abilities (Searcy and Nowicki 2005, Maynard Smith and Harper 1988), a reduction in available resources will change an individual's ability to

invest in defense differently between these two classes, such that the foraging behavior of dominant birds is expected to be less affected by fluctuating resource availability (Figure 9).

The black-crested titmouse (*Baeolophus atricristatus*; hereafter titmouse or titmice) is a socially monogamous passerine native to Texas and northern Mexico. Male titmice have a conspicuous dark crest that can be prominently elevated or discretely laid flat on top of the head. Observations suggest that the crest is frequently displayed during agonistic interactions (Grubb 1998), suggesting a possible status signaling function to this ornament. Furthermore, this species is a year-round resident that appears to maintain territories throughout the year, with little change in territorial location between years (personal observation). Because this species is not migratory, individuals have to compete over food resources that fluctuate in quantity and quality throughout seasonal shifts. As a result, this species provides an excellent system in which to study the use of a potential signal of status during competition for food, and how that signal is utilized when competition for food varies over time.

I conducted two studies on status signaling and resource access in the black-crested titmouse. In the first study, I tested the hypothesis that males with large crests are dominant over males with smaller crests during competition for access to food, and I predicted that males with larger crests will have greater access to experimentally provided seed-feeders, and that these large crested-males will be better at monopolizing individual feeders. In the second study, I tested the hypothesis that dominant individuals --as assessed by their success in monopolizing feeders-- suffered fewer costs when there was an experimental increase in competition for food. To test these hypotheses, I attached a passive integrated transponder (PIT) tags to individual birds and recorded their foraging behavior within an array of eleven seed-feeders outfitted with radio-frequency identification (RFID) devices. I first compared crest size to access and

monopolization of experimentally provided feeders during the post-breeding season. During the following pre-breeding season (approximately 6 months later), I again compared crest size to competitive outcomes. In addition, I tested whether an individual's competitive ability during a period when there was an abundance of resources (when all eleven feeders were available), predicted access and monopolization of resources when we increased competition for access to food by reducing the number of feeders by approximately half. These tests allow me to test whether signals, as well as previous dominance status, are consistently used to mediate dominance in dynamic environmental contexts where food resources vary temporally.

Methods:

Study species

The Black-crested titmouse is a year-round resident of Texas and north-eastern Mexico. During the non-breeding season (July-February), Black-crested titmice form small family groups and forage in mixed species flocks. These groups are likely composed of breeding pairs and young from the previous breeding season (personal observation). During the breeding season (March-June), males behave territorially towards other males (Paton and Smith 2008) with frequent songs and aggressive behavioral displays, and this behavior is seen at artificial feeders located within overlapping home ranges.

General

The studies were carried out at an approximately 50 ha private ecological preserve in Kendalia, TX (29°58'44.0"N, 98°32'49.6"W). The first study on crest size and foraging behavior

was conducted from May 27th - July 15th, 2013. The second study comparing both crest and dominance to competition after resource manipulation was carried out from February 1st – 20th, 2014 at the same location. Between May-June 2013, I captured birds using funnel traps placed around seed feeders. Upon capture, I measured basic morphological features (tarsus, wing, bill) and body mass to assess body size and condition. Birds were banded with USGS metal band, individualized color bands, and a 12 mm PIT tag was attached to the color bands on one of the bird's leg. I captured and tagged 13 adult (after hatch-year) males and 10 juvenile (hatch-year) males for the purpose of these two experiments. Only adults were used in the first study because the juveniles had juvenal plumage. 1 of the tagged individuals did not appear in the RFID data. In the second study, I monitored, 7 of the same adults from the previous study, and added 7 of the tagged birds that were previously juveniles-- these birds had aged into second-year birds and developed adult plumage (in the Sept-Oct molt).

Crest length was measured digitally using standardized photos in which the crest was flattened and held parallel to the camera sensor. A size scale was included in each picture. Image J was used to measure the linear distance between the exposed culmen to the tip of the flattened crest. We measured crest length during May-June 2013, immediately before the first experiment (post-breeding comparison of crest to foraging success). We used these same crest measurements in the second experiment that occurred 199 days later (pre-breeding comparison of both crest and dominance to foraging success). Because titmice molted their crest feathers between these experiments, we rely on crest measures taken pre-molt; however, we have found no systematic change in crest size between years (unpublished data) and so our use of a previous year's measure provides a reasonable estimate of crest size after molt. All analyses use raw crest length

because there was no correlation with crest to body size in our population of males (least-square linear regression: tarsus on crest length, $p = 0.48$, $n = 11$)

Recording foraging data with radio-frequency identification (RFID)

I created an array of 11 feeders outfitted with RFID antennae (impedance = 1.3-1.4 mH) and processors programmed using code available online (Bridge n.d.). Each feeder was modified so that only one feeding port was accessible, thus allowing feeders to be monopolized while an individual was foraging in the area. Each time a tagged titmouse fed from a feeder, its unique ID was stored as a data file, along with the time and date. In this species, each visit to the feeder represents the consumption of a single seed: when landing on a feeder, a titmouse removes a single seed and then flies to nearby vegetation to process and consume the seed (personal obsv.). As such, the sum of foraging visits represents the quantity of feeder-provided seed consumed by an individual.

I quantified foraging behavior in three manners: 1) the total number of visits to any feeder over the recording period, which relates to overall access to the food resource; 2) number of feeding stations that were utilized over the recording period, which relates to the size of foraging range; and 3) the degree of monopolization of a single feeder. The degree of monopolization of a single feeder represents investment into resource defense. This monopolization measure was calculated as the percent of an individual's total visits at their most-heavily used feeder (i.e., an individual had a 75% monopolization score if it ate 750 seeds from a feeder while three other titmice together ate 250 seeds from the same feeder). MATLAB was used to calculate all foraging measures.

Does crest size related to access to resources during the post-breeding season?

To test for a relationship between crest size to access to resources, I compared crest length to three measures of access to resources (number of feeds, number of feeders, % monopolization) over 19 consecutive days during the post-breeding season (June 27-July 15, 2013) which is during the period when family groups remained together. The RFID readers acquired data on foraging visits during all daylight hours (approx. 14 hrs per day). There were two occasions in which data from a single feeder was lost (either due to loss of seed or due to damage by mammals). When this happened, data during this time-period were removed from all 11 feeders so that all feeders recorded over identical periods. I compared foraging data to the crest length of 11 adult males. One male was removed from the analyses because his crest was missing the distal half of the feathers (presumably from a previous injury), preventing an accurate measurement of crest length.

Does both crest size and dominance relate to access to limited resources during the pre-breeding season?

For the second experiment on the relationship between crest size and access to resources, I re-deployed feeders 199 days after the initial experiment. To then test how a reduction in available resources affected foraging behavior of adult male titmice, I removed approximately half of the available feeders. Specifically, I collected 10 days of baseline foraging data using RFID antennae at 11 feeders (hereafter this period will be referred to as 'F-11'), after which I removed 5 of the available feeders (hereafter this period will be referred to as 'F-6'). Feeders were removed in a manner that ensured that the remaining feeders were evenly distributed throughout the property. We balanced which feeders were removed so that there was not a bias

in the number of dominant or second year birds that lost their preferred feeder. In other words, the number of subordinates that lost their primary feeder (as assessed by % monopolization during F-11) was similar to the number of dominants that lost their feeder. Similarly, neither adults or young birds were more likely to lose their primary feeder during the experiment

To increase competition after F-11, the five feeders were removed at night during a non-foraging period. Immediately after feeders were removed, F-6 began and data were collected in the same manner as listed above during the baseline period (i.e., during all daylight hours). During F-6, I collected 10 days of foraging data. There was one instance where a feeder was emptied of seed for 7 hours during F-11. Data from all other feeders during these hours were removed from the F-11 dataset, and a corresponding period of data of equal duration was also removed from F-6 that corresponded to the time-sequence that data were missing during F-11.

To assess the effect of competition on defense of foraging resources, I measured how each individual changed its foraging behavior (number of feeds, number of feeders, % monopolization) during F-6. To do this, I compared the loss of access to seed during F-6 by calculating a 'relative change' for each bird subtracting a bird's total visits during F-6 from its total visits during F-11, and divided by its total visits from F-11. Thus, this relative change in feeding accounted for the relative loss of access to food experienced by each individual. This measure of relative change in foraging was used instead of absolute foraging to accurately reflect how behavior changed relative to an individual's baseline. This was done because a bird that fed more during the baseline period might have reduce its absolute total visits in F-6 simply because it had more feeds to lose compared to a bird who had a lower baseline. To quantify dominance during F-11, I used total visits to all feeders and % monopolization of the most-used feeder during the baseline period. I then tested whether both crest length and dominance status (as

measured by total visits and % monopolization) were related to relative-change in foraging behavior between F-11 and F-6,

Statistics

For the first study, which compared crest length to foraging behavior during the post-breeding season, I used a linear regression to compare crest size to the measures of foraging success (total number of visits, number of feeders utilized, percent monopolization of most-used feeder). For the second study, I first compared crest length to our measures of relative changes in foraging success using linear regression. Second, I compared our measure of dominance from F-11 (total number of visits, number of feeders utilized, percent monopolization of most-used monopolization) to our measures of relative changes in foraging success using linear regression. I used t-tests to compare foraging behavior between F-11 and F-6 to quantify the overall change in foraging behavior between the two periods. To assess what other factors may influence competitive outcome, I additionally tested for a relationship between aspects of the phenotype that can influence competitive outcome, including body size (tarsus length), mass, and residual mass (residuals from regression of mass on tarsus) to both crest length and foraging behavior using linear regression. All statistics were performed in JMP 11.

Results

Does crest size related to access to resources during the post-breeding season?

I recorded a total of 9,412 foraging events from 11 male titmice over 19 the day recording period in the post-breeding season. Adult males had an average of (mean \pm STDEV)

856 \pm 440 total visits throughout the study period, visited an average of 3 \pm 1.2 feeders, and the average percent monopolization was 21.2 % \pm 11.1 %.

Crest length was positively correlated with total number of visits across all feeders (least-square regression, $p = 0.04$, $R^2 = 0.40$, $n = 11$, Figure 2) and % monopolization ($p = 0.049$, $R^2 = 0.36$, $n = 11$, Figure 3). Crest size was not significantly related to number of feeders utilized ($p = 0.82$). There was not a significant relationship between crest length and body mass ($p = 0.75$, $n = 11$), body size ($p = 0.48$, $n = 11$) or residual body mass ($p = 0.99$, $n = 11$). There was not a significant relationship between body mass and total visits ($p = 0.36$), total feeders ($p = 0.97$), and % monopolization ($p = 0.77$), nor was there a significant relationship between body size and foraging behavior (sample size 11 for each analysis: total visits $p = 0.13$; total feeders $p = 0.29$; % monopolization $p = 0.28$). There was not a significant relationship between residual body size and total visits ($p = 0.77$), total feeders ($p = 0.57$), and % monopolization ($p = 0.84$).

There was a significant positive relationship between % monopolization and total visits during the post-breeding study ($p = 0.0001$, $R^2 = 0.84$, $n = 11$, linear regression, Figure 4) indicating that individuals that were more effective at monopolizing a feeder gained access to more food.

Does both crest size and dominance relate to access to limited resources during the pre-breeding season?

During the 10-day recording period of F-11 (11 feeders available), I recorded 4,222 foraging events from 14 adult male titmice. These 14 males were composed of the same 7 males from the post-breeding study, and 7 additional males that had aged into adulthood since they were first captured as yearlings in the previous year. These males visited an average of 301 \pm 186

times, visited an average of 2.2 ± 1.1 feeders, and the average % monopolization was $32.0\% \pm 22.0\%$. During the 10-day recording period of F-6 (6 feeders available), I recorded 2066 foraging events from 14 male titmice. These were the same 14 males recorded in F-11. These males visited an average of 148 ± 107 times, visited an average of 1.2 ± 0.6 feeders, and the average % monopolization was $19.0\% \pm 14.0\%$.

During F-11, there was not a significant relationship between crest length (as measured from previous molt) and total visits ($p = 0.72$, $n = 14$), total feeders ($p = 0.85$, $n = 14$), or % monopolization ($p = 0.20$, $n = 14$). During F-6, there was a positive trend between crest length and % monopolization ($p = 0.073$, $n = 7$), but no significant relationship between crest length and total feeders ($p = 0.096$, $n = 14$), or total visits ($p = 0.18$, $n = 14$).

All foraging measures decreased from F-11 to F-6 (paired t-test (by individual band number), $n = 14$ in all analyses: total visits $p = 0.0009$; number of feeders $p = 0.009$; % monopolization $p = 0.02$). Between F-11 and F-6, crest size was significantly positively related to an individual's ability to maintain foraging access: individuals with larger crests had lower relative reduction in total visits ($p = 0.02$, $R^2 = 0.71$, $n = 14$, Figure 5). Crest size was not significantly related to relative reduction in % monopolization ($p = 0.53$, $n = 14$) and total feeders ($p = 0.14$, $n = 14$).

Dominance in F-11 (as measured by % monopolization) was significantly positively related to an individual's ability to maintain foraging access after a reduction in available food: individuals that had higher monopolization scores in F-11 had a lower relative reduction in total visits ($p = 0.01$, $R^2 = 0.41$, $n = 14$, Figure 6), indicating that dominant birds suffered less from the decreased availability of food. Neither total number of visits, nor number of feeders utilized correlated with relative changes in foraging behavior ($p > 0.10$, $n = 14$).

During F-11, % monopolization was unrelated to total visits ($p = 0.80$, $R^2 = 0.0055$, $n = 14$, Figure 7). This is in contrast to findings during the post-breeding season. However, when competition was increased during F-6, % monopolization was positively correlated with total visits ($p = 0.0001$, $R^2 = 0.71$, $n = 14$, Figure 7) indicating that during increased competition, that birds that were more successful at defending feeders gained access to more food.

The number of feeders used (a measure of a bird's feeding range or feeding effort) during F-11 was uncorrelated with total visits ($p = 0.76$). However, birds that fed from more feeders during F-11 reduced the number of feeders used during F-6 relatively more than other birds ($p = 0.006$, $R^2 = 0.48$, $n = 14$), indicating that birds that foraged widely in the first period were less able to do so when competition was experimentally increased.

Discussion:

Status signals mediate conflict over resources by reducing the need of costly fights. This signal function may be particularly useful in times of high competition that may arise through seasonal fluctuations in resource availability. I investigated whether adult male titmice use their crests to signal status over food resources during both the post- and pre- breeding season. These times of the year are separated by approximately 5 months and vary dramatically in annual precipitation, and so are also likely to vary in food abundance. During the post-breeding season, birds with longer crests were more successful at resource defense (measured by % monopolization, Figure 3)) and had greater access to food (measured by an individual's total visits, Figure 2) than birds with shorter crests. These relationships are consistent with the hypothesis that male crest length signals dominance of male titmice and indicate that individuals with longer crests may be able to minimize the time and energy spent fighting and thus reduce

the cost of competition over food resources (*sensu* Rohwer 1975). Similar relationships are found in other species, wherein a plumage or bare-part ornament is used to signal status over key resources (Evans and Hatchwell 1992, Lemel and Wallin 1993, Laucht et al. 2010, Pryke and Andersson 2003, Jones and Hunter 1999).

We then tested whether the crest was also used to mediate competition approximately 5 months later during the pre-breeding season. During this period, we failed to find a correlation between crest length and our measures of access to resources. This lack of relationship suggests that the use of the crest is not consistent through the annual cycle and may indicate that the crest is only selectively beneficial during periods of intense competition. The lack of a relationship during the pre-breeding season could be explained because of seasonal increase in natural food availability, or because these birds were no longer traveling in family groups and so competition for access to each feeder was lower (*i.e.*, there were fewer individuals in a cooperative unit attempting to feed from a single source). To further explore the idea that the crest is only used as a signal of status during periods of high competition, we experimentally reduced the availability of food to test whether crest length again became a predictor of foraging success. During this second test, I found that birds with longer crests were again better able to maintain access to the feeders: males with larger crests experienced smaller reduction in access to food and a smaller reduction in their ability to monopolize a feeder compared to birds with smaller crests (Figure 5). These results provide compelling support to the hypothesis that crest length mediates competitive interactions, but also suggests that the crest is predominately used to signal status in times of high competition, and that selection for signal utilization can vary on a seasonal temporal scale and that benefits of signaling may only be accrued during discrete times of the year when resources are limited.

In addition to focusing on the communication system in this species, I additionally tested whether dominance (as measured by ability to monopolize a feeder) predicted an individual's ability to maintain access to resources when they were experimentally limited. I found that dominant birds suffered less reduction in access to food than did subordinate birds: dominant birds reduced their access to the feeders less than other birds after the removal of approximately half of the feeders (Figure 6). These findings suggest that dominant and subordinate birds face different costs for resource defense (Figure 9), and that those costs increase more rapidly for subordinate birds (Figure 10), forcing subordinates to alter their defense strategies faster than dominants under high competition.

The finding that large-crested dominant male titmice have prioritized access to food resources when competition is experimentally increased corroborates other findings that show that dominant birds gain greater access to food resources by excluding subordinates. For example, in the winter habitat of hermit thrushes, food availability decreases throughout the winter, and dominant birds (usually large-bodied males) exclude subordinate birds (usually small-bodied females) from territories with the most resources (Diggs et al. 2011). In pied wagtails, some individuals in a population will defend territories and others will join flocks and exploit transient food sources. Territorial birds that exclude conspecifics from their territory benefit from a more diverse diet than gregarious birds, and are also able to join foraging flocks when food on their territories becomes scarce, thus indicating that dominant individuals are better able than subordinates to exhibit a suite of foraging options when resources become scarce (Davies 1976). These studies add support to the hypothesis that dominant birds are better able to buffer against the costs of limiting resources, and that subordinates and dominants face different tradeoffs when maximizing resource intake.

There has also been a wealth of research on the ability of dominant birds to use signals of status to gain access greater resources (Senar 2006). For example, among male black-capped chickadees, individuals with darker and more contrasting achromatic plumage are dominant over other males and gain prioritized access to supplemental feeders by excluding subordinate conspecifics from the resource (Mennill 2003). In crested-auklets, males with longer crests exclude shorter-crested males from penguin carcasses and consume a larger percentage of each carcass (Jones and Hunter 1999). These studies parallel the findings in this study, that dominant individuals are both able to maintain their dominance in the face of increased competition, and that signals are likely used to mediate conflicts during these competitive interactions

An interesting observation in our study is that crest size does not relate to the number of feeders an individual utilizes. Initially, we expected that dominant individuals would have larger home ranges, and thus access more feeders. However, it now seems likely that the number of feeders a bird utilizes is not a good measure of dominance or foraging behavior because there might be multiple factors that influence a bird's use of multiple feeders. For example, a dominant individual might heavily invest in the defense a single feeder, but also invest to some degree in the defense of neighboring feeders. In contrast, a subordinate bird may feed from the same number of feeders, but because it is not able to effectively defend any single feeder, it forages less at any one feeder and spreads its foraging pattern more widely. In this scenario, the dominant bird might feed from several feeders because it is able to defend feeders while it is also able to intrude on other males' feeders, while the subordinate might feed from several feeders because its only option is to forage opportunistically as it avoids dominant birds.

This current study provides evidence that adult male black-crested titmice use their crest to signal status during competition for food resources and that dominant individuals are more

able to withstand an increase in the cost of resource defense and thereby maintain investment in defense of key food resources. We also demonstrate that this potential signal of status may only be used (or may only be responded to) when competition for resources is elevated. More research is needed to bolster these findings. For example, manipulations of the crest itself could provide evidence for its use as a status signal. Furthermore, it is worth considering that the crest of the titmouse can be lowered or raised, and so could signal status in a dynamic way. Dynamic status signals have been identified in other species and often are considered to reflect an individual's immediate ability to invest in a fight (Murphy et al. 2009, Rosenthal et al. 2012, Dey et al. 2013, Pham et al. 2014), compared to static signals, which lack a real-time reflection of phenotypic condition. Thus, the active use of the crest (i.e. rates of lowering vs. raising) may signal different information than the length of the crest itself. It is possible that titmice uses crest in a variety of competitive contexts, and these contexts may vary throughout the year.

Figures

Figure 1: The degree of investment in resource defense is dependent on the costs and benefits of defense. An individual optimizes its investment by maximizing the distance between the benefits and costs of defense such that net benefits maximized.

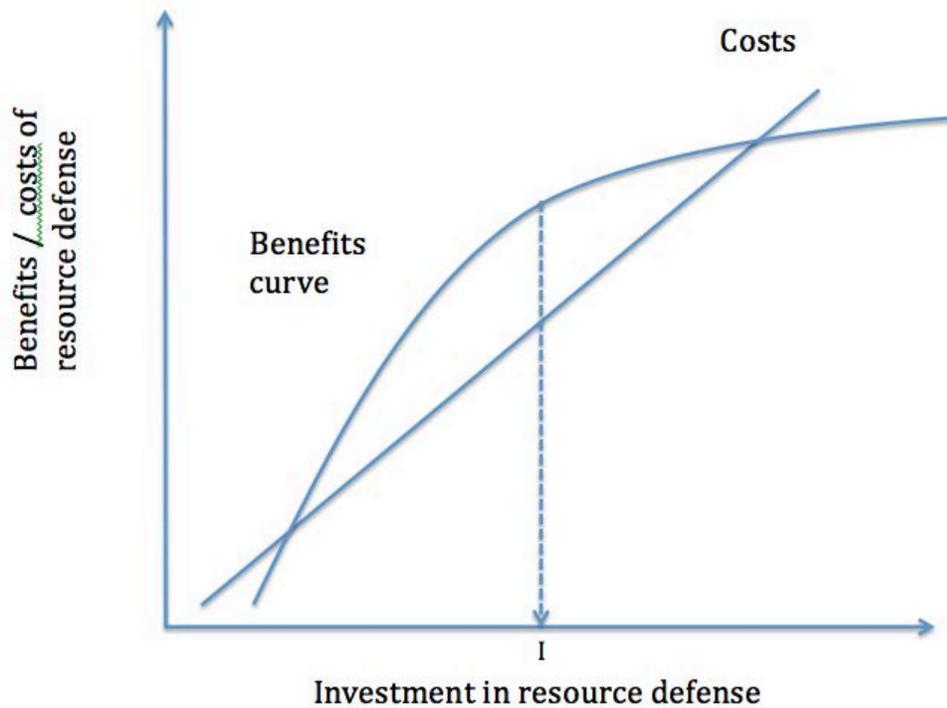


Figure 2: Birds with longer crests had greater access (as measured by total visits) to the 11 supplemental feeders during the post-breeding season

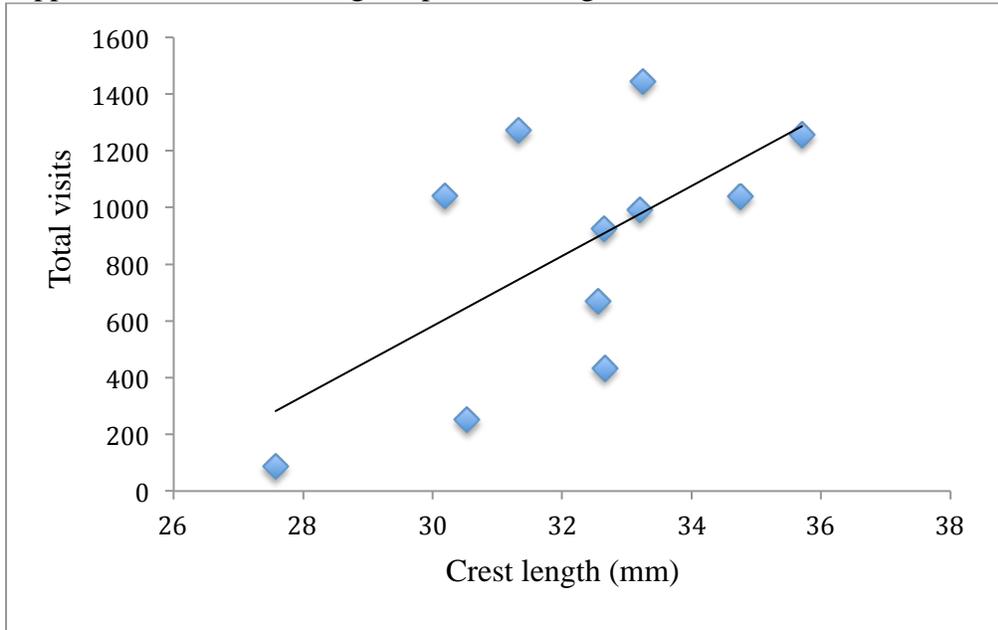


Figure 3: Birds with larger crests invested more in defending their most-used food resource (as measured by % monopolization of an individual's most-used feeder) during the post-breeding season.

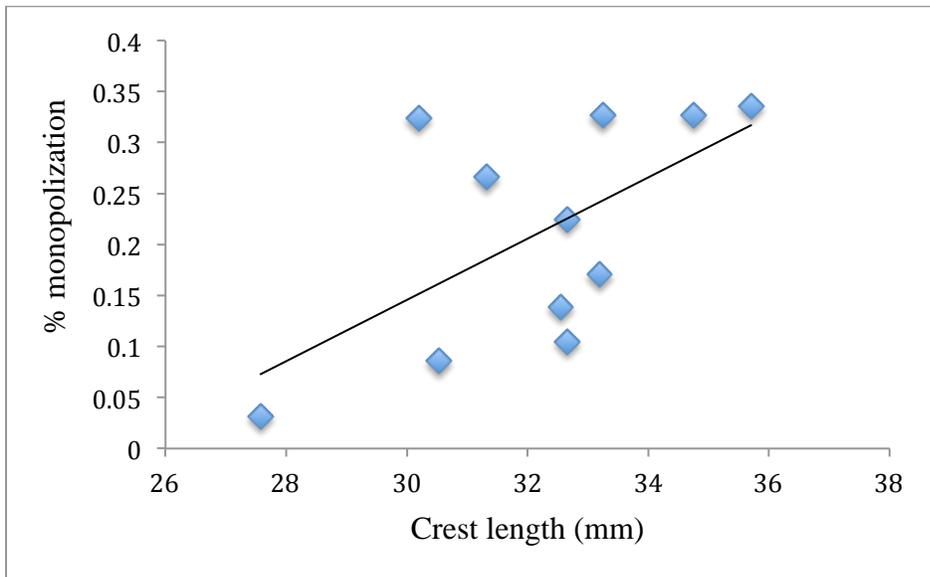


Figure 4: Birds that invest in the defense of their most-used feeder (% monopolization) had greater overall access to food (total visits) during the post-breeding season.

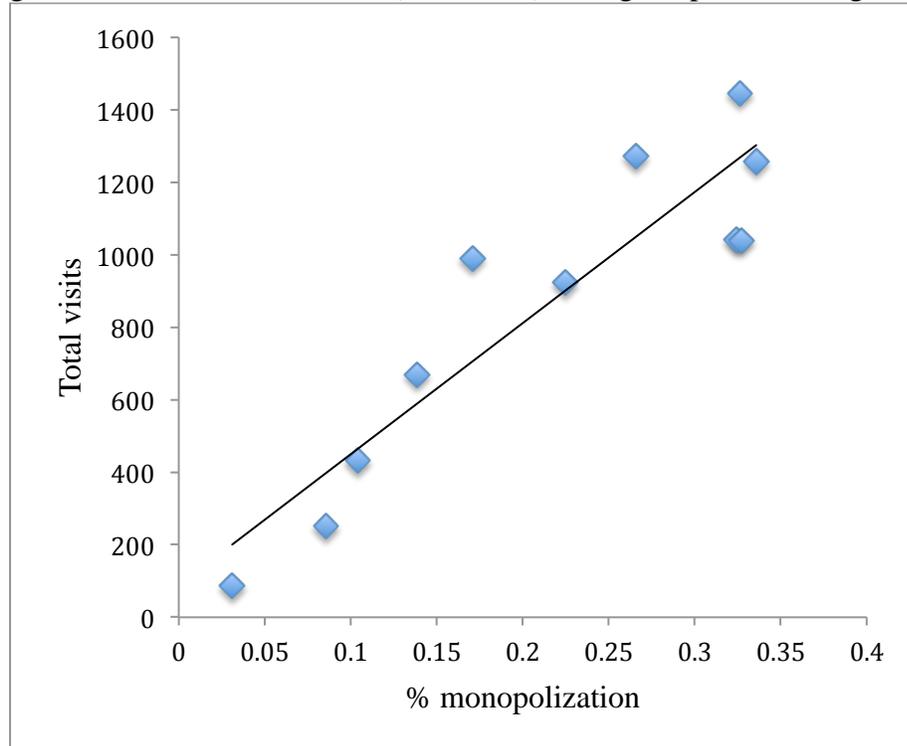


Figure 5: When food availability was experimentally reduced, birds with longer crests (mm) had a lower relative reduction in their access to food (total visits) than birds with smaller crests during the pre-breeding season.

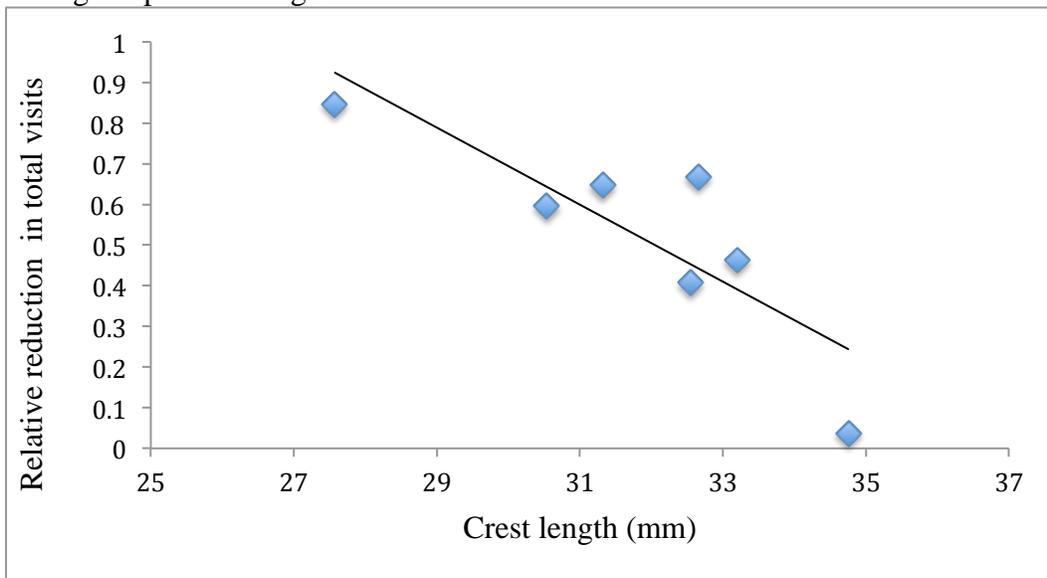


Figure 6: When food availability was experimentally reduced, birds that invested more in resource defense (% monopolization) during F-11 had a lower relative reduction in their access to food (total visits) than birds that invest less in resource defense during the pre-breeding season.

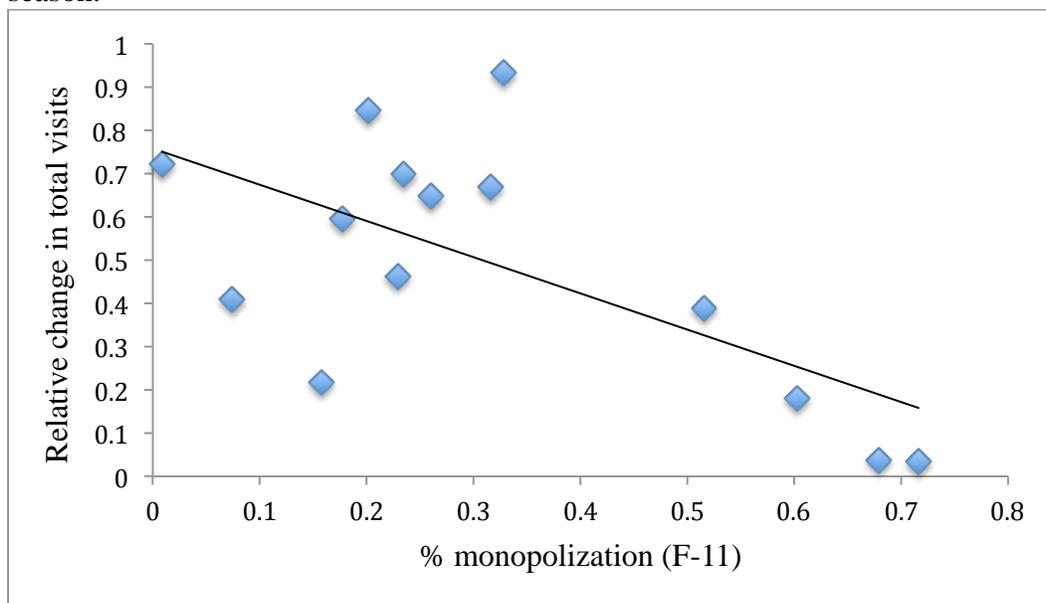


Figure 7: When there are 11 supplemental feeders available during the pre-breeding season, an individual's investment in the defense of their most-used feeder is unrelated to their overall access (total visits).

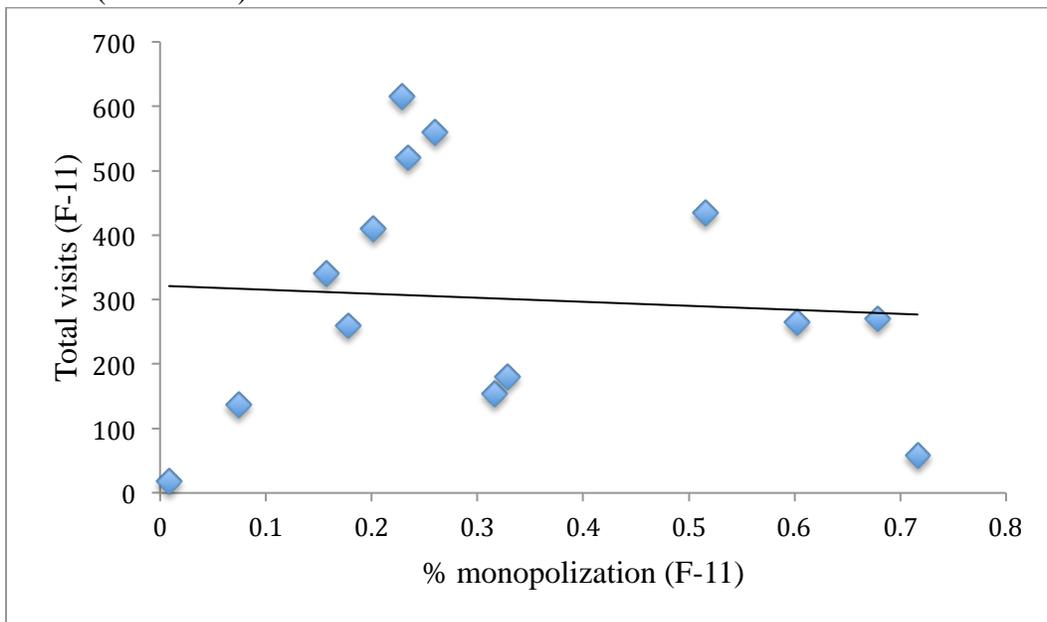


Figure 8: When there are 6 supplemental feeders available during the pre-breeding season, birds that invest more in the defense of their most-used feeder also have greater overall access to food (total visits).

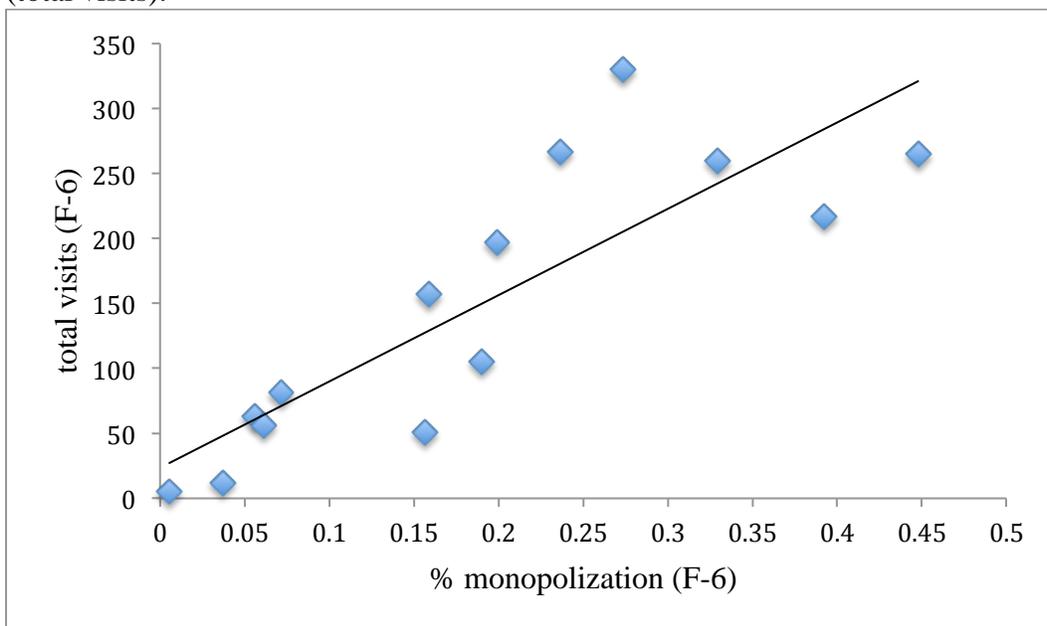
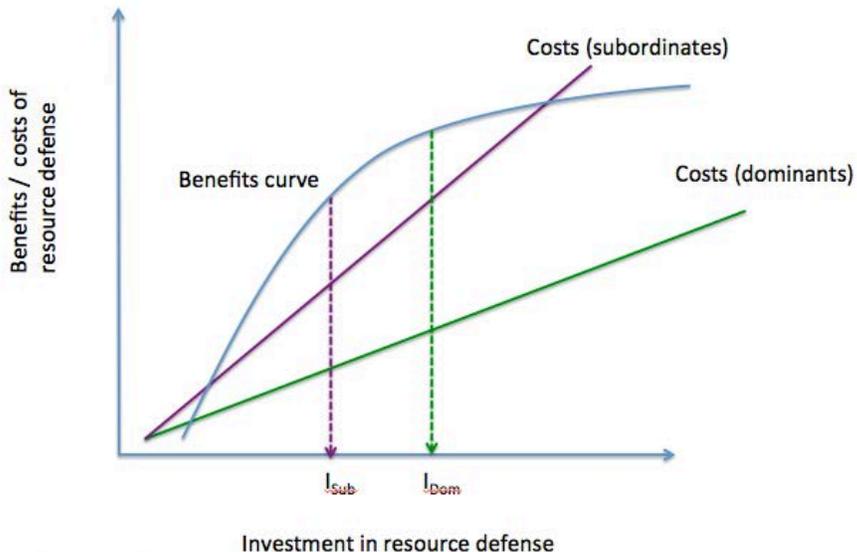
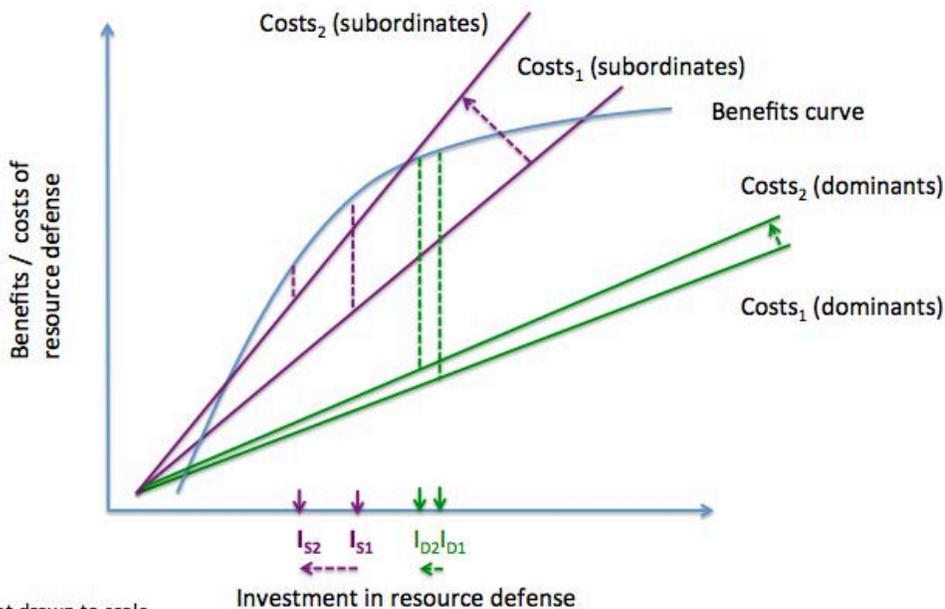


Figure 9: Dominant and subordinate birds face different costs for defending a resource and therefore have different levels of optimal investment in resource defense.



*Model not drawn to scale

Figure 10: As food becomes scarce and competition increases, the costs of resource defense also increase. The costs of resource defense increase more rapidly for subordinate birds than for dominant birds.



*Model not drawn to scale

Chapter 1 References

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