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The Evolution of Sexual Dimorphism: Understanding Mechanisms of Sexual Shape Differences

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1. Introduction

Understanding the origin of biodiversity has been a major focus in evolutionary and ecological biology for well over a century and several patterns and mechanisms have been proposed to explain this diversity. Particularly intriguing is the pattern of sexual dimorphism, in which males and females of the same species differ in some trait. Sexual dimorphism (SD) is a pattern that is seen throughout the animal kingdom and is exhibited in a myriad of ways. For example, differences between the sexes in coloration are common in many organisms [1] ranging from poeciliid fishes [2] to dragon flies [3] to eclectus parrots (see Figure 1).



Figure 1. A) Male Eclectus (© Stijn De Win/Birding2asia)
B) Female Eclectus (© James Eaton/Birdtour Asia)

Sexual dimorphism is also exhibited in ornamentation, such as the horns of dung beetles [4], the antlers of cervids [5], and the tail of peacocks [6]. Many species also exhibit sexual differences in foraging behavior such as the Russian agamid lizard [7], and parental behavior and territoriality can be dimorphic in species such as hummingbirds [8, 9]. Another common pattern is that of sexual size dimorphism, such as is observed in snakes [10] and monk seals [11].

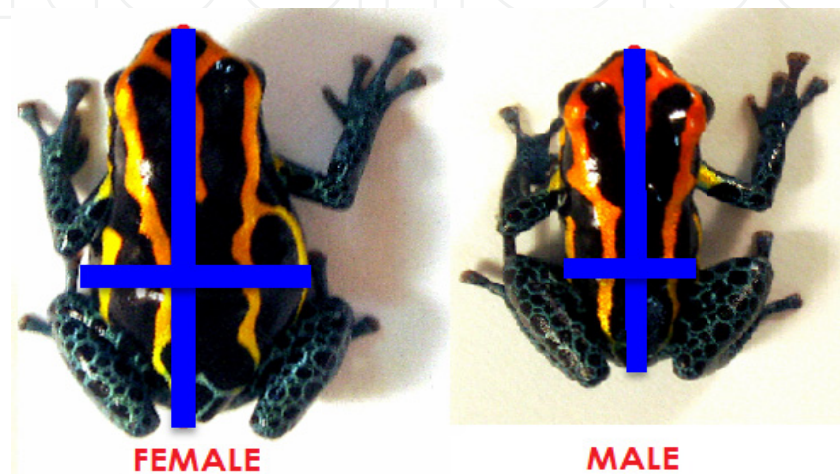
There are many mechanisms that drive the evolution of SD, the most accepted mechanism being sexual selection [12-14], which enhances fitness of each sex exclusively in relation to reproduction [15, 16]. This states that SD evolves in a direction such that each sex (especially males, see 17) maximizes reproductive success in two ways: by becoming more attractive to the other sex (inter-sexual dimorphism) or by enhancing the ability to defeat same-sex rivals (intra-sexual dimorphism), in both cases such that each sex increases the chances to mate and pass genes on to the next generation. Many researchers have argued that competition for mates is at the very heart of sexual selection because these rivalries greatly influence mating and fertilization success. Indeed, competition for mates has been shown to be the major factor impacting SD in several taxa [18]. However the complexity of SD cannot be explained by a single mechanism.

Mate choice is an important proximate mechanism of sexual selection. Often the sex with the higher reproductive investment is the 'choosy' sex. Patterns then emerge, such as those consistent with the 'sexy son' hypothesis [19], where females prefer mates with phenotypes signifying fitness. The females prefer males that are phenotypically 'sexy' to ensure that the genes of their offspring will produce males that will have the most breeding success, propagating her genes successfully [16, 20]. Taken further, sometimes females prefer males that exhibit very extreme phenotypes within a population. Over evolutionary time these traits become increasingly exaggerated despite the potential fitness costs to the males themselves, termed Fisherian runaway sexual selection [19]. Examples include the tails of male peacocks, plumage in birds of paradise and male insect genitalia [14, 21, 22].

Alternatively, ecological mechanisms, such as competition for resources, may exert distinct selective forces on the sexes resulting in the evolution of SD [23]. Here, intraspecific competition in species-poor communities may allow divergent selection between the sexes (rather than between species), resulting in sexual niche segregation [12, 24-26]. In this case morphological traits often change to minimize this intersexual competition. Other ecological hypotheses have been proposed to explain patterns of SD, such as the influence of sex-specific divergence in response to environmental gradients (i.e., intersexual niche packing; sensu 27]. For example, both sexes of fruit flies *Drosophila subobscura* increase in body size with latitude, however in South America these size increases are less steep and weaker in males as compared to females [28]. Another study found weaker latitudinal clines in males as compared to females in houseflies *Musca domestica* [29], and yet another study found geographical variation in climate that corresponded to a change in the magnitude of sexual size dimorphism between males and females [30]. Hypotheses continue to be proposed and the explanations for the evolution of SD may not be mutually exclusive but instead, may operate in a synergistic or antagonist fashion to shape these patterns.

2. Processes and patterns of sexual size dimorphism

Sexual size dimorphism is a frequent phenomenon where the size of males and females of the same species differ (see Figure 2), driven by one or more of the mechanisms mentioned above. When these processes occur in closely related species, distinct patterns of among-species size dimorphism can result, one of which is termed 'Rensch's Rule' [31]. Rensch's rule is a pattern wherein the degree of sexual size dimorphism increases with body size in species where males are the larger sex, and conversely decreases in those species where females are the larger sex (see Figure 3).



Photograph by: <http://www.joshsfrogs.com/catalog/blog/category/poison-dart-frog-care>

Figure 2. Sexual size dimorphism in poison dart frog.

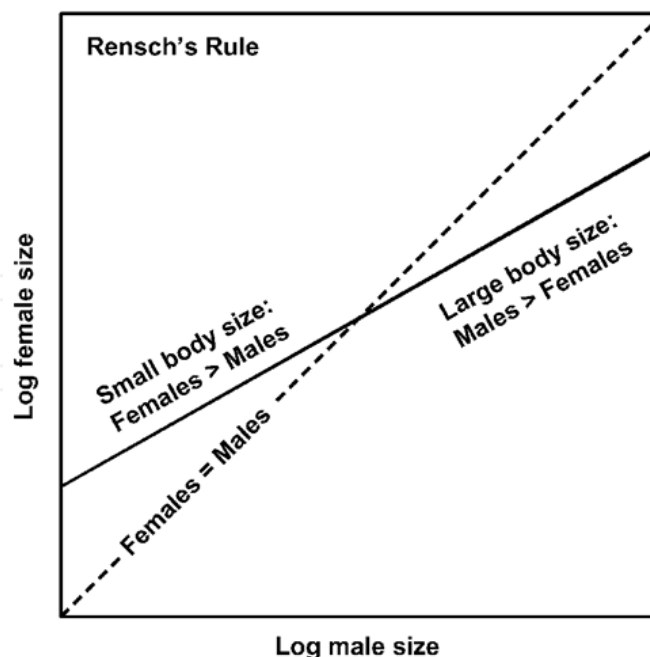


Figure 3. Rensch's Rule, where in species above the broken line (broken line denoting where female and male sizes are equal) females are larger than males and below, males are larger than females. From R. Colwell, Am. Nat., 2000.

Several hypotheses have been proposed to explain Rensch's rule. One proposes that the combination of genetic correlations between male and female size with directional sexual selection for larger male size will cause the evolution of larger males relative to female body size [13, 32, 33]. Another argues that sexual size dimorphism evolves through intraspecific competition between the sexes when foraging is related to size [15, 26]. Finally, many researchers have hypothesized that this pattern is due to female fecundity, where the larger female will have bigger eggs and a greater capacity to reproduce successfully [15, 34, 35]. Examples of Rensch's rule and support for all three hypotheses abound in nature in organisms as diverse as hummingbirds [36], hummingbird flower mites [36], water striders [32], turtles [37], salmon [38] and shorebirds [39].

Another such pattern is that of 'adaptive canalization', where the larger sex has less plasticity compared to the smaller sex. This is due to directional selection for a large body size and individuals with sub-optimal body sizes will have lower fitness [40, 41]. Alternatively, there may be condition-dependence, where the larger sex is under stronger directional selection for a large size and will be more affected by different environmental factors as compared to the smaller sex. This indicates that sexual size dimorphism should change with changing environments. These hypotheses and studies have led to much understanding of the patterns and processes underlying sexual size dimorphism.

3. Sexual shape dimorphism

In addition to sexual size dimorphism, males and females often differ widely in shape [42, 43]. Curiously, although shape can contribute meaningfully to various functions such as feeding, mating, parental care and other life history characteristics, patterns of sexual shape dimorphism have historically received considerably less attention than sexual size differences [12, 44, 45, 46]. Examining the size and shape of traits together provides a much more complete quantification of sexual dimorphism, as the two components are necessarily related to one another. As such, shape analysis allows a deeper understanding of mechanisms underlying SD, because different parts of the body can serve multiple functions and be under distinct selective regimes.

Shape is defined as the specific form of a distinct object that is invariant to changes in position, rotation and scale [46, 47], and many methods have been proposed to study shape. For instance, sets of linear distances may be measured on each individual (e.g., length, width and height) to represent shape (Figure 4A), as well as angles (Figure 4B) and ratios of these measurements.

Sets of linear distances do not always accurately capture shape because of shortcomings that limit their general utility. For instance, it is possible that for some objects the same set of distance measurements may be obtained from two different shapes, because the location of the measurements is not recorded in the distance measures themselves. For example, if the maximum length and width were taken on an oval and teardrop, the linear values might be the same even though the shapes are clearly different (see Figure 5). Additionally, it is not possible to generate graphical representations of shape using these measurements alone

because the geometric distances among variables is not preserved and aspects of shape are lost [48]. As a result of these shortcomings, other analytical approaches for quantifying shape have been developed.

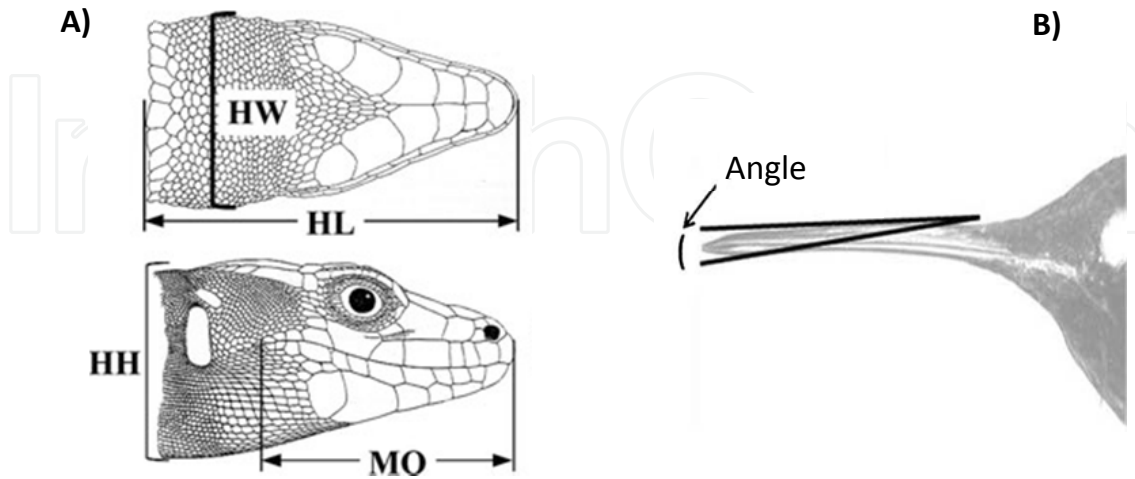


Figure 4. A) Sets of linear distances: Head length (HL), head width (HW), head height (HH), and mouth opening (MO) and B) Measurement of angle. A): adapted from Kaliontzopoulou et al. 2012. B): adapted from Berns and Adams, 2010

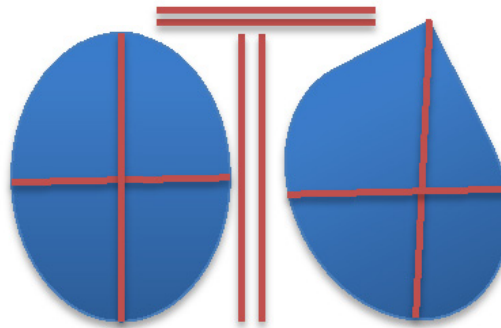


Figure 5. Maximum height and width taken on two different shapes results in the same linear measurement on both

A major advance in the study of shape is landmark-based geometric morphometric methods, which do not have these difficulties. These methods quantify the shape of anatomical objects using the Cartesian coordinates of biologically homologous landmarks whose location is identified on each specimen (Figure 6). These landmarks can be digitized in either two- or three-dimensions, and provide a means of shape quantification that enables graphical representations of shape (see below).

Geometric morphometric analyses of shape are accomplished in several sequential steps. First, the landmark coordinates are digitized from each specimen. Next, differences in specimen position, orientation and size are eliminated through a generalized Procrustes analysis. This procedure translates all specimens to the origin, scales them to unit centroid size, and optimally rotates them to minimize the total sums-of-squares deviations of the landmark coordinates from all specimens to the average configuration. The resulting

aligned Procrustes shape coordinates describe the location of each specimen in a curved space related to Kendall's shape space [49, 50]. These are then projected orthogonally onto a linear tangent space yielding Kendall's tangent space coordinates [47, 51, 52], which can then be treated as a set of shape variables for further analyses of shape variation and covariation with other variables [e.g., 53, 54, 55].

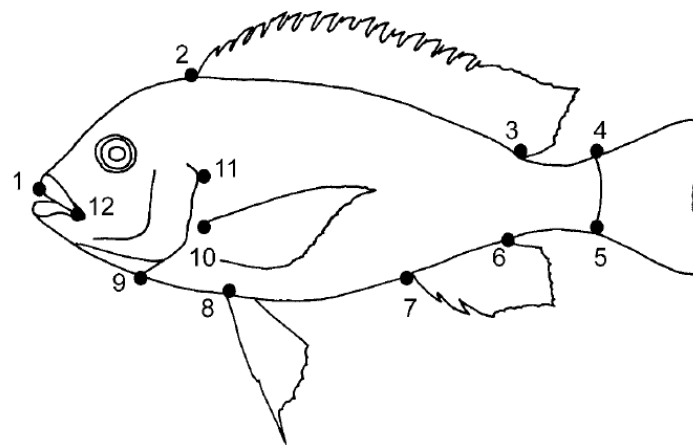


Figure 6. Example of biologically homologous landmarks From Kassam *et al.* 2003

In terms of sexual shape dimorphism, dimorphism, sets of both linear measurements and geometric morphometric methods have been utilized to identify patterns of shape dimorphism in numerous taxa, including fish [56], turtles [57], birds [58-61] and lizards [62, 63]. In addition to quantifying sexual shape dimorphism, identifying the potential mechanisms that generate these patterns is a current focus of many evolutionary biologists. For instance, one central hypothesis for the evolution of sexual shape dimorphism is that males and females diverge phenotypically due to intersexual competition for similar resources. Here, functional morphological traits diverge between the sexes such that the sexes partition resources. Under this scenario, SD is more strongly influenced by natural selection than sexual selection. For example, in the cottonmouth *Agkistrodon piscivorous*, sex-specific prey consumption as a function of prey size is directly correlated with differences in head morphology between males and females [64]. Thus natural selection, and not sexual selection, maintains both foraging and morphological differences between the sexes in this species.

By contrast, sexual shape dimorphism can be the result of sexual selection. For example, in the tuatara *Sphenodon punctatus*, Herrel *et al.* [65] tested the hypothesis that sexual shape dimorphism is due to niche differentiation between the sexes, rather than driven by the territoriality of males. Head shape is much larger in males as compared to females and this may be functionally tied to the larger prey of males. The authors suggested that sexual selection for male-male combat may play a role, but that bite force differences between males and females may be impacting the maintenance of these sexual differences. Interestingly, it was found that males do have a greater bite force relative to females, but that these differences and their maintenance are the result of sexual selection, as bite force is correlated with good male condition but not with female condition [66].

Another study also rejects the hypothesis that differential niches maintain sexual shape dimorphism. Feeding, territory, and mate acquisition have been proposed as functions for the bill of the Cory shearwater *Calonectris diomedea* [61]. The bill morphology is such that sexual differences are related not to feeding ecology, but to sexual selection and antagonistic interactions. On the other hand, the Purple-throated Carib *Eulampis jugularis* hummingbird exhibits the clear link between function and the different food preference of males and females, suggesting that the longer and more curved bill of the female as compared to the male is due to the division of resources [67-69]. In other species of hummingbirds that exhibit sexual size and shape dimorphism in their bills however, it is unclear whether interspecific competition and niche differentiation, sexual selection, or some other force drives this sex-specific morphology [58, 60].

One study investigated the relative contributions of intersexual resource partitioning and sexual selection in the amagid lizard *Japalura swinhonis* [63]. Here, sexual shape dimorphism was not correlated with diet, however limb size and shape were associated with perch habitats. These findings are inconsistent with the hypothesis of intraspecific competition for resources, but provide evidence for the 'fecundity advantage' hypothesis. Under this hypothesis, a large mother can produce more offspring than a small mother, and can give her offspring better conditions through directional selection [14]. For instance, an increase in abdominal volume can arise with an increase in overall body size, seen in some mammals and amphibians [70, 71], or in the abdomen's relative proportion to overall body size, like that of some reptiles [72]. Olsson *et al.* [73] examined SD in the heads and trunk length of an Australian lizard *Niveoscincus microlepidotus* to address the hypothesis that head morphology dimorphism had evolved via sexual selection for male-male combat and that trunk length evolved due to fecundity selection. Results did not uphold one part of this prediction however, as sex divergence in head morphology was genetic and not specifically due to sexual selection. Evidence was presented in favor of the prediction that difference in trunk length is driven by fecundity advantage, and that sexual selection favored males with smaller trunk size. Studies such as these suggest that sexually dimorphic shape traits may be driven by the combination of natural selection for fecundity advantage and by sexual selection.

Evidence supporting fecundity advantage is weak or not existent in many systems however. For instance, investigators examining the tortoise *Testudo horsfieldii* hypothesized that the wider shells of the females provided more room for eggs, but were unable to provide conclusive evidence for fecundity advantage. Instead, the patterns of sexual shape dimorphism seemed to be due primarily to locomotive constraints of mate seeking and male-male combat [74]. In two species of crested newt *Triturus cristatus* and *T. vulgaris*, results somewhat support fecundity advantage, however researchers suggest there are more underlying processes driving the evolution of sexual shape dimorphism than simply fecundity selection [75]. Evidence presented by Willemsen and Haile [76] outright reject the fecundity advantage hypothesis. Three tortoise species *Testudo graeca*, *T. hermanni*, and *T. marginata* have differing courtship behaviors and display differing magnitudes of sexual shape dimorphism dependent on their specific courtship display. In contrast to previous

studies, the authors suggest that these results indicate that sexual shape dimorphism is driven not by fecundity advantage and natural selection, but rather by sexual selection. From the inconcordant results of studies such as these, it remains unknown whether patterns of the evolution of sexual shape dimorphism are primarily driven by natural selection for fecundity advantage or by some other mechanism.

Environmental conditions are also hypothesized to drive the evolution of different shapes between the sexes. Evidence for one environmentally-driven hypothesis is presented in a study looking at environmental gradients underlying SD and parallel evolution of a species of guppy *Poecilia reticulata* [28]. Results indicate that populations experiencing high predation were made up of males with smaller heads and deeper caudal peduncles. Open canopy sites resulted in selection for females with smaller heads and distended abdomens, whereas both sexes in high flow sites had small heads and deeper caudal peduncles. Males and females showed some shared responses to the environmental gradients, thus indicating that environmental variables may be responsible for sexual shape dimorphism more than sexual selection pressures might be. More support for the hypothesis that environmental processes drive variation in sexual shape dimorphism is found in the Greater Antillean *Anolis* lizards that exhibit sexual size and shape dimorphism. Males and females use habitats differently and although sexual size dimorphism is not highly related to habitat use, sexual shape dimorphism is [77]. Further study on West Indian *Anolis* lizards also suggests environment as a major factor driving the patterns of sexual shape dimorphism. Concordant with the Greater Antillean *Anolis* lizards, the shape dimorphism clearly reflects the different niches occupied by males and females [43].

Although these and numerous other examples demonstrate the influence of environment on the evolution of sexual shape dimorphism, a recent study examined sexual shape dimorphism in the snapping turtle *Chelydra serpentina*, and found no evidence that environmental condition was correlated with shape dimorphism. Unlike sexual size dimorphism, shape dimorphism was evident at hatching and at 15.5 months, where both males and females exhibited this pattern under optimal and suboptimal conditions. When adults however, sexual size dimorphism was present and differed under conditions such that there is increased plasticity of the larger sex as compared to the smaller. Interestingly however, sexual shape dimorphism still did not vary with differing conditions [57]. It has been suggested for over a century that environment is a major driver of morphological differences [78, 79], and new evidence such as this presents an opportunity to further understand the variables at play in the evolution of shape dimorphism.

Broadly, allometry (defined as a change in shape related to a change in size: 45) has also been suggested as having an influential impact on sexual shape dimorphism [80, 81]. In an example of evolutionary allometry, Gidaszewski *et al.* [45] examined sexual shape dimorphism in the wings of nine species of *Drosophila melanogaster* in a phylogenetic framework. Sexual shape dimorphism diverged among the nine species, however the evolution of sexual shape dimorphism was constrained by evolutionary history. This provides evidence that, while allometry is a large part of the evolution of sexual shape dimorphism in this system, it is not the main factor driving shape dimorphism.

Kaliontzopoulou *et al.* [82] studied heterochronic patterns of allometry in two species of lizard, *Podarcis bocagei* and *P. carbonelli*. Here, allometry did influence sexual shape dimorphism such that males and females actually differed in allometry with respect to head shape and body size, where change in male size increased disproportionately relative to head size and dimensions. Yet another recent study on sexual shape dimorphism in the stalk-eyed fly *Teleopsis dalmanni* found conclusive evidence for the impact of allometry on sexual shape dimorphism, where the size of the eye bulbs decreased with an increasing eye span and eyestalks became more elongated as they became thinner (Figure 7; 83).

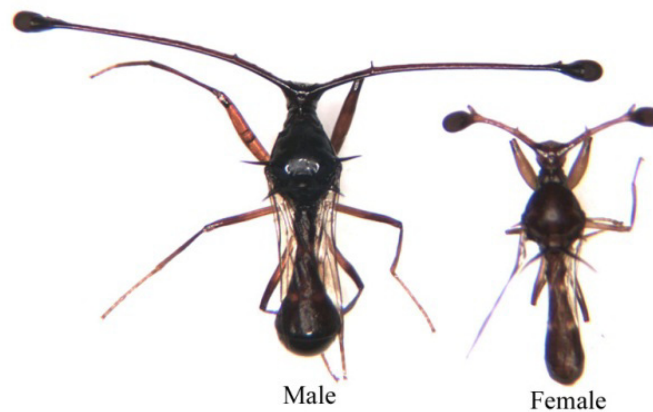


Figure 7. Sexual shape dimorphism in eye stalks of *Teleopsis dalmanni* (Photo credit: Jerry Husak)

Exceptions continue to be found however. For instance, in a recent study examining sexual size and shape dimorphism in the bill morphology of two hummingbirds *Archilochus colubris* and *A. alexandri*, Berns and Adams [58] examined a model that included an allometric component. This model was found to be inferior to those that included size, shape, and sex. When graphically depicted, it was clear that allometry is a less influential factor in the evolution of sexual shape dimorphism. However, as shown by the studies above it seems that allometry is generally an important process driving the patterns of evolution in sexual shape dimorphism.

Conserved genetics may be yet another factor driving patterns of sexual shape dimorphism. Sexual shape dimorphism has been studied in the piophilid fly *Prochyliza xanthostoma* (Piophilidae) and the neriid fly *Telostylinus angusticollis* (Neriidae) to address the impact of conserved genetic factors on patterns of sexual shape dimorphism [84]. These related species share similar patterns of sexual shape dimorphism, but have drastically different ecological and functional requirements as well as male-female interactions. Given that shape dimorphism is the similar trait in these three species, these flies may have congruent patterns of shape variation interspecifically, not due to common life-history requirements [84]. Bonduriansky suggests that this may be due to conserved genetics common to both species, or a reflection of interspecific variation in selection. In 2007, Bonduriansky [85] performed another study on *Telostylinus angusticollis* to examine condition-dependence and genetic variation. Sexual dimorphism is significantly correlated with the condition such that these two traits share a common genetic (and developmental) base. Therefore, it is possible that in this, as well as other systems, sexual shape dimorphism is a pleiotropic effect where

sex-linked genes determine the allocation of traits differently in males and females. Any variation of these genes due to plasticity may then determine the genetic relationship of sexual shape dimorphism and differing conditions. Many genetic hypotheses continue to examine sexual size dimorphism and just recently is sexual shape dimorphism receiving attention.

4. Conclusion

Although studies are currently underway, many questions about sexual shape dimorphism still remain. For instance, how frequently is sexual shape dimorphism exhibited and how is this related to ontogenetic and biomechanical influences? Worthington *et al.* [83] propose that the sexually dimorphic patterns seen in the stalk-eyed fly are due to sexual selection, but also to biomechanical and possibly ontogenetic constraints. However, more information is necessary before a conclusion can be made about the actual process underlying the pattern of sexual shape dimorphism. Kaliontzopoulou *et al.* [82] suggest that a lack of sexual differences in cranial development of *Podarcis* species may indicate an ontogenetic limitation on both sexes, but also note that the habitat appears free of head constraint. The examination of ontogenetic development as well as biomechanical constraints on sexual shape dimorphism may reveal much about the causes and selective forces of these patterns, many of which are still unknown.

Does sexual shape dimorphism follow well-known patterns of sexual size dimorphism, such as Rensch's Rule? How much impact does allometry have in driving the evolution of sexual shape dimorphism? Although patterns such as these have been suggested as a component of sexual shape dimorphism, only recently have researchers begun to investigate these patterns. Is allometry in sexual shape dimorphism common? Berns and Adams [58] did not find a significant effect of allometry, whereas Worthington *et al.* did [83]. In species of *Drosophila melanogaster*, allometry did not explain the majority of evolutionary divergence of sexual shape dimorphism [45], while in *Podarcis bocagei* and *P. carbonelli*, Kaliontzopoulou *et al.* [82] showed that allometry was present and even differed in males and females. These inconcordant results suggest that there is a multifaceted interaction between sexual size dimorphism, sexual shape dimorphism and allometry. Examining size alone shows only a piece of the mechanisms contributing to allometry, thus attention needs to also focus on allometry and it's relationship with sexual shape dimorphism.

As seen in the examples in this chapter, much of the evidence on processes underlying sexual shape dimorphism is incongruent. One area needing attention is that of the correlation between sexual shape dimorphism and fecundity advantage, as shape may impact egg carrying capacity as size does. More work is needed to assess genetics and sexual shape dimorphism, and studies continue to argue that sexual selection causes sexual shape dimorphism due to male-male combat and mate choice, while others argue for natural selection via environmental factors and interspecific competition. No doubt that all of these factors play a role in influencing the evolution of sexual shape dimorphism, but what are the patterns? Do vertebrates tend to follow one trend while invertebrates follow another? In

closely related species, does body size impact the effect of condition dependent sexual shape dimorphism? Just how much can natural selection and sexual selection be teased apart?

We are just beginning to test the questions about the role evolutionary history plays in patterns of sexual shape dimorphism. How do phylogenetic relationships effect sexual shape dimorphism? What role does sexual shape dimorphism play in microevolutionary patterns and what are the mechanisms underlying these patterns? What might result when these patterns are scaled from micro- to macroevolution? One way to address these questions is to take a sequential comparative approach: first examining patterns of dimorphism in two closely related species, then scaling up to family, genera, and so forth. It is now also possible to ask if rates of evolution differ between species and if these rates differ more broadly between different sexually dimorphic traits. What effect do habitat and environmental gradients play in assessing rates and patterns of sexual shape dimorphism evolution? By examining the possible correlation between sexual shape dimorphism and habitat variables in a phylogenetic manner, it is possible to quantify hypotheses such as these. With the advent of new phylogenetic techniques, morphometric methods, and statistical testing, we can further examine the details of the evolution of sexual shape dimorphism.

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