Why are sexually selected weapons almost absent in females?

Anders BERGLUND*

Department of Ecology and Genetics/Animal Ecology, Uppsala University, Norbyv. 18d, 752 36 Uppsala, Sweden

Abstract In sex role reversed species, predominantly females evolve sexually selected traits, such as ornaments and/or weapons. Female ornaments are common and their function well documented in many species, whether sex role reversed or not. However, sexually selected female weapons seem totally absent except for small wing spurs in three jacana species, present in both males and females. This poor female weaponry is in sharp contrast to the situation in species with conventional sex roles: males commonly have evolved sexually selected weapons as well as ornaments. At the same time, females in many taxa have naturally selected weapons, used in competition over resources or in predator defence. Why are sexually selected weapons then so rare, almost absent, in females? Here I briefly review weaponry in females and the function of these weapons, conclude that the near absence of sexually selected weapons begs an explanation, and suggest that costs of sexually selected weapons may exceed costs of ornaments. Females are more constrained when evolving sexually selected traits compared to males, at least compared to those males that do not provide direct benefits, as trait costs reduce a female’s fecundity. I suggest that this constraining trade-off between trait and fecundity restricts females to evolve ornaments but rarely weapons. The same may apply to paternally investing males. Whether sexually selected weapons actually are more costly than sexually selected ornaments remains to be investigated [Current Zoology 59 (4): 564–568, 2013].

Keywords Sexual selection, Female weapons, Female ornaments, Sex role reversal

1 Introduction

Traits used as weapons in fights between individuals are common in animals, and are found in both males and females of many species (Emlen, 2009). Weapons (for definitions, see Box 1) may serve functions in for instance predator defence, defence against suitors, in resource competition, or in mating competition. For females, some additional explanations to weapon evolution have been suggested: they may exist due to a genetic correlation with the same trait in males (interestingly, the reverse has not been suggested, i.e., males possessing weapons due to a genetic correlation with the corresponding female trait). Moreover, another suggestion for the evolution of female weaponry, the male mimicry hypothesis, is about avoiding intimidation of sons by weapons in adult males – if the mother is also armed, sons may be less scared by adult males and stay with the mother for longer (Estes, 1991). So which of these functions do female weapons serve? I will briefly go through some well researched taxa, and discuss how female weapons are used. I will not dwell on differences between adaptive and non-adaptive (i.e., genetic correlations between the sexes) explanations, and I will not try to differentiate between the explanations relying on natural selection (e.g., anti-predator, resource defence, male mimicry), but I will contrast natural selection explanations with sexual selection ones.

2 The Use of Female Weapons

In bovids (cattle, sheep, goats and antelopes) males typically have horns, but in many species females also possess such weapons, albeit usually smaller and differently shaped (Caro et al., 2003; Bro-Jørgensen, 2008; Stankowitch and Caro, 2009). In male bovids, horn evolution is thought to be driven by male-male competition for females, whereas female horns may serve as defence against predators or in female-female competition over territories (Roberts, 1996; Stankowitch and Caro, 2009). Indeed, horn size in females has been used to quantify the proportion of male weaponry that can be due to natural selection, the remainder is then assumed to be sexually selected (Bro-Jørgensen, 2007). Large, conspicuous, open-living bovids typically have females with horns used in predator defence, and such horns are thought to have evolved repeatedly in this family (Stankowitch and Caro, 2009). In smaller, inconspicuous territorial bovids, such as many duikers, females defend their territories against other females aided by their horns. Horns of this type are thought to have
evolved once, and then only among the duikers (Stankowitch and Caro, 2009).

In cervids (deer), females have antlers in only one species, the reindeer, but these are again thought to be naturally selected. Females use them to establish dominance, in particular over males. In fact, females keep their antlers for longer than males, thus securing feeding sites for themselves and their calves (Espmark, 1964).

Other ruminants also seem to lack sexually selected weapons (Box 1) in females: ossicones (horn-like skin-covered protuberances) in giraffes are used in male-male “necking” fights, whereas females have proportionately smaller ossicones, skulls and necks and are not known to use them in combat or dominance (Simmons and Scheepers, 1996). In the related okapi, however, females are territorial (Hart, 1992) and may use their ossicones in territory defence against other females. In pronghorns, finally, female have pronghorns but presently seem not to use them at all, although these horns have been suggested to be anti-predator devices against now extinct predators (Byers, 1999). Thus, in no ruminant species females are known to use their horns in intrasexual combat over males, presumably because sex role reversal (Box 1) seems absent in this taxon.

The lack of sexually selected weapons in females seems in fact to be the rule in all mammals. For instance, in boars, elephants and rhinos females use tusks and horns as tools or anti-predator devices, i.e. these traits are naturally selected or due to a genetic correlation with male traits (Estes, 1991). In male narwhales tusks may be used in aggressive encounters (Silverman and Dunbar, 1980). Some females may also develop tusks, but their function, if any, is unknown.

Birds pose a much more interesting taxon for the search for female sexually selected weapons. Several sex role reversed species exist, especially among waders such as phalaropes and jacanas. Unfortunately birds are seldom heavily armoured, but spurs exist in many species. In three species of jacana, the wattled, the northern and the pheasant-tailed jacana, males as well as females have wing spurs (Fig. 1, Rand, 1954). They are similar in size between sexes (Rand, 1954), but as females overall are larger than males, spurs are proportionately smaller in females. Nevertheless, females may use their spurs in displays at mating time, “as if they were attempting to strike each other with their sharp spurs” (Rand, 1954). These spurs are, in fact, the only (likely) sexually selected female weapon I have found, even if the evidence is somewhat anecdotal.

In several species of swans, geese, screamers, plovers and lapwings both sexes may have wing spurs (Rand, 1954), but their function in females is not well known. As these birds typically have more conventional sex roles (Box 1) female spurs are unlikely to be used in female-female fights over males, and their use seems primarily to be defence against enemies or intruders (Rand, 1954), or use in competition over resources for chicks (B. Lyon, pers. comm.). Female rallids (coots, moorhens) have huge claws (as do males), used in fights over territory borders and resources for chicks (B. Lyon,
Current Zoology

Fig. 1  A female northern jacana *Jacana spinosa*, with wing spur
(from http://scienceblogs.com/tetrapodzoology/2010/07/14/spurs-blades-jacanas-lapwings/)

pers. comm.). The spurs in gallinaceous birds (fowl), located on the tarsus, are found in males only (Rand, 1954).

In some reptiles, for instance horned lizards (*Phrynosoma*) and thorny devils *Moloch horridus*, both males and females have spiny horns (Emlen, 2008), but these function primarily in predator defence (Young et al., 2004). In fish sexually selected weapons are quite rare, and I know of no case where females possess such in spite of sex role reversal being not uncommon (e.g., many pipefish species, Berglund and Rosenqvist, 2003). In some crustaceans females are armed, like in the snapping shrimp *Alpheus armatus*, but those weapons are used in territory defence (Knowlton and Keller, 1982). In several beetles females possess weapons, sometimes even larger than those in males. This is for instance the case in the dung beetle *Onthophagus sagittarius*, but these females use their horns in contests over dung (a resource for reproduction), not in fights over access to males (Watson and Simmons, 2010).

3 Why Are Sexually Selected Weapons So Rare in Females?

Female sexually selected weaponry thus seems almost non-existent. Rather, when females possess weapons, they are naturally selected, used in competition over resources other than mates, in predator defence, or are non-functional (Caro et al., 2003; Bro-Jørgensen, 2007; Emlen, 2008). In other words, female weapons may often belong to the realm of social selection (West-Eberhard, 1983; Lyon and Montgomerie, 2012; Tobias et al., 2012), but not to that of sexual selection as defined in Box 1. Still, females in many species have sexually selected ornaments, attractive to males (e.g., Clutton-Brock, 2009). Even if the endeavour to explain the lack of something may seem strange, I still think the paucity of female sexually selected weaponry, in the face of frequent female ornamentation, begs an explanation. The question is then, why do females have ornaments, but typically not weapons, to aid them in acquiring males? One possibility is of course if weaponry and sex role reversal for some reason are found in different taxa – if so, females would remain unarmed in the context of sexual selection. This is perhaps a possibility in mammals where sex role reversal is uncommon (but see e.g. Kuester and Paul (1996) for a possible exception), but cannot apply to birds, fish or insects, where we find both sexually selected weapons and sex role reversal within lineages. Another possibility is that females, for some reason, engage in mate attraction and in dominance interactions, but not in direct fights with other females over males. If so, sexually selected weapons would of course be superfluous in females. However, females of many species are indeed aggressive towards one another and do engage in direct fights over resources as well as mates (e.g., Andersson, 1994; Eens and Pinxten, 2000; Clutton-Brock, 2012).

To take one step back, we first need to understand if costs and benefits of sexual selection differ between males and females. If we compare non-investing males (Box 1), who do not provide females or offspring with direct benefits such as paternal care or nuptial gifts, with females, sexual selection definitely operates differently in the two sexes. In addition to all possible costs associated with developing and possessing sexually selected traits that apply to both sexes, females always face an additional cost: that to their fecundity. Resources allocated to a sexually selected trait will trade off with resources allocated to egg production in all females, and also to any further offspring care if provided. This will constrain the evolution of sexually selected traits in females: they need to trade ornaments for offspring (Fitzpatrick el al., 1995; Clutton-Brock, 2009; Tobias et al., 2012). Exactly the same trade-off will be present in
males, if they provide females or offspring with direct benefits (Fitzpatrick et al., 1995). In other words, anisogamy suffices to constrain trait evolution more in females than in males, and any further parental investment (sensu Trivers, 1972) provided for the offspring by the females may amplify the constraint. Conversely, a reversal in the difference of the direct benefits provided by the parents, so that male parental investment exceeds that of females, may reverse the constraint on trait evolution to operate more strongly on males. Still, even under the last scenario, females will always produce eggs, and so never can rid themselves from the trade-off between fecundity and sexually selected traits. Moreover, benefits from sexually selected traits may also differ between the sexes. Payoffs from such traits may be lower in females than in males if for instance anisogamy thwarts the value of additional matings more in females than in males. Again, this would act to produce less extreme traits in females.

So, can this constraint on trait evolution in females explain why they evolve ornaments rather than weapons? Possibly, but only if sexually selected weapons are more costly than ornaments. We expect females to evolve “cheap” traits so as not to compromise their fecundity, and if weapons are more expensive than ornaments that would explain the paucity of the former. So are weapons expensive? This is not known and for now remains a speculation. I think it would be odd if energetic or other production costs of weapons were prohibitive, as many females possess naturally selected weapons. Can the cost of provoking and entering real fights with other females, risking injury, be prohibitive? If this is the case costs and benefits from sexually selected traits could look like in Fig. 2. Here, a steep rise in costs with trait size for sexually selected weapons compared to ornaments, together with females being more cost-sensitive than non-investing males, prohibits females from evolving weapons but permits the evolution of ornaments. Maximizing the difference between benefits and costs in Fig. 2 would render sexually selected weapons in females unfeasible, in contrast to male sexually selected weapons and male and female ornaments. A similar argument could be raised when comparing investing with non-investing males (Box 1): we would expect sexually selected weapons in the former to be absent or small, and ornaments to prevail, i.e., the cost curves in Fig. 2 may look similar for females and investing males. For simplicity the benefit curve in Fig. 2 is drawn similarly for females and non-investing males. However, benefits may likely be lower in females if they typically gain less from multiple matings compared to males. Again, this would further reduce the likelihood that females develop sexually selected weapons.

4 Conclusion and Future Directions

Sexually selected weapons in females are near-absent, but female ornaments are not uncommon. As the evolution of sexually selected traits in females is compromised by effects to their fecundity, females are typically very cost-sensitive. If sexually selected weapons somehow are more costly that ornaments, this may explain the paucity of weapons in females relative to males. We now need to understand several things to explain the absence of female sexually selected weapons. First, we need more clearly to understand the function of female weapons. It is not uncommon to find explanations to weapons in terms of their value to females in defending resources for themselves and their offspring, but when males have the same weapons and defend the same resources they are said do so to attract females. Thus, female weapons would automatically become “naturally selected” and male weapons “sexually selected”! To avoid such just-so stories we need much better insights into how and why weapons are used. Second, we need to compare costs of sexually selected weapons and ornaments. This may not be an easy task—often one and the same trait functions as both a weapon and an ornament (Berglund et al., 1996), so disentangling the two may be a formidable task. Moreover, costs must be measured in terms of costs to individual fitness, and such measures are notoriously difficult to obtain. Nevertheless, if we succeed, we can finally understand why something hardly exists, namely female sexually selected weapons.

Acknowledgements I thank Bruce Lyon for fruitful discussions on this topic and for good comments on the manuscript.
References


