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The Effect of Exogenous Testosterone on Dominance and Status Signaling in the Female American Goldfinch (*Spinus tristus*)

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THE EFFECT OF EXOGENOUS TESTOSTERONE ON DOMINANCE AND STATUS
SIGNALING IN THE FEMALE AMERICAN GOLDFINCH (*SPINUS TRISTUS*)
DANIELLE FREUND

A DEPARTMENT HONORS THESIS SUBMITTED TO THE
DEPARTMENT OF BIOLOGY AT TRINITY UNIVERSITY
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR GRADUATION WITH
DEPARTMENTAL HONORS

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The effect of exogenous testosterone on dominance and status signaling in the female American
goldfinch (*Spinus tristus*)

by

Danielle Rose Freund

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Table of Contents

<i>Acknowledgements</i>	5
<i>Abstract</i>	7
<i>Chapter 1</i>	8
<i>Direct selection of female aggression: The adaptive costs, benefits, and mechanisms resulting in female specific behavior</i>	8
Behavioral Trade Offs That Regulate Female Aggression	11
Individual Condition Costs	11
Reproductive Costs of Aggression	15
Adaptive Benefits of Female Aggression	17
Individual Survival	17
Aggression, access to mates, and mating success	20
Aggression and Offspring Survival	24
Mechanisms Underlying the Regulation of Aggression	27
Dehydroepiandrosterone (DHEA)	27
Progesterone	29
Estrogen	31
Testosterone	33
Genetic control of aggression	36
Conclusion	37
<i>Chapter 2</i>	40
<i>The effect of exogenous testosterone on dominance and status signaling in the female American goldfinch (Spinus tristus)</i>	40
Introduction	40
Methods	44
General Procedures	44
Rank Assessment: Flock Hierarchy Establishment	45
Assignment to Dyads	47
Testosterone Manipulation	47
Bill color Assessment	48
Dyad Behavioral Trials	49
Behavioral Analysis of Dyad Trials	49
Verification of the Efficacy of Testosterone Injection Concentrations	49
Statistical Analysis	51
Results	51
Discussion	54
<i>Chapter 1 References</i>	59
<i>Chapter 2 References</i>	72

Abstract

Studies on aggression and status signaling have traditionally focused on the male sex. As a result, the function of female aggression and status signaling is not nearly as thoroughly understood as it is in males. Although testosterone is characteristically known as a “male hormone,” recent evidence has suggested that in many species females develop testosterone linked fighting potential and ornamentation. In this thesis, I report the results from an investigation on the influence of testosterone on female dominance and status signaling. The female American goldfinch is aggressive year-round over limited resources such as food, and at times females are observed to be more aggressive than males. Additionally, American goldfinches have a dynamic bill color that has been correlated to testosterone and has been shown to serve as a status signal in females. Females were placed into dyads consisting of a testosterone treated individual and a control treated individual of similar dominance. Behavioral observations were recorded over a monopolizable food source, allowing us to determine which female was dominant within each dyad. Additionally, bill color was measured using a spectrophotometer before and after treatment. Although testosterone treated females won a majority of the trials that took place, testosterone did not significantly predict the outcome of the dyad trials. Interestingly, wing size was an accurate predictor of winning, with over 80% of the winners having larger wings. Therefore, it may be that wing was so tightly correlated with winning that it overshadowed our ability to detect any influence of testosterone on competitive potential. Testosterone did not significantly influence bill color in this study. Taken together, these findings indicate that wing size may be a more important mediator of aggression than testosterone within this species.

Chapter 1 - Direct selection of female aggression: The adaptive costs, benefits, and mechanisms resulting in female specific behavior

Introduction

Aggression is part of an intricate set of behaviors that widely varies across species. The behavioral definition of aggression has been outlined in multiple ways within scientific literature, and has been studied under many different environmental conditions. In its simplest form, however, animals exhibit aggression when the interests of two individuals do not align, resulting in a conflict (Soma et al., 2008). Visual or auditory displays are often used to resolve conflicts without resorting to physically fighting; however fighting does occur frequently in many species. Indeed, there are many species specific mechanisms underlying aggressive behaviors that allow individuals to survive and compete for resources in specialized ways that maximize their reproductive fitness (Trainor, Kyomen & Marler, 2006). Male aggression has been heavily studied in reproductive contexts that influence evolution and physiological mechanisms. The study of female aggression, on the other hand, has been slow to gain momentum within scientific interest and literature (Stockley & Campbell, 2013).

The scientific community has long considered female traits, including aggression, as a non-adaptive trait that arose due to shared genetics with the male (Lande & Arnold, 1983; Møller et al., 2005). This genetic correlation hypothesis has been a prevailing explanation for female aggression in biology since the formalization of evolutionary thought, when Darwin provided an adaptive explanation for ornamental traits and aggression in males but not females (Darwin, 1872; Tobias, Montgomerie, & Lyon, 2012). Today, the genetic correlation hypothesis is described as the phenomenon when shared genes between the sexes affect traits and behaviors in males and females in a manner that is not sex-linked. This leads to parallel trait and behavioral

expression in the sexes, although females can express reduced versions of male-like traits (Møller et al., 2005). For decades the correlative hypothesis provided the best explanation for elaborate female traits. As a result, the adaptive value and function of female aggression and ornamentation has been long overlooked in scientific research, and only recently has there been a rise in interest in female aggression (Clutton-Brock, 2009; Murphy, 2007; Stankowich & Caro, 2009; Stockley & Bro-Jørgensen, 2011; Tarvin & Murphy, 2012).

Female aggression is often not as conspicuous as it is in males (Stockley & Campbell, 2013). However, female aggression can range from physical fights to threats, and is often elicited over different resources than male aggression. Female aggression extends outside of the usual evolutionary forces posed by sexual selection, with females frequently competing more intensely over ecological resources than males (Cant & Young, 2013; Gill, Alfson & Hau, 2007; Murphy et al., 2009; Rosvall, 2013b). Therefore, aggression in females likely has different costs and benefits than in males, resulting in distinct selection on life history traits (Cant & Young, 2013; Rosvall, 2011a; Tobias, Montgomerie & Lyon, 2012). Such female behaviors are found across the animal kingdom, indicating that aggression is likely heritable, evolutionarily significant, and advantageous to females. Recent interest in female aggression has led to the hypothesis that female aggression is under direct selection in species where such behaviors are present (Rosvall, 2013b).

The evolution of female aggression by direct selection is often a result of broader forms of ecological pressures than just sexual selection. If there is variation in females' ability to acquire resources that enhance survival and reproduction then natural selection may favor aggressive traits regardless of whether the competitive context is related to mate or resource acquisition (Cain & Langmore, 2016). Such forms of selection have been termed social selection,

with sexual selection deemed as a subset of this farther reaching variable (West-Eberhard, 1983). According to social selection, the intensity of resource defense is expected to change depending on the value of the sexual or non-sexual resource, and it is predicted that more aggressive females will have better access to resources (Cain & Langmore, 2016; West-Eberhard, 1983).

Although the scientific community has long neglected the phenomenon of female aggression, female dominance poses a unique adaptive and mechanistic evolutionary system. Although female aggression is prominent amongst many species, such antagonistic behavior is also associated with costs. The costs females face has created interesting adaptations beginning at the genome and culminating in specific social interactions. Specifically, it has been proposed that aggression is more costly to females than males, providing an evolutionary explanation for the fact that female aggression is often not as conspicuous as it is in males. An individual's fitness is directly influenced by their surviving offspring, and females typically have more to lose from the impacts of environmental and physiological stressors due to their higher parental investment. Female aggressive behaviors are therefore constrained by such costs, leading to a large variety of aggressive behaviors that stem from female specific forms of natural selection. However, as female aggression is prevalent within the animal kingdom, we can infer that females are likely to accrue benefits that counteract such costs (Hrdy, 2013). This review will outline female specific adaptive costs and benefits of aggression. Specifically, this review will focus on the adaptive function of a range of female aggressive behaviors such as threat displays and infanticide, as well as the hormonal mechanisms that underlie such behaviors. Studies on female aggression provide untapped insight into the evolution of female behavior, and provide important knowledge on how intrasexual selection shapes behavioral traits.

Behavioral Trade Offs That Regulate Female Aggression

Engaging in agonistic behaviors is often associated with costs, as aggression can involve the risk of injury or death (Campbell, 2013). Trade offs of aggression can be related to energy depletion, decreased parenting ability, decreased attractiveness, decreased immunity, and increased predation risk. When costs of any of these categories are high enough, they can constrain the evolution of aggressive behavior (Briffa & Sneddon, 2006; Cain & Ketterson, 2013). The fact that females incur such costs in a variety of taxa and in a variety of ways suggests that female aggression is under direct selection --and is associated with counterbalancing positive benefits-- rather than arising as a byproduct of genetically encoded male phenotypes (Rosvall, 2011b). Below, major forms of costs imposed on females will be outlined, providing support for female specific forms of natural selection on aggressive behaviors.

Individual Condition Costs

When a behavior such as aggression leads to greater marginal costs for low quality individuals (Grafen, 1987), the behavior is known to be condition dependent. Condition dependent behaviors are likely to evolve because only the highest quality individuals can overcome the costs associated with them (Price, Schluter & Heckman, 1993). If female aggression is condition dependent, then variation in female aggressiveness should map onto an individual's available energy reserves and health. Variation in behaviors is the raw material upon which selection acts, supporting the idea that female aggression is indeed under direct selection (Rosvall, 2011b). The fact that female aggression tends to be highly costly leads to the evolution of diverse forms of the behavior in many species.

Although it seems that female aggression would facilitate resource acquisition through a greater likelihood of competitive success, the relationship between female aggression and

resource holding appears to be more complicated. In high quality, uniform habitats aggressive female superb fairy wrens (*Malurus cyaneus*), were shown to produce more offspring (Cain, Cockburn & Langmore, 2015). Cain, Cockburn and Langmore tested whether the costs of female aggression can be altered by resource availability. Resource defense theory postulates that the benefits of aggression should increase when a territory is of more variable quality and there is a lower number of competitors (Venter, Grant & Carrigan, 2005). However, Cain, Cockburn and Langmore (2015) found that females in lower quality habitats had higher intensities of aggressive response than what was found in high quality habitats. Additionally, these highly aggressive females in low quality habitats had lower reproductive success than less aggressive females in low quality habitats and more aggressive females in high quality habitats. As a result, female aggression may be detrimental in some contexts and not others depending on resource availability. If there is limited food in an area, it may be more beneficial for females to trade off defense for food acquisition. However, if females utilize aggression to occupy a higher quality territory, then the trade off between energy investment and defense is less (Cain & Langmore, 2016).

In contrast to resource defense theory, the “desperado effect” of contest theory predicts that when the costs of losing to an intruder are very high for low quality females that are unlikely to acquire another territory, females will increase aggression despite the potential associated costs (Cain & Langmore, 2016). Low levels of resource availability may therefore alter the rules of female contests, affecting the relative costs of aggressive behavior. This theory may provide an explanation for the behavior seen above in superb fairy wrens. Such an idea has been tested in female jumping spiders (*Phidippus clarus*) and compared to males. Female-female contests resulted in higher rates of injury and death than male-male contests, indicating an elevated cost

associated with female aggression and resource acquisition. Specifically, low quality females less likely to acquire territories in the future had a higher rate of aggression despite the potentially deadly costs (Elias et al., 2010).

Both the case of the superb fairy wrens and the jumping spiders illustrate that the costs of female aggression in terms of resource acquisition can vary depending on the quality of the individual and the relative value of the resource. If females are of high quality, then they can invest in more aggression because they have the available energy reserves. However, if females are of low quality they may also invest in aggression because the cost of not obtaining a resource is higher, and the resources are essential to their survival. Therefore, the cost of female aggression in terms of resource acquisition seems to be heavily dependent on an individual's condition, supporting the idea that female aggression is indeed variable and condition dependent.

The previous two examples illustrate that individual condition can influence how females utilize aggression to acquire resources, but availability of resources can directly influence an individual's condition and therefore their aggressive behavior. Specifically, condition is defined as an individual's ability to meet its energy demands through the attainment of resources (Rowe & Houle, 1996). In tree swallows (*Tachycineta bicolor*) it was found that more aggressive females have a higher body mass, indicating that smaller females do not have the energy reserves to compensate for the energetic cost of maintaining aggressive behavior (Rosvall, 2011b; Rosvall, 2010). Tree swallow aggression is characterized by rapid aerial chases and dive bombs illustrating how energetically taxing elevated aggression can be. It is therefore likely that larger females have the available energy reserves to expend on aggression, where smaller females do not because they cannot withstand the costs of such behaviors. Such reserves may allow females

to have higher endurance during competition or just participate in energetically costly behaviors in general (Rosvall, 2011b).

Equally as important to individual condition as resource acquisition and energy reserves, is the ability to evade and escape from predators. Aggression has been correlated to decreased overall survivorship and increased mortality because aggressive behavior can often make individuals more conspicuous to predators (Marler & Moore, 1988). Although larger tree swallows were able to sustain the energetic costs of aggression more efficiently than smaller females, they also had a larger carrying load relative to their wing length (i.e. greater wing loading). This additional cost was found to inhibit larger females' flight ability. These larger more aggressive females presumably have an increased likelihood of being predated, as they showed decreased flight speed. Although the study did not take into account maneuverability, speed often plays an important role in escaping predators (Rosvall, 2011).

Intrasexual aggression can also have negative effects on condition due to the potential for injury when females attempt to reject a male, resulting in an aggressive conflict. In the Lake Eyre dragon (*Ctenophorus maculosus*), males use forced copulation as a mating strategy. Although more aggressive females may prevent unwanted copulations, posing a potential benefit to their behavior, attacks by rejected males also cause more aggressive individuals to suffer injuries. In a study that observed such ramifications, several females that did not cooperate were observed to have open wounds, and one female died after an unusually fierce interaction. On many instances of forced copulations, researchers observed successful attacks by hawks (*Accipiter*) and Gould's monitor lizards (*Varanus Gouldii*). The researchers concluded that when females were more likely to fight back against a male's copulation attempts, the conflict made them more conspicuous to predators, increasing the likelihood of predation (Olsson, 1995).

Reproductive Costs of Aggression

Due to females' larger parental investment, aggression often has a direct trade off with offspring production, because aggressive behaviors may divert energy away from rearing and producing future generations (Campbell, 1999; Packer et al., 1995). The cost of female aggression on offspring production and rearing has been tested in the tree swallow (*Tachycineta bicolor*), where female aggression serves to obtain nesting cavities necessary for reproduction (Rosvall, 2008; Rosvall, 2011b). Females were found to suffer the costs of aggression in terms of the quality of their offspring rather than the quantity. In other words, more aggressive females produced nestlings of lower mass, although they did not produce fewer nestlings over all (Rosvall, 2011b). Interestingly, larger female mothers were more aggressive, but had smaller offspring than what would be expected for their size. Despite the fact that Rosvall (2010) did not monitor the nestlings into adulthood, previous studies have found that smaller nestlings are less likely to survive and reproduce when they come to reproductive age (Alatalo & Lundberg, 1986; Tinbergen & Boerlijst, 1990). This finding indicates that females have a significant fitness cost associated with aggressive behavior that directly influences the perpetuation of their genes into subsequent generations (Rosvall, 2010).

The costs of female aggression on offspring can occur both pre and post hatch for nestlings. For example, in an experiment looking at the effects of maternal aggression on offspring, the negative effects of maternal aggression were most apparent when offspring were both conceived and fully reared by an aggressive mother (Rosvall, 2010). In terms of pre hatch costs associated with aggression, there may be a trade off between female incubation and aggressive behavior. Female tree swallows (*Tachycineta bicolor*) that have experimentally elevated testosterone and high levels of aggression decreased the amount of time they spent incubating their nests and had decreased hatching success (Rosvall, 2010). A similar conclusion

was found in dark eyed juncos (*Junco hyemalis*)(Cain & Ketterson, 2013). Both defense of resources against same sex competitors and female parental effort are critical to the reproductive success of female tree swallows in their short breeding period (Rosvall, 2013a). However, these findings suggest that when females tip the balance of behavior towards aggression and away from parenting, their overall fitness suffers as low nest temperatures have been shown to reduce offspring growth and development (Perez et al., 2008). Females therefore have to trade off their time spent caring for eggs for participating in aggressive behaviors.

As mentioned above, maternal aggression may also mediate post hatch costs for nestlings. For example, the amount of food an offspring receives is the most important predictor of offspring growth and development (Altmann & Alberts, 2005; Nowicki, Searcy & Peters, 2002; Quinney, Hussel & Ankney, 1986), and evidence suggests that aggressive females feed their offspring less (Rosvall, 2010). These studies explicitly illustrate a negative relationship between female aggression and offspring provisioning. Interestingly, male provisioning does not seem to counter the costs of female aggression on offspring production post hatching, indicating an asymmetry in the costs associated with male aggression and female aggression. Specifically, if females are aggressive and do not provision their offspring, it is likely their offspring will not be as successful. However, males do not bear this same cost. The importance of maternal care and the costs associated with female aggression are therefore more pertinent in determining offspring success, and the persistence of female aggression throughout generations (Rosvall, 2009).

The examples outlined above provide evidence for the substantial reproductive costs associated with female aggressive behavior. Specifically, more aggressive females divert energy away from offspring production, producing smaller offspring that are less likely to survive

(Alatalo & Lundberg, 1986; Rosvall, 2010; Tinbergen & Boerlijst, 1990). Additionally more aggressive females spend less time taking care of offspring pre and post hatch, limiting individual's survival potential (Cain & Ketterson, 2013; Perez et al., 2008; Rosvall, 2010). The fact that these costs substantially influence overall fitness, and males likely do not bear the same costs, supports the idea that female aggression is favored by direct selection.

Adaptive Benefits of Female Aggression

In contrast to the correlative hypothesis, selection should result in female aggression if some variance in fitness is accounted for by variance in competitive ability (Rowe & Houle, 1996). The fact that a variety of aggressive behaviors are seen across many taxa, despite the costs outlined above, indicates that aggression likely provides some evolutionary benefit that is female specific (Tobias, Montgomerie & Lyon, 2012). It is generally the case that female mating success and the number of offspring they produce is dependent on the quality of both their sexual and non-sexual resources rather than the quantity (Altmann, 1997; Petrie, 1983). Although the payoff for female competition may be lower than males, it is likely still beneficial for selection to favor female competition and aggression, as it can help them attain better resources which will ultimately increase their fitness (Rosvall, 2011a). The following section will outline the adaptive value of female aggression and the benefits that it can provide for an individual's fitness, ultimately specifying evidence that female aggression is indeed favored by natural and sexual selection in many species.

Individual Survival

As illustrated above, aggression in females is often mediated by the availability of resources that influence survival. However, unlike the examples previously outlined, aggression can often allow individuals to acquire more resources. Specifically, female aggression amongst

certain species may increase when food is rare, allowing more aggressive females to gain access to highly contested resources. The relationship between aggression and food availability was explored in female collared lizards (*Crotaphytus collaris*). The frequency of female aggression was found to be higher in higher density populations where resources were scarce (Baird & Sloan, 2003). Similarly, in female Soay sheep aggressive interactions increased when local population density was high, indicating that female aggression is related to resource availability (Robinson & Kruuk, 2011).

Further supporting the idea that the benefits of female aggression are dependent on resource abundance is the fact that when resources are not limited, aggression between females may decline. Ueda and Kidokoro (2002) found that when female flies (*Drosophila melanogaster*) are exposed to an abundance of food resources, they show lower levels of aggression. This is likely because aggression allows individuals to acquire sought after, limited resources (Grant, Gaboury & Levitt, 2000). As a result, the benefits of female aggression are likely to only be large enough to counter the costs outlined in the previous section when resources are limited. This provides evidence that the benefits of female aggression can vary depending on environmental conditions.

The direct benefits of obtaining resources through aggressive behaviors has been heavily studied in primates, where the ability to gain resources is often directly related to the rank of an individual in a hierarchical social system. Female chimpanzees (*Pan troglodytes*) communicate aggression via pants, grunts, and agonistic interactions, which serve as reliable indicators of dominance. In wild female chimpanzees, where such forms of female aggression usually occur over contested food resources, higher ranked females were found to have a higher diet quality

and spent less time foraging. Subordinate females often faced periods of “food scarcity” due to aggressive interactions resulting in food competition.

“Food scarcity” may be a result of subordinates and their inability to maintain a territory (Murray, Eberly, and Pusey, 2006). Subordinates have an increased likelihood of occupying lower quality habitats as a result of avoiding dominant females. Dominant females therefore outcompete subordinate females, gaining greater access to contested resources (Murray, Mane & Pusey, 2007; Kahlenberg, Thompson, & Wrangham, 2008). In support of the conclusion that female aggression is linked to food resource acquisition, Pusey et al. (2005) found that dominant female chimpanzees tend to weigh more and have a more consistent body mass than subordinate females. Furthermore, dominant aggressive females were found to have more offspring that mature more quickly than less aggressive females (Pusey, Williams & Goodall, 1997). As a result, female aggression provides the advantage of higher mass through resource acquisition, which translates into inclusive fitness benefits.

In some species, such as the chacma Baboon (*Papio cynocephalus ursinus*), female aggression has not been shown to be related to food resources (Ron, Henzi, & Motro, 1996). In contrast to the cost of aggression increasing the chances of predation described above, the risk of predation and competition over safe locations within a group seems to play a more important role in determining female aggressive behavior and overall condition within the chacma baboon. Through observations of intense female aggression, Ron, Henzi, and Motro (1996) found no significant correlation between time spent foraging and dominance. However, the researchers did find a positive correlation between dominance and centrality within the troop, suggesting that more aggressive females were better protected from predation. Dominance was also related to mortality with only lower ranked females dying within the time period the troops were observed.

As a result, rather than aggression causing individuals to be more conspicuous to predators, it allows female baboons to secure a safer location within their social system. This pattern spans taxa with the frequency of female aggression in eiders (*Somateria mollissima*) significantly predicting central location within the coalitions rather than structural size, body weight, age, and clutch size (Ost, Jaatinen & Steele, 2007). The individual adaptive benefit of female aggression therefore seems to be wide and far reaching across taxa, varying depending on the life history of each species.

Aggression, access to mates, and mating success

From the conclusion above stating that female aggression is likely to increase when population density increases, one can deduce that it is also expected that female competition and aggression is greater in species where the operational sex ratio (OSR) is female biased. This is likely because there is a surplus of females, with a limited pool of available males to reproduce with (Eens & Pinxton, 2000). Female aggression can therefore provide the benefit of securing access to mates.

In some species, female aggression has been correlated to the number of available males within a population. In the two-spotted goby (*Gobiussculus flavescens*) female competition superseded male competition when the number of males in the population declined, creating a rapid sex role reversal. As a result, more aggressive females would likely be able to gain more mates through intrasexual competitive interactions, as the number of males dwindled (Forsgren et al., 2004). Similar findings have been found in Roosevelt Elk (*Cervus elaphus roosevelti*), where females also vie for male mates in a mixed sex group when there is a lower proportion of males (Weckerly, Ricca & Meyer, 2001). Interestingly, in a study conducted on sand gobies (*Pomatoschistus minutus*) the authors tested the potential of the OSR and population density to

elicit female aggression, but found that only a female biased OSR increased female aggression, not population density (Kvarnemo, Forsgren & Magnhagen, 1995). In this particular species, female aggression was not found to be influenced by non-sexual resource availability as seen above, rather only the sexual resource of available mates. These studies illustrate that in terms of available mates, it is the ratio of males to females that influences female aggression rather than the overall size of the population.

It is possible that females do not compete for the number of mates (i.e. number of copulations), but rather the benefits their mates provide (Price, Schluter & Heckman, 1993; Zuk et al., 1990). One such direct benefit is parental care. Females that prevent the reproduction of other females through aggressive means may increase their own overall reproductive success by securing undivided parental care for their offspring (Sagsvold & Lifjeld, 1994). This can lead to the maintenance of certain mating systems. For example, in facultatively polygynous European starlings (*Sturnus vulgaris*) females that elicited more aggressive attacks to potential female competitors were more likely to maintain a monogamous relationship with their mate (Sandell, 1998). A similar pattern has been observed in the Caribbean cleaning goby (*Elacatinus evelyna*). Female gobies that were more active at mate guarding were more likely to mate with larger males, which typically provide more parental care (Takegaki & Nakazono; Whiteman & Cote, 2003).

When males do not provide any direct benefits such as parenting, females may also elicit aggression when there is competition for indirect benefits, such as viability genes that may increase offspring survival. Leks are the ideal system to study female competition over indirect benefits because males provide absolutely no direct benefits to females and offspring. In the topi antelope (*Damaliscus lunatus*) females exhibit higher rates of aggression at the center of the

lekking arena where preferred males are located. Interestingly, resources and predation risk in the lekking area were not found to be an important predictor of female aggression (Bro-Jorgensen, 2002). Female aggression in the topi antelope therefore likely serves to solely secure the genes of high quality males for their offspring. Although not as straightforward, similar patterns have been observed in the non-lekking species, White's skink (*Egernia whitii*). Female aggression was found to be related to promiscuity, and thus the indirect genetic benefits gained from extra pair copulations (While, Sinn & Wapstra, 2009).

Mating success of females may not be determined by mates themselves that they choose, but rather the nesting sites they acquire through aggressive means (LeBas, 2006). In the common goby (*Pomatoschistus microps*), males provide exclusive parental care. However, female-female competitive behaviors such as pushing, chasing, or displaying was shown to be negatively correlated to the number of available nesting sites, rather than a decrease in potential mates (Borg, Forsgren & Magnhagen, 2002). Similarly, when the number of available nesting cavities for a tree swallow (*Tachycineta bicolor*) population was experimentally diminished, Rosvall (2008) observed that more aggressive females were more likely to obtain a nesting cavity. This is particularly important in this species because females that do not obtain a nesting cavity do not have alternative options for reproduction (Rosvall, 2011b; Whittingham & Dunn, 2001). Females can therefore elicit aggression to obtain physical resources that affect their mating success.

Female aggression can manifest itself in extreme ways in order to gain a mating advantage. Within community living species, female aggression includes physiological suppression of subordinate competitors so they physically cannot mate. Meerkat (*Suricata suricatta*) social groups are characterized by a single dominant female that monopolizes reproduction, and produces the majority of offspring that survive. The dominant female elicits

aggression towards subordinate females resulting in elevated glucocorticoid adrenal hormone levels, reduced conception rates, and increased abortion rates. Interestingly, this sort of aggression seems to only occur when the dominant female is pregnant, targeting females that pose the greatest threat to her offspring such as older, pregnant, and distantly related females. It is therefore likely that this period of aggression elicited by dominant females serves to compromise the fertility of other females while the dominant female is attempting to breed (Young et al., 2006). Such forms of extreme aggression are therefore modulated to temporally maximize the benefit of aggression over the cost, allowing aggressive individuals to gain extraordinary reproductive benefits.

Another extreme manifestation of female aggression is the use of female induced infanticide to increase one's chances of mating. Female house sparrows have been observed committing infanticide when taking over a nest of a previous female owner. Veiga (2004) suggested that female house sparrows were initiating their aggression in search of mates. In the Black-Billed magpie (*Pica pica*), female non-parental infanticide was attributed to the attempt of neighboring nests to gain access to more valuable territory (with a water pool) and future breeding sites. The particular population where infanticide was observed was one of the most densely populated magpie populations studied, causing the authors to conclude that in dense populations territorial expansion would be adaptive for future breeding attempts (Lee et al., 2011). The large benefits associated with such severe forms of female aggression, such as complete monopolization on community reproduction or territory expansion, provide evidence that female aggression can be exceptionally beneficial. As a result, it is likely that these behaviors evolved via species specific forms of direct selection on females.

Aggression and Offspring Survival

Fitness, in its simplest terms, is defined as the ability of an organism to survive and reproduce (Orr, 2009). Therefore, female aggression in the context of protecting one's offspring and promoting their longevity can be functionally adaptive. Although aggression can be highly costly to offspring, it is not likely that aggressive behaviors would persist in a population without some fitness benefits.

It is important to note that similar to the costs of female aggression, the benefits of such behavior on offspring survival can vary from season to season depending on external factors. Cain and Ketterson (2012) found that more aggressive dark eyed junco's (*Junco hyemalis*) were more likely to produce a successful nest. However, the research group later found that more aggressive females spent less time brooding their nests. This has been shown to be a detrimental fitness cost to aggressive females, as it decreases the viability of offspring. However, more aggressive females also fed their offspring more often. The overall consequences of aggression, measured by egg mass, varied from year to year. One year there was a positive correlation between egg mass and aggression, and another there was a negative correlation. These findings suggest that aggression does provide a large benefit to offspring production, however that benefit is inconsistent (Cain & Ketterson, 2013).

As established above, females have been shown to moderate the costs of aggression temporally depending on resource availability. Additionally, females can also change their behavior based on the likelihood of their offspring survival and the stage of their offspring's development. Specifically, female aggression may vary depending on the degree to which male mates provide direct benefits to females that assist in offspring survival. If males provide offspring care, it is less likely that females will be aggressive during offspring upbringing because they have the benefit of paternal protection and assistance. In contrast, if it is just the

mother taking care of the offspring females will likely be more aggressive after offspring birth when they are highly vulnerable. This pattern is observed through the different life histories of mammals and birds (Rosvall, 2011).

In many bird species female aggression is at its highest just before females lay their eggs and declines when offspring are being reared. Female aggression in the red-necked grebe (*Podiceps grisegena*) has been shown to decline after nest establishment and the beginning of laying regardless of the surrounding population density (Klatt, Nuechterlein & Buitron, 2004). In an analogous study comparing the aggression of two bird species, the hen harrier (*Circus cyaneus*) and the Mantague's harrier (*Circus pygargus*), both species were found to be more aggressive in the early season and most of the aggression was intraspecific. The authors concluded that this temporal pattern of aggression is likely a product of females competing for access to mates that will provide their offspring with care as described previously (Garcia & Arroyo, 2002).

In contrast, females in many mammal species are most aggressive when they are rearing their offspring because males do not provide direct benefits such as protection and food for offspring. In banded armadillos (*Dasypus novemcinctus*), females were found to exhibit aggressive behaviors towards juveniles and other females during pregnancy and lactation (McDonough, 1994). McDonough (1994) suggested that these aggressive behaviors were a result of females providing the sole protection of current litters, facilitating dispersal of previous years litters to decrease potential competition amongst offspring. Intrasexual aggression between grey seal females (*Halichoerus grypus*) was related to the location of the female's pup she was rearing. Females did not show the same pattern of aggression towards males. Additionally, female grey seals were less aggressive during the end of lactation when weaning occurs. Female

aggression in mammals is likely temporally adapted to protect their offspring when they are most vulnerable, whereas female aggression in birds most often occurs during the rearing phase when females and offspring do not have extra assistance from fathers (Boness, Anderson & Cox, 1982).

As described above, there are adaptive benefits when aggressive females induce infanticide to gain mating opportunities. However, females may also utilize aggression to fend off infanticidal threats of their own young, thus increasing the likelihood of their offspring survival and their own fitness. In northern elephant seals (*Mirounga Angustirostris*), Christenson and Le Boef (1978) found that female aggression increases after birth, and was most extreme in smaller areas where interaction with alien females was common. Female aggression in this species is correlated to proximity of potential killers indicating the adaptive value of intrasexual female aggression to decline infanticide. Female aggression can accordingly provide benefits both to enact and prevent infanticide, increasing the likelihood of an individual producing successful offspring.

According to the correlative hypothesis, female aggression resulting from similar genomes with males does not provide any positive selective benefit (Lande & Arnold, 1983; Møller et al., 2005). However, the cases outlined above illustrate some of the evolutionary benefits of female aggression. Although female aggression can negatively impact offspring survival in some aspects, it can also ensure offspring survival in others, thus favoring maintenance of the behavior within females of those species. It is therefore likely that female aggression is not solely a result of correlative genetic inheritance, and is rather under direct female specific selection.

Mechanisms Underlying the Regulation of Aggression

The balance between female hormones and the resulting phenotypic and behavioral variations are the result of the costs and benefits associated with the viability, fecundity, and selection of hormone-induced characteristics. Additionally, hormones are now largely recognized as mediators of life history trade offs. Specifically, hormones regulate transitions between life history stages, serve as communicators of environmental information, and can have pleiotropic antagonistic effects that induce different trade offs amongst individuals (Gill, Alfson & Hau, 2007).

As a result, hormones are essential to understanding the adaptive costs and benefits associated with female aggressive behavior. Although testosterone has accurately formed the reputation of controlling aggression, there are other hormonal mediators that play a large, if not more meaningful role in the modulation of female aggression. Similar to the behavioral costs and benefits outlined above, hormonal mechanisms regulating female aggression are seen in a variety of forms across taxa.

Dehydroepiandrosterone (DHEA)

Research investigating the neuroendocrinology of aggression has long been focused on the reception of testosterone and other gonadal hormones in the brain. Although this research does pose important scientific merit, recent research has been uncovering important alternatives (Soma et al., 2008). DHEA is one such alternative that is being explored as a possible mediator of aggressive behavior (Cloutier et al., 1997). DHEA is a steroid precursor that can be quickly metabolized into androgens and estrogens within target tissue where the necessary amount of steroidogenic enzymes are present (Mo et al., 2004). Although an intracellular receptor specific to DHEA has not yet been isolated and there is little evidence that one exists at all, DHEA has

been found to bind with low affinity to androgen, progesterone, estrogen, glucocorticoid, and mineralocorticoid receptors (Soma et al., 2008; Widstrom & Dillon, 2004).

Although many avian species exhibit distinct yearly breeding and non-breeding patterns of aggression, competitive behaviors in species that are characterized by year round aggression may be controlled independently of gonadal hormones such as testosterone (Goodson et al., 2005; Soma & Wingfield, 1999). This is because most birds have regressed gonads outside of the breeding season, and therefore likely do not secrete large amounts of sex hormones to regulate aggression. In the spotted antbird (*Hylophylax n. naeviioides*), DHEA is produced in the adrenal gland, making it a possible candidate for eliciting female aggression in the non-breeding season. Spotted antbirds make an ideal species to study female aggression mediating hormonal alternatives because both sexes defend territories year round. Using simulated territorial intrusions with live experimental species-specific decoys, Hau, Stoddard and Soma (2004) tested if females were aggressive during the non-breeding season and if DHEA was present within plasma at that time. Females were very aggressive, specifically to other females, and had higher levels of plasma DHEA than testosterone and estrogen. Furthermore, the same results in terms of DHEA concentrations were found for captive birds, and testosterone levels were not detectable whatsoever. The authors concluded that DHEA may serve as a precursor to sex steroids in order to modulate year round aggression (Hau, Stoddard & Soma, 2004).

Melatonin may be an important stimulator of DHEA production, and thus DHEA induced aggression. In both female Syrian hamsters (*Mesocricetus auratus*) and Siberian hamsters (*Phodopus sungorus*) longer duration of melatonin secretion, characteristic of shorter day endocrine patterns, causes an increase in aggression (Demas et al., 2004; Fleming et al., 1988). This is particularly interesting because during short day periods both species have regressed

gonads, and gonadectomy does not reduce circulating DHEA concentrations in Syrian hamsters (Fleming et al., 1988; Pieper & Lobocki, 2000). Although the effects of melatonin on hamster adrenals has not yet been investigated, in mice administration of melatonin in vitro has been shown to increase DHEA secretion (Haus et al., 1996). Despite the fact that more studies need to look for a connection between DHEA and melatonin, melatonin may mediate non-reproductive aggression by upregulating DHEA secretion (Soma et al., 2008).

DHEA has also been explored as an important mediator of aggression in human females. In females 15 to 17 years of age, individuals with conduct disorder scored higher on an aggression questionnaire than controls, and had higher DHEA and testosterone levels (Pajer et al., 2006). A study looking at females with congenital adrenal hyperplasia attempted to isolate DHEA and its link to aggression in female humans. This disease was chosen because females with congenital adrenal hyperplasia (CAH) have elevated plasma DHEA levels. Berenbaum and Resnick (1997) found that CAH individuals were more aggressive than controls. It is therefore likely that DHEA plays an important role in modulating female human aggression to some extent.

Progesterone

There is evidence indicating that progesterone may play a similar role in modulating female aggression as testosterone does in males, but through an inverse relationship. Specifically, declines in progesterone may lead to increases in aggressive behavior (Wingfield et al., 1990; Goymann et al., 2008). Goymann et al., (2008) used female black coucals (*Centropus grillii*) to study progesterone modulation of female aggression. Although black coucals are a sex role reversal species and females compete over males that raise offspring, males have higher levels of testosterone than females reflecting species with conventional sex roles. Additionally,

GnRH challenges did not raise female testosterone levels, indicating testosterone may not be the hormone responsible for female territoriality behaviors.

By evoking female aggressive behavior through the use of simulated territorial intrusions and measuring hormone blood levels, Goymann et al. (2008) were able to identify progesterone as the primary hormone affected by such interactions. Specifically, females challenged with the stimulus had significantly lower levels of progesterone than control individuals, suggesting that short term aggressive interactions led to a decline in circulating progesterone levels. To further establish the link between a decrease in progesterone and female aggression, progesterone or control implants were administered to female black coucals. Three to four days after implantation, simulated territorial intrusions were re-introduced to females. Interestingly, progesterone treated birds were less responsive to the decoys (Goymann et al., 2008).

Similar results were found in female California mice (*Peromyscus californicus*). Both female and male California mice show territorial behavior, however like the black coucal there is little evidence indicating that male and female hormones act in the same way to modulate aggressive behaviors. By conducting trials utilizing intruders and then measuring individuals circulating hormone levels, Davis and Marler (2003) found that female progesterone decreased as a result of aggressive behaviors. Interestingly, no other hormone measured (estradiol, corticosterone, and testosterone) showed any change in concentration.

The negative relationship between progesterone and female aggression is not consistent across taxa. In female Galapagos marine iguanas (*Amblyrhynchus cristatus*), the opposite correlation between progesterone and aggression was observed. Progesterone levels increased in female Galapagos marine iguanas after territory defence (Rubenstein & Wikelski, 2005). Furthermore, in other species such as the female song sparrow (*Melospiza melodia*) progesterone

levels showed no change after simulated territorial intrusions (Elekonich & Wingfield, 2000). The decline of progesterone may therefore serve to fine tune aggressive behaviors in some species, but not others.

The exact mechanism in which progesterone influences female aggression is not fully understood and likely varies amongst species. Goymann et al. (2008) suggested that progesterone and testosterone are dual players in hormone mediated aggressive behaviors. Such a hypothesis was tested in female rats (Albert, Jonik & Walsh, 1992). Females were given hormonal implants containing estradiol, testosterone, and progesterone or just estradiol and testosterone to mimic circulating levels during the last week of pregnancy. Females with implants of estradiol and testosterone alone showed higher rates of aggression than females with these hormones and progesterone. One week later, estradiol and testosterone implants were replaced with low dosage versions and the progesterone implant was removed to mimic the level of hormones characteristic of parturition. After the low dosage manipulation, females that previously had progesterone implants were much more aggressive than those that did not. These results suggest that progesterone acts as a mediator of female aggression throughout the oestrous cycle. Clearly there is a complex interaction between the sex hormones involved in aggression in this particularly species, which may allow females to maintain the proper sex hormone levels in the oestrous state while still being capable of responding to social challenges, and the costs aggression poses on individuals (Albert, Jonik & Walsh, 1992).

Estrogen

Unlike progesterone, estrogen seems to follow the same pattern as testosterone in controlling female aggression. In fact both seem to be somewhat connected in their ability to modulate female aggression within some species (Simon & Gandelman, 1978). Estradiol and

estrogenic metabolites themselves have also been shown to be important in modulating male typical behavior (Ogawa et al., 1997). As a result, despite its possible connection to testosterone, estrogen may in fact be more important than androgens such as testosterone in females (Adkins-Regan, 1999).

In a study that looked at neonatal estrogenization in female mice, females were given estradiol benzoate on the day of birth and then gonadectomized as adults. Over ninety percent of treated females showed aggressive behaviors as adults, whereas only twenty-five percent of control females elicited the same behavior. The authors concluded that the administration of estrogen to young mice promotes the differentiation of androgen mediated mechanisms of aggression (Edwards & Herndon, 1970). However, other studies on prairie voles (*Microtus ochrogaster*) and golden hamsters (*Mesocricetus auratus*) have concluded that administration of estradiol does not influence female aggression (Bowler, Cushing & Carter, 2002; Edwards & Burge, 1971; Floody & Pfaff, 1977).

In the sex role-reversed spotted sandpiper (*Actitis macularia*), females are subjected to high degrees of intrasexual competition and exhibit typical androgen mediated aggressive behaviors such as territory defense. Additionally, this species is sequential polyandrous with females seeking out additional mates after the first clutch. Despite this sex role reversal in behavior, the circulating hormonal concentrations of male and female spotted sandpipers are reflective of the classic male/female testosterone levels; males have higher circulating testosterone concentrations than females. The spotted sandpiper, like the black coucal described earlier, therefore provides an interesting model to investigate hormonal mechanistic controls of female aggression (Fivizzani & Oring, 1986). In their study Fivizzani and Oring captured and collected blood samples from nesting spotted sandpipers. Pre-incubating males had much higher

circulating levels of testosterone than females. In contrast, estradiol levels were significantly higher in females than males. Fivizzani and Oring hypothesized that this difference may be a result of enhanced receptivity of female neural centers to moderate levels of androgens or estrogens. Additionally, differing patterns of enzymatic conversion of hormones in the brain may also be responsible. It is thus likely that male and female spotted sandpipers have altered action in neural centers relating to the conversion of testosterone. Estradiol is the product of testosterone being converted via the aromatase enzyme. The distribution of the aromatase enzyme varies between species; in amphibians and birds it is found throughout the brain, and in mammals it is mainly centralized to the hypothalamus and limbic brain regions (Balthazart et al., 1990; Naftolin, Horvath & Balthazart, 2001; Shen et al., 1995; Trainor, Kyomen & Marler, 2006). The fact that females differ in their neural response to hormones mediating aggression, such as progesterone, indicates that female aggression is likely under direct selection that has resulted in female specific forms of endocrine function.

Testosterone

Although there are important alternative hormones to consider when investigating female aggression, testosterone is the most heavily studied and has been shown to play an important role in some species. In fact, testosterone was one of the first physiological mechanisms discovered to mediate aggression (Trainor, Kyomen & Marler, 2006). Testosterone is produced via the hypothalamus pituitary axis, also known as the reproductive axis. The hypothalamus releases GnRH to stimulate the pituitary. The pituitary then secretes luteinizing hormone which signals the gonads to secrete testosterone and other sex hormones (Schoech et al., 1998). Female circulating testosterone levels are specifically dependent on developing follicles (Goymann & Wingfield, 2014). Furthermore, as mentioned in the previous section, testosterone is a precursor

of estradiol which is an essential hormone in female reproductive physiology. Thus, testosterone and estradiol are likely to be intertwined in their modulation of female aggression (Bentley, 1998).

Despite this possible connection between testosterone and other endocrine factors, many studies have looked at the sole effect of testosterone on female aggression. In a cooperatively breeding cichlid fish (*Neolamprologus pulcher*), Desjardins et al. (2005) presented males and females with an intruder of their respective sex, allowed them to interact, and then took blood samples in order to measure testosterone, 11-ketotestosterone, and estradiol levels. Resident experimental females that interacted with the intruder showed both elevated testosterone and 11-ketotestosterone, whereas males only showed elevated 11-ketotestosterone when compared to controls. Additionally, females had higher levels of aggression and androgens than males. Neither males nor females showed changes in estradiol suggesting that the relationship between testosterone and estrogen is not as an important factor in determining aggressive behaviors within cichlids (Desjardins et al., 2005).

The connection between female dominance and testosterone is supported by the fact that circulating testosterone has been shown to peak at times of the year when females are observed to be most aggressive. Gill, Alfson and Hau (2007) investigated the relationship between testosterone, aggression, and breeding stage in female buff breasted wrens (*Thryothorus leucotis*). Buff breasted wrens are a neotropical bird that exhibit territorial aggression throughout the year. Females were more aggressive during the pre-breeding period to intruder females and during the breeding period to intruder pairs. Females thus altered their aggressive behaviors towards individuals that posed the highest risk depending on their breeding stage. In the breeding season, females that responded aggressively to intruder females had higher circulating

testosterone than unchallenged females, and females that responded aggressively to intruder pairs had intermediate circulating testosterone levels that fell between unchallenged female testosterone levels and those that were challenged by a single female. Interestingly, aggressive responses to intruder pairs during the breeding period were not associated with elevated testosterone. Testosterone may therefore assist females during the pre-breeding season, but not during the breeding season when other mechanisms are more important. Similar to the conclusions drawn from the costs and benefits of aggression outlined above, testosterone may only influence female aggression during specific temporal contexts when it is most advantageous (Gill, Alfson & Hau, 2007).

There is little evidence supporting the idea that changes in circulating testosterone itself have large effects on testosterone mediated traits in females across vertebrate taxa (French et al., 2013; Goymann & Wingfield, 2014). In mammals where females exhibit highly aggressive behaviors, such as the spotted hyena (*Crocuta crocuta*), current research suggests that organizational effects of testosterone influencing "masculinized" behaviors play a more important role than activational effects. These organizational effects likely lead to more androgen receptors or a higher sensitivity of such receptors, and ultimately higher conversion rates of testosterone (French et al., 2013). In such species where testosterone does play a role in female trait development, local sensitivity resulting from organizational differences may be largely responsible for female testosterone regulation, rather than circulating concentrations of plasma testosterone (Voigt & Goymann, 2007). The difference between male and female sensitivity to testosterone indicate that female modulation of aggression by testosterone is likely subjected to direct selection, that results in different adaptive mechanisms controlling aggressive behavior.

Genetic control of aggression

In terms of genetics, aggression is a result of many genes that are sensitive to the environment. High heritability estimates for agonistic behavior have been observed in some species, indicating that female aggression may be not only linked to condition, parenting, and hormonal factors, but also an individual's personality (Anholt & Mackay, 2012). Personality is a behavioral characteristic of a particular individual that results in steady patterns of behavior that are temporally and situationally maintained (Saetre et al., 2006).

The heritability and genetic effects influencing aggression were demonstrated in vervet monkeys (*Chlorocebus pygerythrus*) using the Intruder Challenge Test which measures impulsivity and aggressiveness (Fairbanks et al., 2004). There were significant genetic correlations for both impulsive approach and aggression with no significant influence of maternal environment between adolescents and adults. Additionally, impulsive approach and aggression had high correlation and appear to be genetically linked. This study is a good example illustrating the strong likelihood that there are susceptible genetic loci controlling aggressive behavior (Fairbanks et al., 2004).

Complex personality phenotypes can be influenced by a multitude of environmental factors and genes. Domestic dogs are a good species to investigate the genetic basis of such aggressive behaviors (Bouchard, 1994; Saetre et al., 2006) because many modern breeds of dogs display specific behavioral differences, and purebred breeds are partially inbred genetic isolates as a result of narrow bottlenecks (Hart & Miller, 1985; Ostrander & Kruglyak, 2000). Out of 16 behavioral traits tested, almost all behaviors were genetically related to others. This provides evidence that there may be shared genetics underlying most behavioral responses in dogs. However, the one exception to this was aggression which was only weakly correlated to other behavioral traits. The genetic underpinnings of aggressive behavior in dogs may therefore not be

linked to other behavioral traits (Saetre et al., 2006). A similar conclusion was found in great tits (*Parus major*), where hand reared individuals and wild caught parental aggressive behavior was measured. The heritability found in mid-parent-mid-offspring regressions was statistically different from zero, indicating that variability in aggression is controlled by variability in genetic inheritance to some extent (Drent, van Oers & van Noordwijk, 2003). Although this study looked at males and females together, it does provide evidence that heritability influences female aggression. However, further research in the area of genetically controlled aggression and personality should focus on identifying the similarities and differences between males and females, in order to provide evidence in support of or against the correlative hypothesis and direct female specific selection (Anholt & Mackay, 2012; Saetre et al., 2006).

Conclusion

Aggression enables individuals to survive by allowing them to maintain a competitive status and obtain limited resources (Anholt & Mackay, 2012). Such resources include food, territory, rearing sites, mates, as well as direct and indirect resources that mates provide. Females often utilize aggressive behaviors over non-sexual resources more frequently than males. However, when females do exhibit aggression over sexual resources, such as mates, it is usually for mate quality rather than quantity due to their lower potential reproductive output (Cant & Young, 2013; Gill, Alfson & Hau, 2007; Rosvall, 2013b). As a result, female aggression often falls under the wider reaching branches of social selection, of which sexual selection is deemed a subset (Stockley & Campbell, 2013).

Both low and high levels of aggression may be detrimental to fitness depending on the condition of an individual and the environmental factors influencing resource acquisition and reproduction (Anholt & Mackay, 2012). The fact that aggression is mediated by such variable

components that are related to fitness illustrates that evolution has worked directly on females via distinct mechanistic and behavioral means (Rosvall, 2011a).

Despite this fact, the personality trait of aggression is shown to be genetically heritable in females and males, providing evidence that the correlative hypothesis may be a viable explanation to explain female aggression (Anholt & Mackay, 2012). However, it is expected that some aspects of female traits are explained by correlative inheritance with males, as females share a majority of their genome with the opposite sex (Ellegren & Parsch, 2007). Although the correlative hypothesis is likely to explain some of the widespread appearance of female aggression, it is not sufficient in taking into account the variety of costs and benefits that modulate the adaptation of female aggression within the animal kingdom. Particularly, the correlative hypothesis reasons that females have the same costs associated with aggression as males, with none of the benefits (Lande & Arnold, 1983; Møller et al., 2005). Specific components of female aggression indicate that female genetics influencing aggression have been selected in ways that have allowed many species to maintain the costly behavior of aggression by maximizing the benefits (Cant & Young, 2013; Rosvall, 2011a; Tobias, Montgomerie & Lyon, 2012).

Researchers are beginning to expand their understanding of female aggression beyond the confines of sexual selection and the correlative hypothesis. Many such results have been presented here, revealing how complex and unique female aggression is across taxa. Further research should focus on identifying the differences and similarities between male and female aggressive behaviors in order to fully outline what degree of female aggression is accounted for by genetic inheritance and/or direct selection. Additionally, studies should focus on bridging the gaps in knowledge within each species between the three sections outlined in this review: costs,

benefits, and mechanisms of female aggression. Obtaining a substantial body of knowledge in each area will allow scientists to draw integrative conclusions about the evolution and adaptive function of female aggression. The research reviewed here shows that female aggression can provide extraordinary fitness benefits, while also posing exceptional costs. Such results provide a basis for future studies to expound upon and develop rich understandings of the biology and evolution of female animals - the 'one animal in all creation about which man knows the least' (Hrdy, 2013).

Chapter 2 - The effect of exogenous testosterone on dominance and status signaling in the female American goldfinch (*Spinus tristus*)

Introduction

Historically, studies on aggression have focused solely on the male sex. Although Darwin began postulating about the evolutionary significance of male dominance in the 1870's, references to 'competition among females' remained rare within literature for another one-hundred years, and did not gain much attention within the biological field until the 1980's (Darwin, 1872; Hrdy, 2013; Hrdy, 1999). Consequently, species that are widely understudied include those that exhibit monomorphic traits and behaviors, or those where the female is more aggressive than the male. The function of female aggression is therefore not as thoroughly understood as it is in males (Amundsen, 2000; Kraaijeveld, Kraaijeveld-Smit, & Komdeur, 2007; Tarvin & Murphy, 2012).

This lack of focus on female aggression is particularly troubling because many aspects of a species' natural history and an individual's fitness are often directly related to behavioral characteristics such as dominance. An individual's dominance can increase their likelihood of succeeding in competition over aggressors, which can thus improve access to limited resources (Cain & Ketterson, 2012). According to Gauthreaux (1978) aggression can shape how individuals interact with others and structure social systems, as dominance hierarchies are a result of individuals varying in their abilities to compete for resources that are critical to survival (Marra, 2000). There is growing evidence that females compete over breeding and non-breeding resources, in similar manners and intensities as males (Cant & Young, 2013; Murphy et al., 2009 a&b; Rosvall, 2013; Rubenstein, 2012). Females participate in aggressive encounters over resources such as food (Crowhurst et al., 2012), territories (Kahlenberg, Thompson, &

Wrangham, 2008; Wolf, 1969), mates (Langmore et al., 1996), and paternal care (Sandell & Smith, 1997; Sagsvold & Lifjeld, 1994). Additionally, in some cases females have been found to compete more intensely for access to non-sexual resources than males (Clutton-Brock, 2009; Gill, Alfson, & Hau, 2007; Murphy et al., 2009 a&b; Tobias, Montgomerie, & Lyon, 2012). Female aggression is therefore widespread and pertinent to understanding what Hrdy (2013) has described as “The ‘one animal in all creation about which man knows the least.’”

It is well known that testosterone is important in the development of secondary sexual characteristics in males, including behavioral traits such as aggression (Adkins-Regan, 2005; Bókony et al., 2008, Lincoln, Guinness, & Short, 1972; McGlothlin et al., 2008, Evans et al., 2000). Although aggression and other testosterone mediated characteristics are generally more prominent in males, in many species females also develop testosterone linked fighting potential (Kraaijeveld, Kraaijeveld-Smit, & Komdeur, 2007; Muck & Goymann, 2011; Pham et al., 2014). However, this relationship in females appears to vary interspecifically. Although testosterone seems to be the major mechanism underlying female aggression in some species as noted above, the hormone is not a reliable predictor of dominance in others (Hau, Stoddard & Soma, 2004; Jawor, Young, & Ketterson, 2006; Goymann et al., 2008; Elekonich & Wingfield, 2006). As a result, the link between this hormone and female contest behavior is not fully resolved (Cristol & Johnsen, 1994; De Ridder et al., 2002; Edwards, 1971; Muck & Goyman, 2011; Zysling et al., 2006). Furthermore, the hormonal mechanisms that mediate female aggression are not well understood, and it appears that female aggression may be influenced by a suite of hormones (Soma, 2006). Female testosterone has been linked to estradiol (Rosvall et al., 2013), luteinizing hormone (Jawor et al., 2007), progesterone (Goyman et al., 2008), and individual androgen, oestrogen, and aromatase receptor expression (Rosvall et al., 2012). The correlation observed

between testosterone and aggression in females is therefore far from universal, and taxa wide generalizations cannot be made about the influence of testosterone on female behavior (DeVries, Winters, & Jawor, 2015; Jawor, Young, & Ketterson, 2006).

Conspicuous ornaments regulated by testosterone can serve as honest signals of aggression because of their ability to candidly reflect an individual's health, and thus their fighting ability (Blas & Perez-Rodriguez, 2006; Buchanan et al., 2001; Martínez-Padilla et al., 2014; Mougeot et al., 2004). Specifically, testosterone is negatively correlated to immune function and body mass maintenance, making its production costly to individuals (Ketterson et al., 2001; Wingfield, Lynn, & Soma, 2001). As a result, testosterone mediated signals can indicate an individual's capacity to produce energetically expensive behaviors involved in aggression (Blas & Perez-Rodriguez, 2006; Buchanan et al., 2001; Martínez-Padilla et al., 2014; Mougeot et al., 2004). Furthermore, testosterone mediated ornaments can directly reflect hormonal-state, and thus provide information on an individual's readiness to act aggressively (Pham et al., 2014). Such traits are known as status signals. Status signals allow communication between competitors that can help mediate aggressive interactions where risk of injury or energy expenditure is high (Garamszegi et al., 2006; Laidre, 2007; Maynard-Smith, 1974; Parker & Ligon, 2002; Rémy, 2010). Specifically, status signals allow individuals to assess their competitors' aggressive potential in competition over resources without entering into an aggressive interaction (Senar, 2006). Elaborate traits can therefore serve as honest signals of fighting ability, or motivation, to potential competitors (Berglund, Bisazza, & Pilastro, 1996; Dey et al., 2017; Furlow & Kimball, 1998; Tarvin & Murphy, 2012; Tibbetts et al., 2015).

Consistent with the lack of attention female aggression has received, the topic of female status signaling has been neglected within scientific research until recently. Although it has been

previously postulated that female ornamentation is likely due to correlated genetic inheritance (known as the correlative hypothesis) (Lande & Arnold, 1983; Møller et al., 2005), evidence has arisen that female ornamentation is likely due to direct sex-specific selection (Chippindale, Gibson, & Rice, 2001; Tobias, Montgomerie, & Lyon, 2012). The correlative hypothesis postulates that the sex under indirect selection suffers the costs of the ornament in question, receiving little or no reproductive profit (Ketterson, Nolan, & Sandell, 2005). This idea is highly unlikely from an adaptationist standpoint because selection acts against traits where the cost is higher than the benefit, and female ornaments that receive no advantage would be selected out of the population to some extent (Swierk & Langkilde, 2013). As female ornamentation is observed in extant species, it is more likely that such phenotypes in males and females are under selection that leads to sex specific forms of evolution. This would result in functional traits that serve unique purposes in each sex to maximally increase fitness (Mank, 2015). The pressure from intrasexual female competition for resources likely favors the direct selection for beneficial female dominance behaviors and status signaling, which can be used to mediate aggressive interactions (Cain & Ketterson, 2012; Tarvin & Murphy, 2012).

American goldfinches (*Spinus tristus*) are a particularly interesting model to study in the context of female aggression and status signaling. American goldfinches have a dynamic, near-monomorphic, carotenoid-based bill that is colorful during the breeding season. The bill color of the female has been shown to positively correlate with circulating plasma testosterone levels (Pham et al., 2014). Experimental evidence indicates that bill color serves as an intrasexual status signal between females (Murphy et al., 2009a); in this study, females preferentially chose to feed next to taxidermic models with experimentally dulled bills as opposed to models with augmented-color bills. Goldfinch bill coloration is also subject to temporal stressors, and bills

become more dull over the course of a few hours after experimentally induced infection (Kelly et al., 2012; Rosenthal et al., 2012). Female bill color is positively related to immunoglobulins and antibodies, indicating a relationship with immunity (Kelly et al. 2012). The fact that bill coloration is linked to circulating testosterone levels and health suggests that bill color serves as an honest indicator of individuals' readiness to fight within this species.

This study will explore the hypothesis that testosterone plays a role in mediating both female aggression and the expression of bill color, a known status signal (Murphy et al. 2009a). We predict that testosterone will mediate female-female dyadic interactions, and that individuals injected with testosterone will be more likely to win competitive interactions when facing a competitor not receiving exogenous testosterone. We additionally predict that testosterone injected females will increase expression of bill color. This study will be the first in isolating the influence of exogenous testosterone on both aggression and signaling aggression within this species, providing an important step in understanding the function of female dominance in a behavioral context.

Methods

General Procedures

The American goldfinch is a socially monogamous passerine in which both sexes contribute to nest defense and participate in intra and intersexual aggressive interactions over resources (Coutlee, 1967). These aggressive behaviors are most prevalent throughout the pre-breeding season when nest sites are being defended, during which time females are observed to be more aggressive than males (Coutlee, 1967; Stokes, 1950). We conducted the study at Queen's University Biological Station in Ontario Canada (44°33'N, 76°19'W) from June to July

of 2016. Peak breeding season of American Goldfinches in southern Ontario occurs from June to July, during which time both sexes develop a rich orange bill color (Coutlee, 1967).

Female American Goldfinches were captured using cylindrical traps placed around Nyjer feeders (fig. 1). Age class was determined based on plumage following Pyle (1997). Upon capture, morphometric measurements were taken following the methods of Murphy et al. (2009a&b). Birds were color banded, but colors that resemble bill and plumage coloration (i.e., orange, red, and yellow) were not used. Initially, females were housed in two flocks of eighteen within outdoor aviaries (6'x12'). Each aviary contained a water dish and 2 hanging feeders with more feeding stations than birds present in the flock. Birds were given carotenoids (Kemin FloraGLO Lutein and DSM OPTISHARP natural Zeaxanthin) and vitamins in their water, as well as ad libitum black oil sunflower and nyjer seed. These flocks were housed for 3 weeks before the experiment began in order to acclimatize them to captivity.

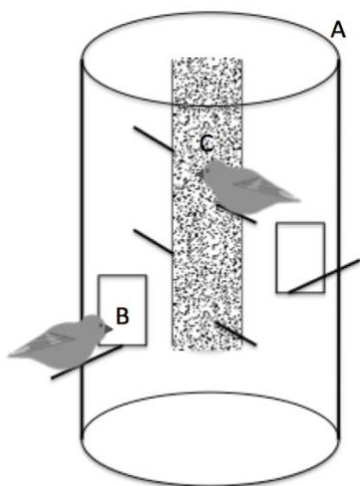


Figure 1. Schematic diagram of method used for trapping female American Goldfinches. A: Cylinder surrounding feeder - Sides of the cylinder were constructed with chicken wire, and the top and bottom of the cylinder was constructed with plastic hardware cloth. B: Tunnels - Tunnels were cut into the side of the cylinder and perches were placed at the bottom of the tunnels allowing birds to fly into the cylinder. C: Feeder - A nyjer feeder with perches was hung from the top of the cylinder for birds to perch on. A larger door was cut into the side of the cylinder and a removable flap of plastic hardware cloth was placed over it to allow removal of the birds from the trap (not depicted).

Rank Assessment: Flock Hierarchy Establishment

Before dyads of testosterone-augmented and control birds competed against each other (see below for more on dyad competition) individual rank was established among each flock of 18 so that dyads could be matched for similar dominance. To do this, we assessed natural

dominance (before hormone manipulation) within each flock by first depriving food for ca. 10hrs (overnight), and then assessing competitive interactions when food was reintroduced into the aviary. The two feeders introduced into the aviary were small bowls that could be monopolized by one or two birds at any one time (fig. 2). Separate hierarchies were established among the 2 flocks of 18 females by scoring dominance behaviors exhibited over the food. One aviary was analyzed at a time. Each aviary had two observation periods, separated by 3 days. Dominance interactions consisted of hold-offs, displacements, and fights (Ardia et al., 2010; Coutlee, 1967; McGraw et al., 2007). Individuals that initiated aggressive behavior and received a submissive response from the receiver were considered winners of that particular interaction.

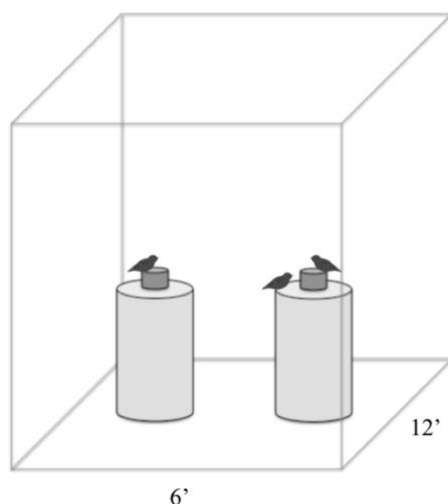


Figure 2. Schematic of outdoor aviary used to conduct flock hierarchy establishment trials on female American Goldfinches (N=18). Two buckets stacked on top of each other. A single food bowl was placed in the center of each bucket tower.

Aggressive interactions at each feeder were observed by two researchers (each watching a predesignated feeder). To record continuous behavioral data, the researchers described the interactions verbally, and two additional researchers recorded the behavior. A video camera was trained on each feeder. In the case that there were ambiguous social interactions, the time was noted, and that portion of the videotape was later reviewed. To calculate rank dominance, we used the Oracle method (Balreira, Miceli, & Tegtmeier, 2014), which is a customizable Markov

ranking method that can consider multiple competitive individuals at once. The Oracle ranking comes from a network where individuals are related according to their interaction. The algorithm is designed to create a group rank order from a context in which information is incomplete, allowing us to take into account the fact that females did not interact with every individual in their flock. The Oracle has been shown to accurately predict ranks in the National Football League (Balreira, Miceli, & Tegtmeyer, 2014), and has been customized to create social hierarchies within green anole lizards (*Anolis carolinensis*) (Bush et al., 2016). The computation for the ranking system was performed using MatLab 2017 (MathWorks, Natick, MA, U.S.A).

Assignment to Dyads

Paired females in dyads were of the same dominance rank within their respective flocks, assessed from the flock trials described above (rank 1 female from flock A was paired with rank 1 female from flock B, and so forth through rank 18) (N=18). This pairing ensured that females were novel to each other and had not interacted previously. Treatment was administered in such a way that testosterone treated females competed against control treated females (see below for more on testosterone treatment). Therefore, each dyad contained a pair of equally ranked females, one of which was experimentally treated with testosterone. One pair did not compete in a dyad because of sickness resulting in a total of 17 dyads. Dyad cages were visually isolated from each other and contained two T perches sitting next to each other, one monopolizable food bowl, and a water bowl.

Testosterone Manipulation

Before the dyad competitions took place, testosterone and control treatments were administered. Females were moved from their flock aviaries to triads of similarly ranked individuals for another experiment (i.e., birds rank 1-3 were housed together, as were 4-6, etc. up

to 15-18). From 7 July to 11 July 2016, while in these triads, females received their respective treatments. Half of the females from each original flock were injected with 15 μ L of 1mg/ml testosterone suspended in peanut oil. The remaining half of each flock was injected with 15 μ L of peanut oil as a control treatment. Testosterone and control treatments were injected subcutaneously above the pectoralis muscle, below the wing. For the first four days of injections, birds were injected once a day with their respective treatment between 3:30 and 5:00 pm. On the fifth and final day of injections, testosterone was administered between 6:30 and 8:00 am. There was no significant morphological difference between testosterone treated females and controls that could influence potential dominance outcomes (Table 1).

Table 1. Summary of independent *t*-tests for pre-manipulation differences in morphological traits between testosterone (T) treated females and control females.

Morphological Measurement	T treated females (mean)	Control females (mean)	t	P
Mass (g)	12.6	12.5	0.46	0.65
Tarsus Length (mm)	13.3	13.3	0.10	0.92
Bill Length (mm)	8.4	8.5	1.43	0.16
Bill Depth (mm)	6.6	6.6	0.81	0.42
Wing Length (mm)	73.2	73.0	0.43	0.67

Bill color Assessment

Bill color measurements were taken after the flock trials (before testosterone administration), and the second to last day of testosterone administration. Measurements followed the procedures of Pham et al. (2014). Briefly, an Ocean Optics USB2000 spectrometer and PX-2 pulsed xenon lamp was used to measure 5 different, randomly chosen 2mm areas of bill. We calculated mean brightness (i.e. luminance; mean *R* from 320 to 700nm), hue, (wavelength where *R* [*R*_{max} *R*_{min}]/2) and yellow-orange saturation ([sum of *R* from 550 to 625

nm]/mean brightness) using RCLR ver. 0.9.33 (Montgomerie, 2010); reference Table 3.2 in Montgomerie (2006) for more information.

Table 2. Summary of independent *t*-tests for pre-manipulation differences in bill color between testosterone (T) treated females and control females.

Color measurement	T treated females (mean)	Control females (mean)	t	P
Brightness	0.27	0.30	1.68	0.10
Hue	546.35	532.76	1.07	0.29
Saturation	0.23	0.23	1.24	0.22

Dyad Behavioral Trials

Females were deprived of food 14 hours before the dyad trials took place. Thirty minutes after the last injections, females were placed into dyads. Food was introduced, and interactions were recorded using video cameras for 1 hour after food introduction to assess dominance.

Behavioral Analysis of Dyad Trials

We analyzed aggressive interactions between competitors in order to determine which female was dominant within each dyad. Measurements included hold offs, displacements, and fights as described above for the assessment of rank within the flocks of 18. The number of interactions won per individual in each trial was summed. Individuals that won 60% or more of the interactions that took place within a trial were considered dominant. The average percentage of interactions won by dominant individuals was 93% (range = 63.64%-100%, SE = 2%), and only 1 winner won less than 80% of the interactions within her dyad.

Verification of the Efficacy of Testosterone Injection Concentrations

To verify that our dosage was effective in raising plasma testosterone within natural circulating limits, different females from the dyad experiment were given varying concentrations

of testosterone treatments from July 1st to July 5th (prior to the treatments administered for the dyad competition). Sixteen females were assigned 3 treatments at random: control (injected with 15 μ L of peanut oil, N=5), low testosterone concentration (injected with 15 μ L of 1mg/mL testosterone suspended in peanut oil, N=6), and high testosterone concentration (injected with 15 μ L of 2mg/mL testosterone suspended in peanut oil, N=5). These treatments were administered once a day, for 5 days, between 6:30 and 8:30 am.

Approximately 28 μ L of blood was collected from the brachial vein before and after injections, to measure pre and post treatment plasma testosterone levels. Pre and post blood samples were taken at the same time on their respective days, with post treatment blood being collected within 2 hours after testosterone injections took place. Blood samples were taken within approximately 10 minutes of disturbance (mean = 4.85 minutes, SE = 0.39 minutes). The 16 female goldfinches were housed in separate cages that were visually isolated from one another. Females were provided ad libitum food and water.

Testosterone was assayed using Salimetrics salivary testosterone enzyme immunoassay kit. This assay has been previously used to analyze passerine plasma (Moser-Purdy et al., 2017) and has been validated for quantifying avian testosterone (Washburn et al., 2007). The Salimetrics protocol was followed except instead of the recommended 25 μ L of sample, 15 μ L of plasma was diluted with 60 μ L of diluent, making our final plasma dilutions 1:4. Plasma samples from each individual were run in duplicates. Intra-assay coefficient of variation (CV) was calculated from standard samples of known concentration ranging from 1.78-5.04 (mean of 3.07). The inter-assay CV was 2.61, and sensitivity was 2.15.

Statistical Analysis

All statistical tests were completed using JMP ver. 10.0.2 or Statplus version v6. A binomial test was used to determine if testosterone treated females won more than 50% of the trials against control-treated competitors. Independent T-tests were used to test if there was a larger bill color change among T-treated females than C-treated females. Paired T-tests were used to test if morphological measurements of the two contestants influenced winning/losing within a dyad (paired by dyad). One-way ANOVA's were used with data from the testosterone dose verification experiment to determine if females in the three treatment groups had statistically different circulating testosterone levels before treatment. Paired T-tests were used to analyze whether there was a change in circulating testosterone levels within each treatment group. One-way ANOVA's were used to test whether females in the treatment groups showed different amounts of delta T (post – pre treatment testosterone concentration). Post hoc independent T-tests were used to assess differences between groups when ANOVAs were significant. All T-tests were two-tailed.

Results

Testosterone treated females won 12 of 17 dyad trials (Binomial test: $p = 0.072$) (fig. 3). In all 5 of the trials where control birds won, control birds won 100% of the interactions that took place. In only 3 of the 12 trials where the testosterone bird won, did the testosterone bird win 100% of the interactions (fig. 4). The testosterone treatment did not have a significant influence on the change in bill color (Table 3). We tested whether other factors could have contributed to winning, and we found that winners had statistically longer wings than their losing competitor irrespective of treatment (Paired T-test: $t=2.20$, $p=0.043$) (fig. 5).

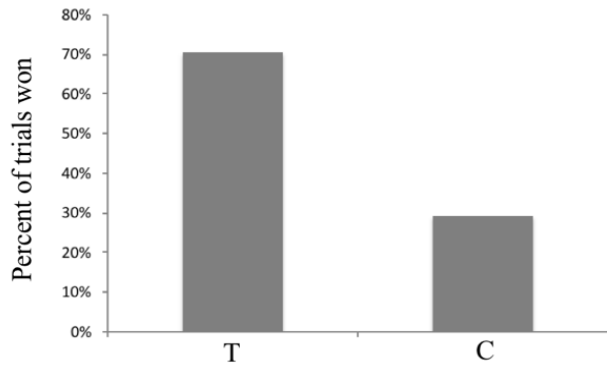


Figure 3. Percent of trials won by testosterone (T) treated and control (C) female American goldfinches (*Spinus tristus*) out of 17 total dyadic competitions.

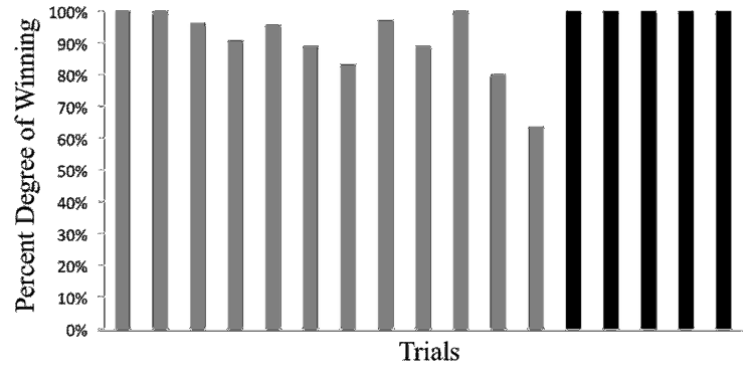


Figure 4. Quantification of winning during a dyadic competition. Grey bars indicate trials where testosterone females won (N=12) and black bars indicate trials where control females won (N=5). Y axis indicates the amount by which the winner won: Percent degree of winning indicates the number of wins of the winner divided by total interactions within a dyad. Each bar represents a different dyadic competition (N=17).

Table 3. Summary of independent *t*-tests for change in bill color (post-pre treatment) between testosterone (T) treated females and control females within dyads.

Color measurement	T treated females (mean)	Control females (mean)	t	P
Brightness	-0.034	-0.055	1.45	0.16
Hue	-50.71	-25.41	0.77	0.45
Saturation	0.002	0.004	0.95	0.35

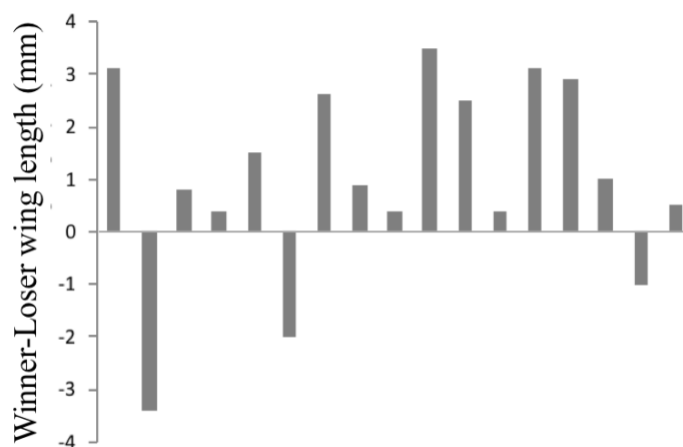


Figure 5. Difference in wing length between winner and loser (winner-loser) in dyadic competition between a testosterone treated female and a control female. Each bar indicates a single trial (N=17).

In the experiment verifying the effect of testosterone injections on circulating testosterone, there was no significant difference between control, low testosterone, and high testosterone treated females prior to injections (ANOVA: $DF=2$, $F=0.60$, $p=0.56$). As per the effect of the injections, control birds did not show a significant difference in testosterone between pre and post treatment (mean \pm SE; pre-treatment = 16.57 ± 4.27 pg/mL, post-treatment= 151.76 ± 68.5 pg/mL; paired T-test: $t=1.88$, $p=0.13$ pg/mL), where low treatment (pre-treatment= 11.94 ± 2.50 pg/mL, post-treatment= $1,619.56\pm395.19$ pg/mL; paired T-test: $t=4.06$, $p=0.01$) and high treatment females did (pre-treatment= 14.44 ± 2.08 pg/mL, post-treatment= $2,015.61\pm382.27$ pg/mL; paired T-test= 5.23 , $p=.006$). In testing whether the three groups showed different delta T, there was a significant difference in delta T between the three treatments (ANOVA: $DF=2$, $F=8.22$, $p=0.005$). Post hoc tests revealed that there was a significant difference in delta T between the controls and the low-T treated females (Independent T-test: $T=3.32$ $p=0.009$), and between controls and the high-T treated females (Independent T-test: $T=4.79$, $p<0.001$) (fig. 6). There was not a significant difference in the delta T between the medium and high treatments (Independent T-test: $T=0.71$, $p=0.50$).

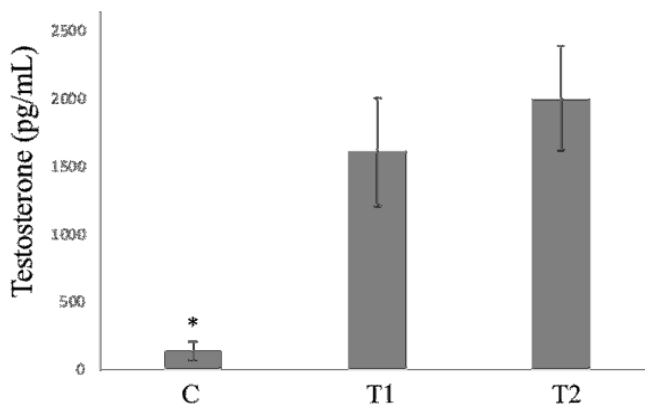


Figure 6. Difference in testosterone treatment (post-pre treatment) between control (C; N=5), low testosterone treated females (T1; N=6), and high testosterone treated females (T2; N=5). Asterisk indicates significant difference, and error bars indicate standard error.

Discussion

Our study explored the relationship between testosterone and female aggression, as well as testosterone and female status signaling in the American goldfinch. Although testosterone is well known to be the hormonal mechanism underlying male aggression and status signaling (Lincoln, Guinness, & Short, 1972), only within the last few decades has focus turned to understanding the role of androgens in mediating female aggression and ornamentation (Cain & Ketterson, 2012; Hau, 2007). Our results indicate that when female American goldfinches were treated with exogenous testosterone, these testosterone-enhanced females won over 70% of dyadic contests against non-hormonally treated females. Although the relationship between hormonal treatment and winning represents a non-significant trend, these results are consistent with previous findings that the expression of the female goldfinch's status signal is correlated with endogenous testosterone (Pham et al., 2014). With studies taken together, these results suggest that testosterone does play a role in contest resolution among female goldfinches.

We also investigated whether other phenotypic characteristics may have influenced dominance outcomes among competing dyads. Body size, as assessed by wing length, was found to be a strong predictor of winning. Among birds, it is not uncommon that body size determines dominance (French & Smith, 2005; Garnett, 1981), and it appears that goldfinches follow a similar pattern. For example, among American redstarts (*Setophaga ruticilla*) larger females are more responsive to territorial intrusions and occupy more desirable mangrove habitats (Marra, 2000). Similarly, larger female tree swallows (*Tachycineta bicolor*) exhibit more aggressive behavior than subordinate females. Female aggression in tree swallows serves to obtain nesting cavities necessary for reproduction, making larger, more aggressive individuals more likely to obtain the limited resource (Rosvall, 2008). Among female tree swallows, smaller individuals do not have the ability to maintain the amount of energy reserves needed to compensate for the

metabolic cost of maintaining aggressive behavior (Rosvall, 2011). Large size can translate into competitive success. For example, if larger individuals have greater muscle strength (Gosler & Carruthers, 1999), or lunge distance (Lange & Leimar, 2003), or alternatively, if large females have the ability to store more energy reserves, they can then invest more into aggressive interactions than small individuals (Rosvall, 2011).

In our study, we were unable to control for the effect of body size on winning in a statistical model because body size shows such tight covariation with winning (i.e., 80% of winners were larger). As a consequence, body size explained most of the variation in competitive success. Our inability to statistically control for body size was compounded by our relatively limited sample size (17 trials). We note that wing length emerged as a strong correlate of winning despite our best efforts to create dyads matched for natural-dominance (i.e., by pairing females based on relative rank within their respective aviaries). This pattern suggests that even small changes in body size may have large effects on dominance outcomes. We note an important consequence of this tight link between body size and winning: we were limited in our ability to detect an effect of testosterone on competitive outcomes because any difference in motivation to fight (a consequence of testosterone) was overwhelmed by differences in the ability to fight (a consequence of body size). This effect of body size on dominance may be especially pronounced in an experimental setup like ours where competitors are food deprived and highly motivated to fight. In this context, displays of aggressive motivation are likely to be disregarded when food resources are so highly-valued and as a consequence, individuals may resolve contests based on actual fighting.

An interesting pattern occurred among the 5 cases where the control female dominated the testosterone female. In all of these cases, the control female dominated her competitor

completely, winning each and every one of the interactions. In contrast, in only 3 of the 12 (25%) trials where the testosterone treated bird won, did the testosterone treated female win all of the interactions. It seems possible that the hormonal treatment had a negative physiological effect on some birds, causing them to lose due to the stress of handling or in response to the testosterone itself. However, upon reexamination of the video tapes, we found no qualitative difference in activity levels between testosterone treated birds who lost versus those who won, indicating that the 5 testosterone treated ‘losers’ were unlikely suffering a pathology due to the injections. To further explore the observation that losers who were testosterone treated lost all of their social interactions, we tested for differences between the birds in the dyad--comparing testosterone treated ‘winners’ to control ‘winners’. There was not a statistical difference in any of the morphological measurements taken, indicating that none of the factors that we measured, except for wing (see above) appear to be driving this phenomenon.

It may be the case that the organizational effects of testosterone, rather than activational, influences an individual’s readiness to fight (Harding, 1981; Hau, 2007; Hirschenhauser & Oliveira, 2006). Such observations have been reported in the sex role-reversed species of the spotted sandpiper (*Actitis macularia*), where females are subjected to high degrees of intrasexual competition and exhibit typical androgen mediated aggressive behaviors such as territory defense. In this species, the less aggressive male sandpiper has higher circulating testosterone levels than the dominant female. Fivizzani and Oring (1986) hypothesized that this difference may be a result of enhanced receptivity and enzymatic conversion of female neural centers to moderate levels of testosterone, accounting for the significantly higher level of estrogen observed in females. Analogous findings have been observed in African black coucals, where testosterone mediated aggression seems to be dependent on the mRNA expression of androgen

receptors (*Centropus grillii*) (Cheng et al., 1999; Voigt & Goymann, 2007). It is therefore possible that testosterone mediated aggression in female American goldfinches is influenced by long term organizational hormonal effects such as the upregulation of receptors. The 5-day treatment administered in this study may not have been long enough to have significant organizational changes. Further research should investigate the temporal sensitivity of testosterone treatment on females.

We found no effect of testosterone treatment on bill color. Although our treatment was given evenly, with control and experimental females having statistically similar bill colors prior to treatment, there was no significant change in bill color within the testosterone treated females. The lack of relationship could have occurred if testosterone requires a longer time-period to have an effect on bill color. Contrary to the findings of this study, previous studies on other species have found a link between testosterone and integument (Ligon et al., 1990; Moreno et al., 2014; Rutkowska, 2005; Setchell et al., 2008). It is therefore plausible that although the bill color of American goldfinches can change rapidly, testosterone may provide the hormonal mechanism behind long term baseline bill color. Factors such as stress that have been shown to quickly change bill color could cause dynamic deviations from the testosterone-controlled baseline (Kelly et al., 2012; Rosenthal et al., 2012).

Our experimental manipulation of testosterone was successful at elevating testosterone; however, our treatment may have raised female testosterone levels above naturally occurring limits. The plasma testosterone levels of manipulated females in this experiment were on average 1000 pg/mL greater than previous studies that have measured natural circulating female testosterone in this species. However, the blood testosterone levels of control females observed post injections were also much higher than previous experiments, indicating that females in this

experiment may have had higher circulating testosterone levels overall (Pham et al., 2014). High levels of testosterone have the potential to cause pathological effects (Evans, Goldsmith & Norris, 2000), yet in this study there was no indication that the treatment negatively affected individuals (i.e., no sickness behavior was observed). Future experiments should attempt to analyze the full range of female circulating testosterone levels, and the effect of different levels of testosterone on natural competitive behavior.

Among female American goldfinches, our results indicate that both testosterone and size are likely to play some role in mediating dominance behaviors. Further research should strive to include a larger sample size to obtain a clearer result. Despite these potential confounding factors, this study represents one of the first steps towards assessing the function of testosterone on aggression within this species, and determining which physiological factors influence female dominance and competition. To further assess this hypothesis, research should attempt to control and isolate testosterone mediated signals within aggressive contexts, specifically focusing on competition mediated by displays that can signal aggressive motivation. The next steps in understanding the mechanisms of female aggression will be to focus on the activational effect of testosterone and other androgen precursors, to establish hormonal feedback that can upregulate receptor production, and finally, to focus on specific pathways that link receptor density to behavior.

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