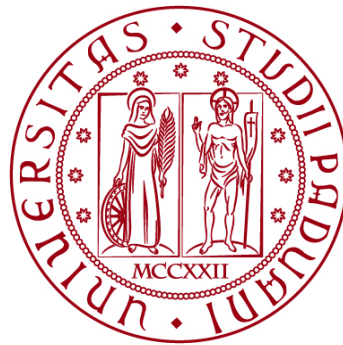


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ELABORATO DI LAUREA

Contemporary perspectives on the armament- ornament hypothesis

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ABSTRACT

La selezione sessuale determina il successo riproduttivo individuale e in questa veste spesso agisce in contrasto con la selezione naturale. La selezione sessuale può determinare lo sviluppo di caratteri sessuali secondari che possono agire all'interno dello stesso sesso con la produzione di armamenti per interazioni aggressive, o intersessuale tramite ornamenti per la scelta del partner. Mentre il funzionamento dei primi può apparire facile da interpretare - monopolizzare le femmine tramite scontri fisici - gli ornamenti agiscono in modo meno diretto. A questa iniziale dicotomia delle funzioni dei caratteri secondari si contrappone il modello 'armament-ornament' che afferma che data la loro linearità nel dare informazioni sulla qualità maschile, un tratto usato come armamento viene poi cooptato dalle femmine ed utilizzato come ornamento. Partendo da questi temi la presente tesi utilizza due studi recenti per vedere nella pratica come questa dicotomia ancora oggi informa lo studio dell'evoluzione. Nel primo studio riportato in 'From ornament to armament' viene studiato il piumaggio appariscente dei maschi di *Malurus coronatus*, arrivando alla conclusione che il tratto 'livrea appariscente' avesse inizialmente una doppia funzione per poi perdere lo scopo ornamentale e funzionare ad oggi esclusivamente come armamento. Il secondo articolo 'In love and war' prende in considerazione due generi di pecilidi ed i loro display della pinna laterale, inizialmente utilizzata come arma e successivamente 'shiftata' a scopo di corteggiamento. I risultati di questi studi indicano la perdita e lo shift di funzione come i due principali meccanismi di coevoluzione tra armamenti ed ornamenti ed inoltre sottolineano la continua rilevanza del modello armament-ornament. L'utilità di questo paradigma viene affermata anche in lavori ancora più recenti che ne considerano l'ampliamento ad altri contesti sociali ed addirittura a strategie anti-predatorie.

Sexual selection shapes individual reproductive success and, under this guise, it can act in contrast with natural selection. Sexual selection can determine the development of secondary sexual traits that can act intrasexually with the production of armaments for aggressive interactions (usually between males) or intersexually through ornaments for mate (usually female) choice. While the function of the former may appear clear - monopolize the females through physical encounters with other males -, ornaments act in a less direct way.

This initial dichotomy between the two functions of secondary traits is challenged by the 'armament-ornament' model which states that, given its linearity in informing on male quality, a trait used as armament will often be co-opted by females and function as an ornament. Starting from these themes, this thesis uses two recent studies to investigate how practically this dichotomy still informs studies of evolution. In the first study reported authors study the use of a secondary sexual trait in *Malurus coronatus* and come to the conclusion that the conspicuous plumage initially had a double function and then lost the ornamental purpose and function, as today it is used exclusively as an armament. The second article takes into consideration two genres of poecilids and their dorsal fin displays, which was initially used as a weapon and then shifted to a purpose of courtship. The results of these studies indicate that the two main mechanisms of co-evolution between

armaments and ornaments are loss and shift of function and emphasize the relevance of the armament-ornament model even today. The usefulness of this paradigm is also affirmed in more recent works that consider its extension to other social contexts and even anti-predatory strategies.

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1. INTRODUCTION

1.1 General introduction

Sexual selection is the mechanism that emerges from the variability in fitness associated with different success in the competition for access to mates, and therefore to reproduction (Shukera & Kvarnemo, 2021). In other words, it arises through preferences for certain characteristics presented by the opposite sex, enhancing an individual breeding chances and the quality of the hypothetical offspring.

As a consequence, sexual selection is the process behind the evolution of elaborated secondary traits. Classically, sexual selection has been hypothesized to work in two different ways: intrasexually, evolving armaments or weapons used in aggressive male-male competition; or intersexually, developing ornaments that will lead to the female choice, as representative of male quality as described by Darwin (1861) and Andersson (1994).

As I will describe subsequently, sexual selection works as an evolutionary drive together with natural selection, but the two might seem to be at times contrasting. If natural selection favours survival by making the individual less subject to predation, the development of secondary sexual traits appears to make it harder to hide and to escape predators. The trade-off between the fitness benefits and the costs of developing such traits shows the important role of this selective force. In this trade-off there is the key to evaluate the current value of the classical armaments/ornaments juxtaposition. In this thesis I will therefore examine how armaments and ornaments have each evolved, and provide a contemporary view of such juxtaposition using as paradigm two recent research studies on the subject.

1.2 The evolution of armaments

The main evolutionary drive behind armaments is easier to understand, as these characteristics have evolved to be more performative in a direct physical encounter. It is also now well known that these traits are involved in trade-offs with other life history and secondary sexual traits (Simmons et al., 2017). All these features contribute to the mechanism known as 'evolutionary arms race', as described by Dawkins & Krebs (1979), stressing the role of competition for the same resource, in this case being females, and leading to more arbitrary directions of weapon evolution.

Thus, this idea supports the hypothesis that weapons evolve independently from female choice, but some studies show otherwise: Emlen (2008) explains that in the majority of the animals studied, armaments had the role of defending crucial resources that had a direct or indirect effect on the chances of mating. The winners of such physical interactions replace their contestant in the social ranking or in the reproductive territory, depending on the species, and are therefore expected to gain benefits in reproduction. Consequently, weapons will be favoured whenever the costs of expressing such traits are less than the benefits, and if we want to translate this in an ecological context, such a thing happens when essential resources are restricted to a limited number of males which are able to monopolize them.

The same article (Emlen, 2008) also explains that, evolutionarily, weapons can start as relatively small traits with a strong utility in aggressive interactions; later variants tend to be much bigger, more complicated, and specifically more likely to be used as status signals, evaluated by rival males. This makes also emerge the need for the coevolution of an assessment behaviour: mutual receivers of such information have to recognise its meaning.

When assessing this topic, it is fundamental to stress the concept of honesty, as Fisher (1930) first explained: weapons signal the differences in individuals' quality, establishing the dominance hierarchy. Consequently, even if at a first glance it could seem beneficial to fake genetic quality in order to gain a higher hierarchic position and reproductive territories, similar individuals will fight against each other for resources: it would be counterproductive for low-quality males to cheat by creating a mismatched armament, because they would be constantly obliged to confront high-level rivals and quickly be recognized as impostors. Therefore, different males undergo different evolutionary drives as the males with the best physical condition are expected to invest more into weapons (Tobias et al., 2012).

Another aspect of interest is the correlation between aspects of the habitat, or the ecology and the types of weapons found. In this context the role of rivals that happen to be present at said space and time, which is not necessary persisting, plays a fundamental role, revealing the sensibility of sexual selection to the changing of events (West-Eberhard, 1983). The authors underline also how this correlation between armament type and environmental factors is only true in animals that fight for a wide range of contexts, and not for similar resources (Tobias et al., 2012).

1.3 The evolution of ornaments

The evolutionary drives behind ornaments are less easily appraised: sexual selection is not essential for these traits to arise as they will be promoted whenever they improve access to resources that are limiting. This happens via social interactions and has the consequence of increasing the fitness of the bearer: direct competition is the strongest and most common social mechanism influencing the evolution of ornamental traits (Tobias et al., 2012).

However, a clarifying explanation of their existence and prevalence can be summarised in the following four hypotheses. (Hill et al., 2014)

1. The species recognition hypothesis, discussed by Wallace (1889). It assumes the simplest role of such ornamentation as species-specific badges and it is based on the fact that mating outside species boundaries is perhaps the worst error a female can make. Nowadays this hypothesis is highly criticised as it should evolve "simple, invariant within a species, and easy to perceive" markers, which are rarely found in nature
2. The sensory exploitation model, stating that ornaments exploit the natural already existing sensory bias towards resources that work in natural selection and trigger the mechanism of positive behavioural response that already exists. A classic example is the presence of a red patch in those

animals that have a diet composed by red fruit; in this way females will naturally tend to approach the coloured males (Rodd et al., 2002).

3. The chase-away model stresses the differences between females and males in mating preferences, with males tending to harass females in order to mate often, with the wrong timing, or with a low-quality partner, enhancing their own reproductive success and not the females'. Thus, this model proposes that, as this preference seems to be inadaptive for females, they are selected to evolve in a way that diminishes their response systems, in order to resist the pressure of males; moreover, this leads to a selection on males for traits that are more and more elaborated in order to reach the female's responsiveness. This model explains that this change in female sensibility happens over evolutionary time.

The strongest proofs for this mechanism, leading to reduced female fitness, comes from an experiment on the mating costs of monogamous versus polygynous breeding in female fruit flies (Rice, 1996). Flies experimentally forced to monogamy lived longer, as opposed to females in which there was a male-male competition for sexual access which showed reduced fecundity and shortened lives. The reported reason was that when multiple mating occurred, what we would call 'sperm competition' would lead males to add toxic constituents to semen to enhance their fitness in spite of females that ended up paying in costs of longevity. Consequently, when sexual selection was removed, the poisonous elements in semen disappeared and females showed normally expected lifetime.

Such relationship of coevolving traits to respond to others' behaviours is perfectly described in the Red Queen Hypothesis (Van Valen, 1973). Even if especially relevant in the relationship between parasites and hosts, it explains that each individual's purpose is to benefit itself: when undergoing a negative effect inflicted in the relationship with another individual, the adaptive changes to respond will be shortly followed by the improvement of the offender. This would lead to a 'race' in developing antagonistic traits that are each generation stronger and more efficient.

4. The runaway model, or Fisherian, supports the idea of a self-reinforcing process between female choice and male ornamentation, which will lead to an exaggeration of the male trait. This mechanism begins when some males "carry genes for a trait that bestows a fitness advantage such as a slightly longer tail that enhances flight ability".

Because of sensory exploitation, some females carry genes that make them prefer such trait, and this is reflected in the offspring, that will inherit more beneficial genes: both the ones for better traits, both those for the characteristic preference in females. This translates in what is defined 'sexy sons': the benefits of producing traits that are primarily driven by natural selection (like aerodynamic tails in birds), start to become secondary to the benefits for producing attractive sons, that will later be advanced in reproduction.

This mechanism leads to an exaggerated elaboration of the trait and to the fact that the preferences of females will be led to an extreme; eventually, the fitness (natural selection) costs in the form of reduced survival and fecundity from having a burdensome ornament, will outweigh the benefits of sexy sons and the runaway process will be halted.

As said before, armaments can also evolve in badges of status and are driven by dominance hierarchies, but this is not prerogative of weapons. For example, the red facial coloration of male rhesus macaques follows the same mechanism, as this trait that predictably evolves under female mate choice also “mediates agonistic interactions with rivals during competition over reproductive opportunities” meaning that dominance rank correlates with facial redness. This implies this trait to be under both inter and intrasexual selection; however, results keep open the possibility of the simpler explanation that “the color variation reflects differences in male condition” (Petersdorf et al., 2017), as producing and maintaining such traits is an important energetic cost, bearable only to the healthier ones.

There can also be a context, age and condition-specificity to ornaments; this is shown in the Black Grouse (*Lyrurus tetrrix*), where the positive correlation between ornament quality and dominance has a specific development in the breeding season: because of the important energetic cost of maintaining such traits for a longer timespan, they are more beneficial for adults that can prioritise ornaments as they have already developed and have more energy to spend. On the other hand, younger males favour a later growth of their ornaments and more importantly they regulate such expression only accordingly to the amount of time spent on the lek, which correlates directly with dominance: when far from females, ornaments would not be needed and therefore less energy can be invested in them (Harris et al., 2018)

1.4 Issues with the dichotomic division between ornaments and armaments

This dichotomic concept dividing sexual traits in two distinct categories gradually changed due to many studies proving that sexually selected traits may have a dual function (Olivera & Custòdio, 1998; Tobias et al., 2011).

As a matter of fact, later research showed that ornamental traits, such as conspicuous plumage or elaborated calls, might function as a badge of aggressive behaviour. Indeed, they can convey information about the quality of their bearer in all those agonistic interactions to obtain mates or other resources.

As stated in Berglund et al. (1996): “some traits classically thought to be weapons, such as the antlers of ungulates or the chelae of the fiddler crabs, may also function as signals revealing the fighting ability of the male and thus serve to settle contests without real fighting.”

As said in chapter 1.2, in this context a great role is played by honesty, that is maintained by male-male interactions and proves its role as only real quality males can afford the high costs of producing such elaborated traits.

Therefore, for a time the most appreciated theory was the armament-ornament hypothesis, which stated that because of their linearity in proving male quality, traits used primarily in male-male interactions get later co-opted by females as rank indicators (Tobias et al. 2011).

On the other hand, some affirm that it has been our own biased view that made us consider weapons as analogous to ornaments for such a long time. As a matter of fact, to our eyes many weapons may seem ornamental, but in reality, the two traits might not be conflated.

This point of view, which doesn't necessarily disagree with what was assumed before, is perfectly summarized in McCullough et al. (2016): the evolution of male ornaments and of male weapons might be expected to proceed differently. This because, if females show a tendency to pick a trait, and if there is genetic variation for both the female preference and such ornament, genetic covariance will arise between the two. By doing so, females with the keenest preferences, will only mate with males that show the most attractive trait themselves.

Another aspect to take into consideration is that weapons and ornaments also participate differently as catalysts in speciation: there is a direct link between female choice and reproductive isolation as such preferences can be a direct barrier to gene flow among population that are diverging; on the contrary male-male competition has no such effect. Indeed, the way they act as driving forces in the creation of new species is yet another distinction not to forget (McCullough et al., 2016).

As a matter of fact, reading more into this topic makes it clear how these changes arise via mechanisms that are interceded by social interactions. This is because, on a first level, they seem to be counterproductive: they charge with costs without contributing with any survival benefits, and they don't act under a strictly survival drive.

As explained in Tobias et al. (2012) the original definition of social selection gives a clarification. It explains that the theory of it approaches social interactions in the widest sense, and this includes all the social contexts that can drive selection, sexual or non-sexual. The best way to approach it, but maybe not the most attainable, would be to divide all these social mechanisms into 'sexual social selection' and 'non-sexual social selection'.

1.5 Purpose of the thesis

The aim of this thesis is to take a step forward in the understanding of the armament-ornament eventual coevolution, and in the evolutionary interaction between them. I also dedicate a section to how the armament-ornament hypothesis remains relevant to these days.

I'm going to assess such themes by analysing articles that expose different hypothesis. The first article is about loss of function and is an experimental study in birds. The second article deals with the shift of function in poecilids using a comparative approach. Both papers are of interest because they further develop the theories by testing them practically.

2 HYPOTHESIS 1: ‘From ornament to armament or loss of function? Breeding plumage acquisition in a genetically monogamous bird’

This article examines how conspicuous seasonal plumage in purple-crowned *Malurus coronatus* males influences their male-male competitive interactions. It asserts that their breeding plumage, which nowadays appears to be used predominantly in male-male interactions, could represent a shift in function from a sexual trait that was formerly selected by females. This concept was elaborated because, as in other phylogenetically close *Malurus*, the male reproductive success and the female extra-pair (EP) mate choice are strongly correlated to the timing males obtain ornamental plumage. However, in most *Malurus* females select the feather colouration via extra-pair mate choice, but not in the monogamous *Coronatus*.

In this first hypothesis, this trait, initially used as an ornamentation, is now maintained by male-male competition because of its evident role in obtaining and defending a breeder position. It functions as an intrasexual indicator of dominance and competitive ability, as the results show “subordinate males in more complete breeding plumage being more likely to win a breeder position”.

Nevertheless, a more compelling alternative hypothesis is that initially this trait had a dual function, and later its ornamental use was lost. The article states that, being used in both female choice and male–male competition, the ornamental function was lost with the disappearing of extreme EP paternity levels and female EP mate choice.

It is important to take into consideration that when an expensive trait loses one of its functions it should theoretically disappear, unless it has multiple roles or changes function. This concept matches the armament-ornament hypothesis above-mentioned: intersexual mate choice co-opts the traits used in intrasexual competition, as they signal individual qualities also in a potential mating view. Moreover, a shift or loss of function can show changes in trait expression or selection, shifting among multiple components of indication. In this case, however, the only remaining use for the trait would appear to be as an armament in male-male competition.

This article shows a greater elasticity in the role of sexual ornaments than commonly appreciated. It also implies independence in losing or gaining functions of ornaments, notwithstanding them being used either in intra or intersexual selection, adding an interesting new perspective to the complexity of this topic.

3 HYPOTHESIS 2: ‘In love and war: the morphometric and phylogenetic basis of ornamentation, and the evolution of male display behaviour in the livebearer genus *Poecilia*

The hypothesis in this case is that there was a shift of a male display from what originated for male-male aggression, which later became a display co-opted for courtship. The traits taken into consideration is “the ornamental dorsal fins in male poecilid fish of the subgenera *Mollienesia* and *Limia*, which exhibit convergent development of an enlarged dorsal fin, and often direct erect fin displays to male and female conspecifics”.

This hypothesis is based on the fact that, phylogenetically speaking, male competitive displays are distributed way more broadly than the courtship displays, an indication that male-male aggression came first; consequently, extreme dorsal fin height “may have arisen secondarily to enhance the vigor or efficacy of male aggressive and courtship displays”.

This would support the armament-ornament hypothesis and would be congruent with an evolutionary switch in the main mechanisms of sexual selection from intra- to intersexual. Moreover, as added proof, the data also shows that species that use fin displays only for male-male competition have males with smaller dorsal fins, and vice versa such traits are larger in those species where fin displays have a dual function (both courtship and competition).

4 METHODS AND RESULTS

4.2 From ornament to armament or loss of function?

To test whether subordinate males succeed in obtaining breeding positions depending on their breeding plumage, the authors used a 6-years dataset on *Malurus Coronatus*, whose males sport a dull brown head plumage in nonbreeding season and purple and black feathers during the breeding season.

They then proceeded with periodical population censuses conducted year-round to monitor the size of groups and social status of the males, in order to establish “the extent of breeding plumage on a scale between 0% and 100%”. The tarsus length (as indicator of male quality) and the territory quality were also periodically measured.

To test whether the strength of territorial defence was affected by the plumage of male intruders, they presented 3D-printed models representing males with different simulated stages of plumage: brown nonbreeding, purple back breeding and a similar size bird belonging to another species as control.

They then measured several aspects like the latency and duration of response, closest approach, time spent within 1 and 3 m of the model and number of songs...; recording other aggressive behaviours such as swooping and pecking.

Subsequently, they took into consideration if the role of breeding plumage in male-male interactions could depend on constitutional and environmental factors (like age, territory quality, within group rank and group size); if it could predict the possibility of subordinates obtaining a breeder position; and whether breeding plumage of simulated male intruders modifies the power of territorial defence by resident breeder individuals, and whether this varies with the plumage state of resident males.

They also tested whether the response in its totality differed between male and female breeders using similar models to those for males.

Eventually, this study shows that older subordinate males, and thus higher ranked in the progression line for the inheritance of breeder position, produced a more elaborated breeding plumage and were therefore more successful in acquiring a breeder position by competing.

As a proof of its role exclusively in male-male interaction, males in breeding colours experience more aggression from resident breeder males than when

showing dull plumage but evoked limited response from females; this is consistent with the idea of competitors in breeding plumage being recognized as a bigger threat to the breeder male. Even though there is not enough proof to exclude or confirm one of the two hypothesis -loss or shift of function, this study resents experimental evidence that a trait lost its use as an ornament, retaining it as an armament.

In other words, the authors show proof that, as of now, a trait which either had a dual function or was selected because of mate choice is maintained thanks to male-male interactions.

4.3 In love and war

For this study, the species of choice are *Mollienesia* and *Limia*, as previously mentioned. They are both in the genus of *Poecilia*, and even though closely related, they have “independently evolved ornamental display structures, and they use comparable displays for courtship and competition”.

A behaviour, characteristic of both aggressive male encounters and courtship display is the S-posture, “a sigmoid body curvature in which they swim parallel or antiparallel to each other with their backs arched and their dorsal fins fully spread”. The phylogenetic approach showed the ancestral status of dorsal fin erection, as it is observed in all species with male-male aggression.

Firstly, they examined how ornamentation, morphology, and behaviour interacted in both species by measuring each trait and adjusting each measurement to the individual's size.

Secondly, they introduced a high ornamentation index (OI) for the measurement of dorsal fin exaggeration. As a matter of fact, this gives a lot more information on the variability of such traits, previously treated exclusively as present or absent and now evaluated in a more nuanced way.

They predicted that a high OI should be “positively correlated with sexual dichromatism and multicomponent courtship displays, and negatively correlated with female-biased sexual size dimorphism and relative gonopodium length, because species without ornate fins tend to have long male intromittent organs and larger females”.

They then proceeded to map the evolution of the continuous index “display behaviour onto a new phylogeny of the two subgenera” via taxon sampling, DNA alignments and molecular dating analysis through various indexes and algorithms.

The OI index suggests that there is a minimum size of dorsal fin height that must be reached in order to develop competition interactions between males, and that “further increased dorsal fin height is a prerequisite in turn for the evolution of courtship displays to females”.

Moreover, as aggression is more frequently observed than courtship among the two species, the conclusion is that the use of two display components like dorsal fin erection and sigmoid body postures in aggressive male interactions should come before the co-option of both elements in order attract females.

Furthermore, the authors particularly stress the importance of a comparative approach to trait evolution and dual-utility traits, highlighting the role of phylogenetic analyses, behavioural observation, and ancestral state reconstruction.

5 Conclusion

5.1 Latest works: further expansion of the dichotomy

In recent years, evidence has further accumulated that despite the use of the above-mentioned model as a theoretical basis, a number of other factors are also in play when considering the evolution of secondary sexual traits. Specifically, natural selection can also influence the function of traits usually considered sexually selected (and vice versa). Whiting et al. (2022) used a similar approach to the armament-ornament model when analysing the deimatic display in the lizard *Phrynocephalus mystaceus*, a species that presents cheek flaps in both sexes that get unfolded to increase the appearance of body size and threaten predators.

Aposematic signals, that get associated with a cost to the attacker by causing an unpleasant experience, and deimatic displays, that exploit the sensory system of the receiver and cause a fear reaction that discourages the attack, frequently have a dual function, and inform the receivers in various ways.

Although the present thesis focuses on the signals used in social and sexual selection, an interesting and rarely investigated relationship is the one taken into consideration in the above-mentioned article between anti-predator behaviour and conspecific social signalling. The authors state that not only deimatic and aposematic signals have this dual function of surviving a predation attempt, but also ornaments or armaments that are normally considered sexual selected traits can be co-opted for natural selection: “any survival benefit from one of these structures could set the stage for selection”.

This cryptic lizard was taken into consideration to study the hypothetical co-option of conspicuously coloured signals from quality indicators to anti-predator defence or vice versa, as both sexual and natural selection can be evolutionary drives for the development of such traits.

Although the study did not find strong evidence of coevolution between the two functions, they discovered context-specific responses, in accord with their hypothesis. They also cite the frill-neck lizard (*Chlamydosaurus kingii*) that uses its frill both as anti-predator response and as a sexual dimorphic secondary sexual trait for social interactions; furthermore, many species of lizards expose brightly coloured mouths during encounters with predators and we still don't know the reason behind it.

The next stage in this line of research would be to deepen the influence of context and to test for multiple signals, as the authors highlight a much more relevant presence of deimatic displays than we think, developing our knowledge in sensory ecology.

Fiddler crabs are another example of the role of sexual and natural selection intertwining (Levinton, Weissburg 2021), as huge claws are both used as ornaments attracting females and as armaments in the interactions between males but have a relevant role also in the killing of preys and as defence from predators via cheliped

autotomy. Autotomy is generally induced as an escape mechanism from predators via the self-induced amputation of a claw, a non-vital organ, in order to distract them and run away; therefore, the regenerated claw shows considerable variation in size and form relative to the other chelipeds. This sometimes results in dishonest signalling to females and possible rivals, because of the presence of relatively weakened regenerated major claws.

As a final example of the role of predation in the dichotomy between armaments and ornaments, the “Love and war” article also mentions the “aggressive spill over” hypothesis as an explanation for the passage in behaviour from an exclusively male-male competition role to the addition of a female mate choice function. This theory suggests that “aggression towards prey “spills over” into the mating context due to genetic constraints on the plasticity of aggression”. In the context of the original article, “more aggressive females more likely catch more prey and grow larger, but also consume courting males and may thus remain unmated” (Golobineh et al., 2021).

Recent work also questions the classic role of breeding colours as quality indicator and thus their function as ornaments reflecting the energetic investment in colour maintenance (McQueen et al. 2021). Superb fairy-wrens (*Malurus cyaneus*) differ from what seen in chapter 2 as early-moulting males do not present more conspicuous colours, nor such colouration is impacted by experimental low body conditions: experimentally testosterone-implanted males didn’t show a difference in plumage colouration from non-implanted males nor there were any variations between control males and those with induced early winter moult (which should suffer harder conditions); furthermore such coloration doesn’t show a comparable trend with aging. The authors suggest that such colours might evolve as they label species identity, are aesthetically attractive or make displays more striking.

An interesting take on the evolution of secondary sexual traits is when the trend in conspicuousness takes the opposite direction. In Spikes et al. (2021) they examine the female preferences for male size, that in *Limia perugiae* favours smaller males. This gives new insight on how secondary sexual traits impact female preference and opens the possibility of a not yet studied coevolutionary relationship.

Therefore, in this case the genetic benefits of mating with larger males must be insufficient for the normally observed trend to appear in this species. In order to explain this unexpected data, they suggest that, because the experimental context eliminates predation risk, the preference for small males could reflect an increased courtship on behalf of the latter which can now compete with bigger males in mating. Although the data appears interesting, the cause behind it clearly still needs to be investigated.

Even if the authors end up not developing one specific theory to explain this, this study excludes the responsibility of pre-copulatory female preferences in the maintenance of male ornaments in this species; furthermore, they affirm that such traits could be “the product of alternative selective forces or may not even be adaptive”, contesting the general knowledge on sexual selection.

In conclusion, we can highlight the relevance of models like poecilids, where the relationship between the trait taken into consideration and the result in sexual selection is easily measurable and often gives precise data on this topic. Such genus also has a widely mapped genome, making phylogenetic comparison very precise.

Furthermore, we can assume the ornament-armament hypothesis to still be relevant to these days and indeed applicable to a wider range of situations than Darwin originally thought, even if such recent works still need to be developed: this hypothesis could be used as a general model for all those situations where a trait gets co-opted and not only in sexual selection.

Although the way the two secondary sexual functions have coevolved still hasn't been unanimously assured, we can nowadays assume two main evolutionary mechanisms, i.e. loss and shift of function, that seem to have acted accordingly to species-specific patterns. Both mechanisms can be investigated and confirmed via the armament-ornament model, thus we could now develop our knowledge in the evolution of social selection by seeking the correlations between the loss of function or shift of function hypothesis and the species where each has been observed and compare them.

All these studies give us a paradigm that expands our point of view in sexual selection and makes such theory not only more modern and nuanced, but also more realistic as we know evolutionary forces to intertwine.

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