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# Adaptations in female songbirds to selective circumstances

An analysis of the evolutionary adaptations that female songbirds have evolved as a result of aggressive, competitive and selective circumstances to better understand the working of sexual selection on females.



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# An assessment of the adaptations in female songbirds to selective circumstances

Ramon J. Robben

Despite the usual focus on males, females too can be subjected to aggressive, competitive and selective situations. Sexual selection is usually viewed from the perspective of the males, where they develop traits used by the female as a fitness indicator to choose the male and used by the males in intrasexual competition. This can happen for females too, however. On evolutionary timescales, females in highly aggressive and competitive situations can be predicted to develop traits much like males to better suit these conditions. The potential variation of these adaptations is quite high, as it can result in either a sexually dimorphic or sexually monomorphic appearance of the species. These findings have recently caused stirs in the current theory of sexual selection, with some researchers suggesting changing the current sexual-selection theory or abandoning it altogether. In light of this gap of knowledge, many studies have been conducted attempting to find results to better understand sexual selection. This study assesses the currently known adaptations of females in aggressive, competitive and selective circumstances, to better understand whether and how sexual selection works in females relative to males.

## Introduction

Charles Darwin (1888) defined sexual selection in two ways: 1. Competition within one sex for members of the opposite sex, and 2. Differential choice by members of one sex for members of the opposite sex (Darwin, 1888). He pointed out that in practise, this usually meant that males would compete for females, and that the females would choose some males over others (Darwin, 1888). The females would make their choice based on certain traits on which the sexual selection would be based. These traits include, but are not limited to: size, ornaments and fighting capability. The males developed these traits in order to compete better and to be chosen by the females and thus gain the ability to reproduce (Trivers, 1972).

Darwin pointed out that these adaptations are mostly found in males (Darwin, 1888). In fact, there generally exists a bias on aggressive behaviour towards males. Due to this bias in sexual selection, aggression is much better studied in males than in females (Andersson 1994; Clutton-Brock, 2007). Moreover, testosterone, the mediator of aggression, is often regarded as a male hormone (Andersson *et al.*, 2004). This would make it seem as if males are the only ones who adapt to better suit the aggressive behaviour to increase their reproductive success by developing traits that allow for better intrasexual competition (Darwin, 1888; Andersson, 1994; Clutton-Brock, 2007). However, theoretically, one would assume that if the females would be placed under the same selective, competitive and aggressive circumstances, they too would develop adaptations better suited for these conditions.

Classical sexual selection theory further notes that males obtain greater benefits from mating multiple times (Bateman, 1948; Andersson, 1994). The theory notes that this is mainly because sperm is cheaper to produce than eggs, because males are generally more fierce competitors and compete more for reproductive success, and because males invest less in parental care than females (Bateman, 1948; Trivers, 1972; Andersson, 1994). This would ultimately cause male-biased expression of secondary traits, such as ornamentations and a bigger size (Darwin, 1888; Andersson, 1994). This further points towards a male bias in sexual selection.

These claims have recently been questioned, as it has been found that in species where both sexes experience similar selection strength, the level of sexual dimorphism of traits used in intrasexual competition is reduced (West-Eberhard, 1983). There is an overall growing awareness for the potential of intrasexual competitive traits in females as a result of selection (Amundsen 2000, Rubenstein & Lovette, 2009; Morales *et al.*, 2014). Despite this, however, much is still unknown about the adaptations females develop as a result of aggressive, competitive and selective circumstances. In some cases, these adaptations can result in very sexually dimorphic species, with usually dull looking females, whereas in other cases the female can be very ornamented. Furthermore, despite sexual selection maybe not being as male-biased as once thought, much is still unknown about the mechanisms that result in the development of intrasexual competitive traits, and

whether this development is similar to that found in males.

Based on available literature and previous studies, one would expect that if males and females were to experience the same selective circumstances, this would result in decreased sexually dimorphic appearances of the species, as the females would develop the same intrasexual competitive traits as the male, such as ornamentation (West-Eberhard, 1983). Moreover, it is predicted that female intrasexual competition occurs when variation in male quality is high or access to reproductive resources is limited (Amundsen, 2000). This would assume, however, that the females would develop the same intrasexual competitive traits as the male to result in a decreased sexually dimorphic appearance of the species (thus a monomorphic appearance). However, if the females were to develop different traits for their intrasexual competition (perhaps as a result of the competition being different), it could result in very sexually dimorphic appearances regardless. The adaptations females develop to allow for better intrasexual competition can thus result in either sexually

dimorphic or monomorphic appearances of the species.

The sexual selection theory has always been a major component of evolutionary studies. Therefore, a better understanding of this theory is important. Because of the male bias, intrasexual competitive traits and its evolutionary development are currently not well understood. Therefore, studying intrasexual competitive traits in females is important to better understand the working of sexual selection on females.

Here, I have assessed the intrasexual competitive traits most used in studies focusing on explaining intrasexual competitive traits and its evolutionary development in females. These main traits are ornamentation and body size. I have also looked at how the evolutionary development of these traits helps explain the working of sexual selection in females relative to males. By looking at the intrasexual competitive traits in females, I will be attempting to answer the question: "How do findings in intrasexual competitive traits in females help the understanding of sexual selection?".

## Ornamentation

Most studies focusing on the evolutionary development of intrasexual competitive traits in females centre their studies around ornamentation, as this trait often determines the degree of sexual dimorphism in species and can thus be used as a measure of selection working on females (Rubenstein & Lovette, 2009; Karubian, 2013; Morales *et al.*, 2014). Because of the previously mentioned male bias in sexual selection, the factors that shape ornamentation and other intrasexual competitive traits in females are much less studied and understood (Karubian, 2013). Thus, a better understanding of female ornamentation has recently become a focus of the behavioural ecology research agenda (Amundsen, 2000; Forgsen *et al.*, 2004; Heinsohn *et al.*, 2005; Rosvall, 2011; Rubenstein, 2012a; Rubenstein, 2012b; Tobias *et al.*, 2012).

### Cooperative breeders

To review whether females develop adaptations suited for aggressive behaviour to increase their reproductive success, a comparative analysis would be needed to compare aggressive females and non-aggressive females. Such a case study could be

provided by cooperative breeders. Generally, the females in cooperatively breeding species are more competitive than the females of non-cooperatively breeding species (Rubenstein & Lovette, 2009). This is because of a much higher reproductive skew that exists in cooperative breeders (Rubenstein & Lovette, 2009). This means that only a few females in such species will reproduce. The females will thus compete for the ability to breed, which results in a selection based on the cooperative traits between the individuals, much like in competitive males (Rubenstein & Lovette, 2009). In comparison, non-cooperative breeders have on average a relatively low reproductive skew, as the females of this species have a rather equal chance of reproducing (Rubenstein & Lovette, 2009). To review the adaptations females develop when in more selective circumstances, the cooperative- and non-cooperative breeders therefore make an excellent case study.

Rubenstein & Lovette (2009) (Figure 1) looked at the socially diverse African starlings (Sturnidae). These starlings have both cooperative (nearly 40% of species) and non-cooperative breeding species,

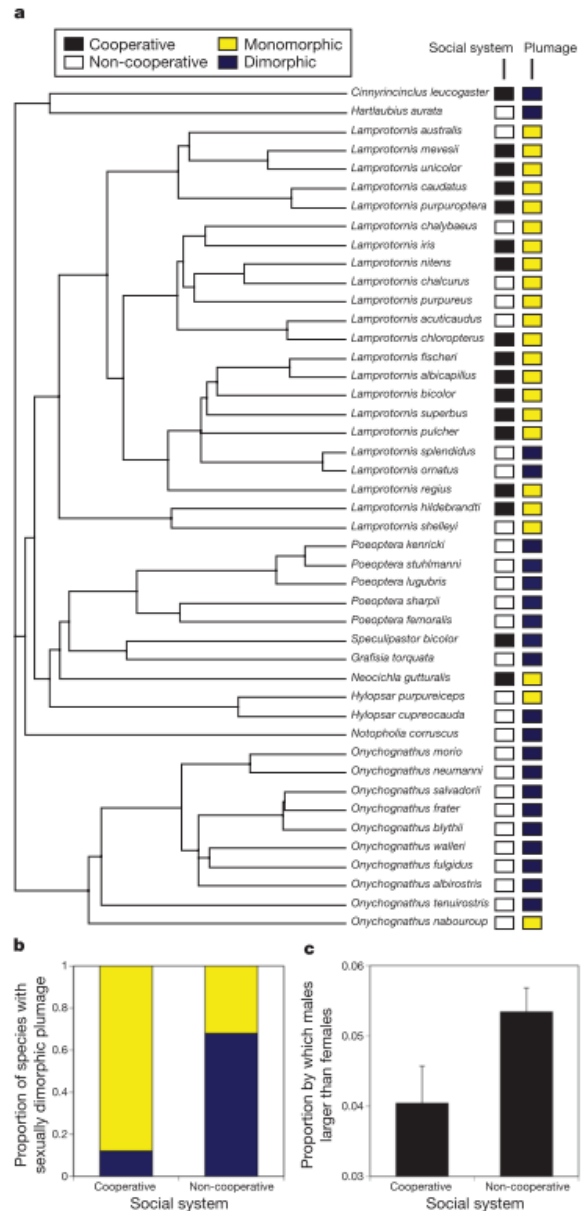
making comparisons between the levels of their sexual dimorphism levels in plumage and body size rather easy (Rubenstein & Lovette, 2009). Rubenstein & Lovette (2009) looked at traits that would help in intrasexual competition such as body size and ornamentation, which would ultimately cause the different species to show different levels of sexual dimorphism. This can be seen in figure 1.

In this study, it was found that females in cooperatively breeding species were more ornamented than those in non-cooperatively breeding species. This translates into the level of sexual dimorphism in plumage being significantly lower in cooperatively breeding than in non-cooperatively breeding starling species (Rubenstein & Lovette, 2009). Thus, they found that the cooperative breeders had sexually monomorphic plumage, whereas the non-cooperative breeders had sexually dimorphic plumage (Rubenstein & Lovette, 2009). While it is also possible that selection is simply weaker on males rather than stronger on females, Rubenstein and Lovette (2009) measured the relative intensities of selection acting on male and female phenotypic traits. They found that selection is acting more intensely on plumage in females, rather than the selection of these traits being weaker in males.

Based on these results, it is safe to say that selection acts more intensely on female intrasexual competitive traits in cooperatively breeding starlings, much like in other group-living species (Irwin, 1994; Badyaev & Hill, 2003; Rubenstein & Lovette, 2009). This is mainly because of the previously mentioned high reproductive skew that exists in these species, where only a few females mate, thus forcing competition for the ability to reproduce (Hauber & Lacey, 2005; Clutton-Brock *et al.*, 2006; Rubenstein & Lovette, 2009). This is further enforced by indirect intrasexual competition through competing for resources such as breeding spots and food (Rubenstein & Lovette, 2009).

### Other sources and breeders

Despite the outcome of comparative study conducted between cooperative and non-cooperative breeders by Rubenstein and Lovette (2009), intrasexual competitive traits do exist in females of non-cooperative species (Morales *et al.*, 2014). The adaptations the female develops can result in either a monomorphic- or dimorphic appearance, depending on the nature of the intrasexual competitive traits the female develops. In non-cooperative breeders, the



**Figure 1. Molecular phylogeny of African starlings with their associated behavioural and morphological traits. a,** The tree is based on combined analysis of mitochondrial and nuclear intron sequences. Social and morphological characters are indicated at each terminal species; a key is given above. **b,** A greater proportion of a non-cooperative species had sexually dimorphic plumage than did cooperative species, suggesting a reduced degree of plumage dimorphism in cooperative species. **c,** Males and females in cooperative species had wings that were more similar in length than those in non-cooperative species (mean s.e.), suggesting a reduced degree of size dimorphism in cooperative species (Figure obtained from Rubenstein & Lovette, 2009).

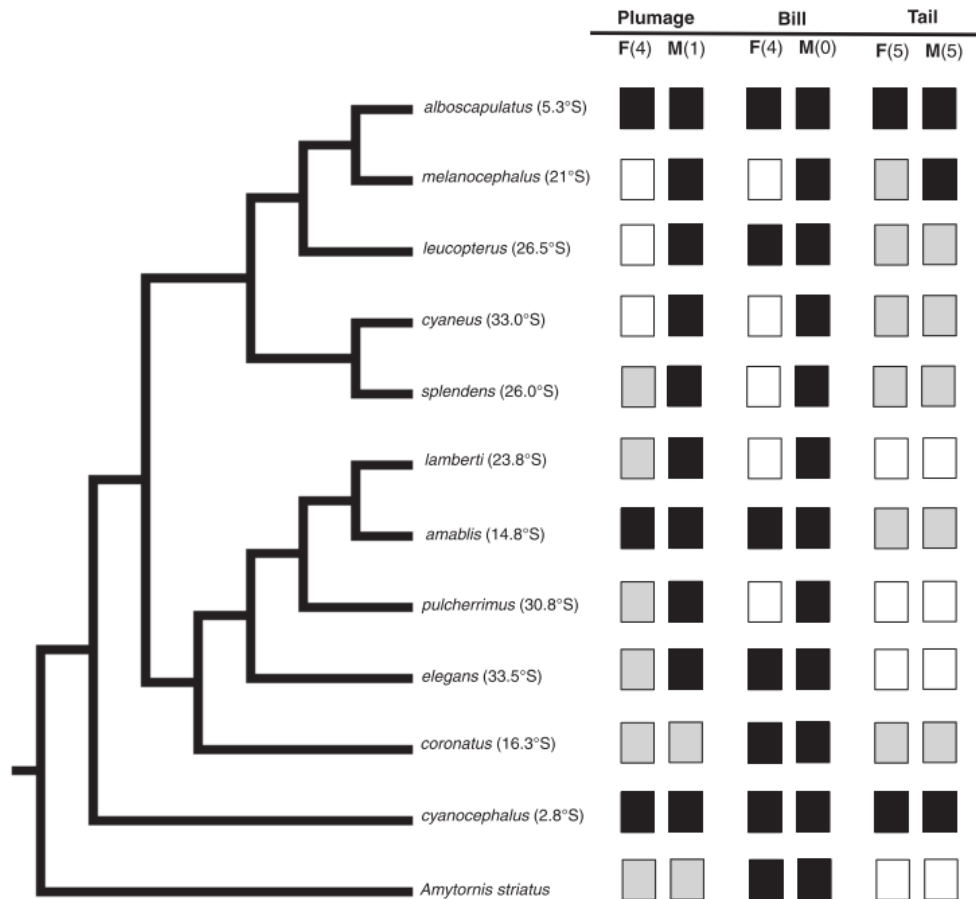


Figure 2. Plumage colouration, bill colouration and tail-length in female fairy-wrens exhibit substantial evolutionary lability. Evolution of tail-length is concordant between the sexes, whereas plumage and bill colouration follow distinctive evolutionary trajectories in males and females. This suggests that patterns of plumage and bill colouration in female fairy-wrens cannot be explained by phylogenetic inertia or genetic correlations with males, and that alternative selective scenarios are likely to apply. Character states for degree of ornamentation exhibited in each trait (black, high ornamentation; grey, moderate; white, low; see Methods) are provided for males (M) and females (F) of each terminal taxon of *Malurus* in the phylogeny of Driskell *et al.* (2011), and for the outgroup (Striated Grasswren, *Amytornis striatus*). The number of evolutionary transitions estimated from character reconstruction is indicated in parentheses for each sex under each trait. Figures in parentheses for each species in the phylogeny are the midpoint latitude of the species range (Figure obtained from Karubian, 2013).

level of sexually dimorphic appearances do not necessarily say anything about the females' development of intrasexual competitive traits, as a species can have monomorphic appearance, without the females having evolved intrasexual competitive traits (Rubenstein & Lovette, 2009). Contradictory, in cooperative breeders, low levels of sexually dimorphic appearances are correlated to high development of intrasexual traits in females (Rubenstein & Lovette, 2009).

Often, systems such as social organisation and mating system affects intrasexual competitive traits because they are mediated by ecological environment (Karubian, 2013). An example of how these systems influence intrasexual competitive traits in females can be found in *Malurus* fairy-wrens (Karubian, 2013). This group consists of non-cooperatively breeding species that can show varying degrees of sexual dimorphism as a result of different amounts of intrasexual competitive traits in the females of the species

(Karubian, 2013). Karubian (2013) studied the ornamentation in female fairy-wrens to give an overview of variation in their ornamentation in relation to phylogenetic, ecological and life-history factors.

Karubian (2013) analysed the species phylogeographically (Figure 2). He found that four out of eleven transitions have taken place in female plumage ornamentation in *Malurus*. Similarly, multiple evolutionary transitions were found between light and black bills. Comparing both plumage and bill colouration to males yields the same result: males showcased little to no evolutionary transition throughout the entire phylogeny in these traits.

Furthermore, Karubian (2013) found that species closer to the equator have an increased degree of female plumage ornamentation. A similar trend was found for females in species closer to the equator displaying more black bills. He thus found a loose

correlation between degree of plumage ornamentation and display of black bill colouration. He therefore concluded that the females of tropical fairy-wren species have developed the highest degree of plumage ornamentation and bill colouration in *Malurus*. For the males, however, the difference in longitude did not seem to matter for plumage ornamentation or bill colouration. These results are in agreement with the idea that ecological environment influences intrasexual competitive traits in females, albeit indirectly through changing e.g. the social competition in the birds (Karubian, 2013).

### (Signals of) Fighting ability

While ornamentation does not directly influence competition, it does so indirectly by e.g. intimidating other individuals. Ornamentation can thus be a signal of fighting capability (Morales *et al.*, 2014). The Iberian population of pied flycatcher (*Ficedula hypoleuca*) has a lower degree of sexual dimorphism in some cases, as the females can sometimes display a white forehead patch, much like males (this can be seen on the "Contents"-page), whereas in European populations, this is absent in females (Morales *et al.*, 2014). As this forehead patch is an intrasexual competitive trait in males, it could very well be one in the females that have this trait as well. Thus, Morales *et al.* (2014) investigated whether this trait plays a role in female-female competition.

From their findings they concluded that the forehead patch does play a role in intrasexual competition

(Morales *et al.*, 2014). They found that females with a patch show greater signs of aggression than females without a patch (Morales *et al.*, 2014). They further noted that if the patch is indeed a signal for fighting ability, the non-patched female most likely avoids the costs of encountering a dominant (patched) female (Morales *et al.*, 2014). The patch thus seems to signal dominance (Morales *et al.*, 2014).

It is predicted that intrasexual competition should occur when either the variation of the opposite sex' quality is high, or when access to resources related to reproductive success is limited (Amundsen, 2000). It was thus thought by Morales *et al.* (2014) that the European population had less variance in the quality of males and better access to reproductive resources (Morales *et al.*, 2014). They further related this to the habitat of the Iberian population, which was more fragmented than its European counterpart (Morales *et al.*, 2014). This could thus potentially mean that habitat fragmentation (and by all extension, humans) can indirectly influence intrasexual competition in females, which could potentially alter the degree of sexual dimorphism in species. This is further enforced by the finding that the ecological environments affect social organisation and mating system in many bird species, which can in turn affect intrasexual competition (Karubian, 2013). Ecological environment can thus, albeit indirectly, affect the level intrasexual competitive traits in females and the level of sexual dimorphism.

## Body size

As mentioned before, many bird species are sexually dimorphic, with the females being duller coloured and are generally smaller in size than the males (Rubenstein & Lovette, 2009). Research suggests this difference in body size is potentially because of opposing selective forces. While social competition may favour larger females, smaller females are favoured for reproductive energetics and thus constrain the selection for larger females (Langston, *et al.*, 1990). Males who are larger than other males will be able to compete better and will thus have better access to females through sexual selection (Darwin, 1888). The same type of competition (and thus selective forces) can apply to females (Rubenstein & Lovette, 2009).

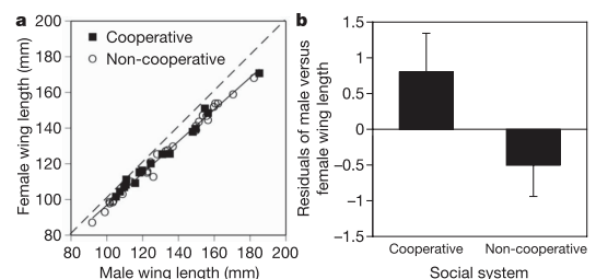


Figure 3. Relationships between male and female wing lengths in cooperatively and non-cooperatively breeding African starlings. **a**, Male and female wing lengths were positively related, but males always had longer wings than females. Cooperative and non-cooperative starlings showed the same relationship (interaction:  $F_{1,40} = 13.97, P = 0.10$ ); the dashed line indicates the line of equality. **b**, The residuals of the phylogenetically controlled relationship between male and female wing lengths were significantly greater in cooperative than in non-cooperative starlings (mean  $\pm$  s.e.), suggesting that in cooperative species, females had relatively longer wings, whereas in non-cooperative species, females had relatively shorter wings (Figure obtained from Rubenstein & Lovette, 2009).

In their study on African starlings, Rubenstein and Lovette (2009) also looked at body size as a component of intrasexual competition. They found that cooperatively breeding species had a significantly lower degree of sexual dimorphism than non-cooperatively breeding species (Rubenstein & Lovette, 2009). This difference in level of sexual dimorphism was not only found in the previously mentioned ornamentation, but also in wing length (body size) (Rubenstein & Lovette, 2009). Their wing size was sexually monomorphic in cooperative breeders, but sexually dimorphic in non-cooperative breeders (Rubenstein & Lovette, 2009). Moreover, while males generally had longer wings than females, the females of cooperatively breeding species had relatively longer wings and the females of non-cooperatively breeding species had relatively shorter wings (Figure 3) (Rubenstein & Lovette, 2009). In his study on the *Malurus* fairy-wrens, Karubian (2013) found that the relative tail-length decreases in both male and female of species that are closer to the equator (Figure 2) (Karubian, 2013).

### Deceptive (competitive) traits

Being larger than your foes is a good advantage to have in intrasexual competition, as it will make it easier to win. It's further assumed that a monomorphic body size indicates that females use this trait for intrasexual competition (Rubenstein & Lovette, 2009). A bigger size is however not necessarily always used in (intrasexual) competition. This can for example be seen in some fairy-wren species, who have bigger tails than the males, without this being used for intrasexual competition.

In many species, males are seen as the bigger sex. Despite this, there are many bird groups where the female is the bigger sex, such as in falcons (*Falconidae*), hawks and vultures (*Accipitridae*), hummingbirds (*Trochilidae*), boobies (*Sulidae*), frigate birds (*Fregatidae*), sandpipers and snipes (*Scolopacidae*) and a handful of other groups (Swaddle *et al.*, 2010). While males are most likely the bigger sex in many species, this example still illustrates the male sex bias quite well, as can be seen in our terminology. When talking about sexual dimorphism, this is usually spoken from the males' perspective, so if body size is sexually dimorphic, this usually means the male is bigger than the female. Consequently, when a species has females that are bigger than the males, this is referred to as a reversed sexual dimorphism (Swaddle *et al.*, 2010). This showcases that the male bias has seeped even seeped into our terminology.

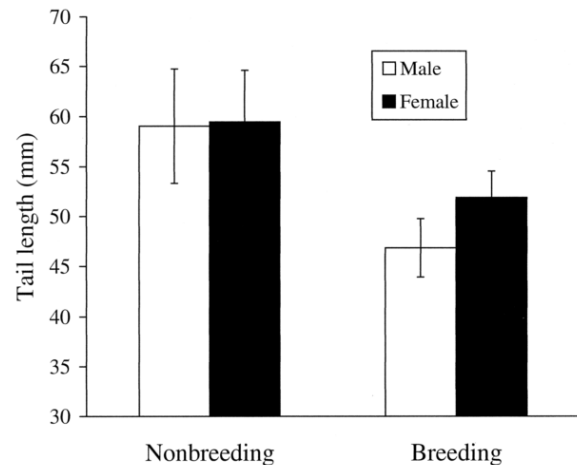


Figure 4.

Mean tail length (mm)  $\pm$  SD in male (hollow bars,  $N = 11$ ) and female (filled bars,  $N = 9$ ) red-backed fairy wrens, in both breeding and nonbreeding plumage. This species exhibits two molts per year, before and after the breeding season. Tails of both males and females are shorter in the breeding season ( $F_{1,18} = 116.82$ ,  $p < .001$ ), but the reduction in tail length varies between the sexes (sex-by-season interaction from a repeated-measures ANOVA:  $F_{1,18} = 6.42$ ,  $p = .021$ ). Tail length in males is shorter than that in females when the males are in breeding plumage ( $t_{18} = 3.36$ ,  $p = .0035$ ) but not when the males are in nonbreeding plumage ( $t_{18} = 0.19$ ,  $p = .85$ ) (Figure obtained from Swaddle *et al.*, 2010).

Swaddle *et al.* (2010) looked at this reversed sexual dimorphism in fairy-wrens (*Maluridae*). They looked at the birds throughout different moments of the year: during the breeding- and nonbreeding season. They found that males had longer tarsi and wings than females, regardless of season. However, males have shorter tail lengths during the breeding season, but in the non-breeding season no sexual dimorphism was found (Figure 4). A "reversed" (or female) sexual dimorphism was thus only found for tail length during the breeding season, other traits either displayed "normal" (or male) sexual dimorphism or no level of sexual dimorphism at all.

Rather than tail length being a female intrasexual competitive trait in this study, Swaddle *et al.* (2010) note that their results suggest that a reduced tail length is the selected ornamental trait in the birds. Thus, whereas in other cases the increased tail length is a trait for which the females choose the males, in this study Swaddle *et al.* (2010) suggest that the decreased tail length is that trait, as it appeared to be advantageous during the breeding season, causing selection for decreased tail length. This study shows that the degree of sexual dimorphism does not necessarily indicate intrasexual competition in females. Traits in birds can be sexually monomorphic and seemingly favoured for the female (such as a bigger tail) without these traits necessarily being used in intrasexual competition in females.



## Viability of classical sexual selection: a discussion & conclusion

As mentioned in the introduction, a better understanding of intrasexual competitive traits is needed to better understand sexual selection, as the current, classical sexual selection theory is rather male-biased (Amundsen, 2000; Forsgen *et al.*, 2004; Heinsohn *et al.*, 2005; Rosvall, 2011; Rubenstein, 2012a; Rubenstein, 2012b; Tobias *et al.*, 2012; Karubian, 2013). Here, I discuss the current controversy surrounding the role of females in sexual selection and the future of sexual selection, as well as giving my own opinion on the matter.

### Female sexual selection controversy

Although controversial, there are currently three main theories that aim to explain intrasexual competitive traits (such as ornamentation) in females (Tobias *et al.*, 2012). The first states that females can display intrasexual competitive traits as a result of genetic correlation between the two sexes (Tobias *et al.*, 2012). This explanation has much support and solid evidence (Lande, 1980; Lande, 1987). Despite this, however, it does not provide a universal explanation and has not received the widespread acceptance that the male-biased sexual selection has received (Tobias *et al.*, 2012). For example, this explanation does not apply in cases where female intrasexual competitive traits differ from those of the males (Karubian, 2013). This explanation further assumes that the traits are selectively neutral or costly (Karubian, 2013). This is at odds with the idea that females evolutionarily rapidly transform from not ornamented to ornamented (Irwin, 1994; Burns, 1998; Hofmann *et al.*, 2008; Karubian, 2013).

The other two explanations are even more controversial. They both state that female intrasexual competitive traits are adaptive in the sense that it affects access to mates through either sexual selection (e.g. mate access) or through natural selection (e.g. resources that indirectly increase reproductive output) (Karubian, 2013). These non-overlapping theories have both been difficult to test however, as the current sexual selection model might be geared to males in such a way that it does not apply to females (Rosvall, 2011).

For example, when looking at males and them maximizing their fitness, we assume them to maximize their number of mates. We expect females however, to focus more on mate quality rather than quantity (because females generally invest more in reproductive output (Bateman, 1948; Trivers, 1972;

Andersson, 1994)). Competition poses a problem as well, as it can be difficult to distinguish when females compete for mates or for resources. Recent studies even suggest intrasexual competitive in females should be less pronounced than in males, because it is less viable for females to invest indirectly in offspring quality by investing in costly ornaments rather than investing directly in fecundity (Kokko & Johnstone, 2002; Chenoweth *et al.*, 2006).

Because of issues and findings like these there has been much discussion about the viability of the current sexual selection theory (Rosvall, 2011). While some proposed to change the current sexual selection theory, others suggested to abandon the current theory of sexual selection entirely (Roughgarden *et al.*, 2006; Rosvall, 2011). For reasons such as these, studies have been conducted and have been called to better understand the development of intrasexual competitive traits in females in a broad perspective to gain better understanding of sexual selection (Hunt *et al.*, 2009; Rubenstein & Lovette, 2009; Cornwallis & Uller, 2010; Robinson *et al.*, 2012; Rubenstein, 2012a; Morales *et al.*, 2014).

Many of the studies mentioned in this paper have tremendously helped the understanding of the development of intrasexual competitive traits in females and the working of sexual selection on females. Despite this, however, it is much harder to understand the entirety of sexual selection on females. While one singular explanation regarding sexual selection for males might have been applicable in the classical theory of sexual selection, it is clear that the same does not apply to females. Sexual selection in females has many different explanations, most of which have been applicable (Rosvall, 2011; Karubian, 2013). For this reason, understanding sexual selection in females is important to get the full picture of the working of sexual selection. At the same time, however, the working of sexual selection on females has sparked heavy debate of the theory.

### Sexual Selection 2.0 (?)

It is safe to say that the sexual selection theory has undergone some heavy controversy following the increase of attention of the working of sexual selection on females. While some argue that the theory needs to be updated or abandoned altogether, others argue that the theory still holds up today and thus does not require much change. This controversy is best illustrated in the [frankly rather amusing] back

and forth between Roughgarden and Clutton-Brock (together with a few others) that has been going on for a few years (Roughgarden *et al.*, 2006; Kavanagh, 2006; Clutton-Brock, 2007; Clutton-Brock, 2009; Carranza, 2009; Roughgarden & Akçay, 2010; Clutton-Brock, 2010).

While both Roughgarden and Clutton-Brock agree the current sexual selection theory needs a change, their opinions differ in the nature of this change. Roughgarden and Akçay (2010) suggest the need for a sexual selection 2.0 and aim to entirely replace the current sexual selection theory, rather than update it. They support this idea with three main claims. For example, they first argue that relationships between the characteristics of females and males and sex differences in gamete and offspring investment, variance in breeding success, and potential rates of reproduction are all riddled with inconsistencies and irregularities (Trivers, 1972; Wade & Arnold 1980; Clutton-Brock, 1988; Clutton-Brock *et al.*, 1988; Clutton-Brock & Parker, 1992; Roughgarden & Akçay, 2010). Their two other main arguments are based on sex differences in reproductive variances and female mating preference (Roughgarden & Akçay, 2010).

Clutton-Brock (2010), on the other hand, is not in agreement with the need for a sexual selection 2.0. He thus counters the arguments given by Roughgarden and Akçay. For Roughgarden & Akçay's (2010) first argument on the inconsistencies in sexual differences in characteristics and investment, Clutton-Brock notes that while these problems do exist, they have been recognized for years and are a vital part of modern sexual selection theory that are refinements rather than flaws of the theory (Campbell, 1972; Clutton-Brock, 1983; Andersson, 1994; Gowaty, 2004; Kappeler & van Schaik, 2004; Clutton-Brock, 2010). The other main arguments are also countered by Clutton-Brock, pointing out how Roughgarden and Akçay exaggerated criticisms and ignored studies (Clutton-Brock, 2010).

Halfway through his paper, Clutton-Brock proposes his own solution for the future of sexual selection (Clutton-Brock, 2010). He suggests focussing on selection between males and females and its components, intensity and targets, rather than distinguishing between natural and sexual selection (let alone Roughgarden and Akçay's (2010) social selection) (Clutton-Brock, 2010). This further

illustrates the difficult position sexual selection is currently in. There are many different opinions, ideas and ways to adapt, update or replace the current theory, but there is much discussion to be had with, as of yet, little progress towards an actual agreement.

### A bias is not necessarily wrong

Finally, I will address the male bias this paper began with. Darwin's sexual selection theory has of course been a fundamental part of evolutionary studies, and still is today. Many researchers looking into the working of sexual selection on females started their paper with addressing the male bias that exists in current literature and in the theory, myself included (e.g. Rubenstein & Lovette, 2009; Karubian, 2013; Morales, *et al.*, 2014). However, despite his focus on males, Darwin was fully aware that sexual selection operates in both sexes (Darwin, 1871). The same goes for Bateman's fundamental principles in his original study on sexual selection in *Drosophila*, who too, had a male bias in his study (Bateman, 1948). Bateman (1948) argued that mating with multiple mates significantly increases reproductive success in males, but not in females. This has however been found to not always be true (Tang-Martinez & Ryder, 2005; Snyder & Gowaty, 2007). Despite this however, Bateman's fundamental principles still stand, as in many species Bateman was correct about the amount of mating partners having a stronger effect of fitness in males than in females (Clutton-Brock, 1988; Rios-Cardenas, 2005; Mills *et al.*, 2007; Clutton-Brock, 2010). The same goes for Darwin's classical sexual selection theory. While it has been proven to not always be the case, the fundamental principles of the theory still remain intact. For this reason, I agree with Clutton-Brock on the notion that the sexual selection theory needs to be updated and improved upon, rather than replaced entirely by a sexual selection 2.0.

There is still much we do not know about sexual selection. Research conducted to study the intrasexual competitive traits in females have helped this field tremendously. Therefore, to better understand sexual selection, this kind of research needs to be continued. After all, "to understand the evolution of sex differences in behaviour and morphology, we need to understand the operation of sexual selection in females as well as in males" (Clutton-Brock, 2009; Clutton-Brock, 2010).

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