

## REVIEW

**Male–male competition, female mate choice and their interaction: determining total sexual selection**

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**Abstract**

Empirical studies of sexual selection typically focus on one of the two mechanisms of sexual selection without integrating these into a description of total sexual selection, or study total sexual selection without quantifying the contributions of all of the mechanisms of sexual selection. However, this can provide an incomplete or misleading view of how sexually selected traits evolve if the mechanisms of sexual selection are opposing or differ in form. Here, we take a two-fold approach to advocate a direction for future studies of sexual selection. We first show how a quantitative partitioning and examination of sexual selection mechanisms can inform by identifying illustrative studies that describe both male–male competition and female mate choice acting on the same trait. In our sample, the most common trait where this occurred was body size, and selection was typically linear. We found that male–male competition and female mate choice can be reinforcing or opposing, although the former is most common in the literature. The mechanisms of sexual selection can occur simultaneously or sequentially, and we found they were more likely to be opposing when the mechanisms operated sequentially. The degree and timing that these mechanisms interact have important implications for the operation of sexual selection and needs to be considered in designing studies. Our examples highlight where empirical data are needed. We especially lack standardized measures of the form and strength of selection imposed by each mechanism of sexual selection and how they combine to determine total sexual selection. Secondly, using quantitative genetic principles, we outline how the selection imposed by individual mechanisms can be measured and combined to estimate the total strength and form of sexual selection. We discuss the evolutionary consequences of combining the mechanisms of sexual selection and interpreting total sexual selection. We suggest how this approach may result in empirical progress in the field of sexual selection.

**Introduction**

Sexual selection arises from variation in reproductive success, and can be regarded as an evolutionary process distinct from natural selection. This Darwinian separation arose because, more often than not, natural and sexual

selection are in conflict with natural selection ultimately limiting the elaboration caused by sexual selection (Darwin, 1859, 1871). Darwin further provided two mechanisms through which sexual selection operates: male–male competition and female mate choice. Even though Darwin emphasized the importance of both of these mechanisms for the evolution of sexually selected traits, from the outset most researchers focused on one mechanism at a time in their studies. Early considerations of sexual selection focused almost exclusively on male–male competition as female mate choice was

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dismissed as an implausible process (Huxley, 1938). The 1980s, however, brought a reconsideration of the potential independence of female behaviour and resulted in a plethora of studies documenting the existence of female mate choice (Andersson, 1994). Theory and models of how female mate choice results in the evolution of elaborate characters stimulated empirical research into mate choice (Mead & Arnold, 2004; Andersson & Simmons, 2006; Kokko *et al.*, 2006). Without fear of eliciting much dissent we can declare Darwin was right: both male–male competition and female mate choice are important mechanisms resulting in sexual selection.

Students of sexual selection have long realized that controlling for male–male competition is an important component of investigating mate choice (Halliday, 1983). This is because male–male competition and female mate choice rarely act independently (Bradbury & Davies, 1987; Berglund *et al.*, 1996; Qvarnström & Forsgren, 1998; Wong & Candolin, 2005). Studying a single mechanism or both mechanisms in isolation and controlling for the other is valuable in that it identifies the occurrence of one or both mechanisms. Such studies can also identify how they occur and which traits are affected. However, studies of mechanisms in isolation obfuscate a critical aspect of sexual selection: how do the mechanisms interact to result in total sexual selection? The strength and form of selection imposed by male–male competition and female mate choice frequently differ (Bradbury & Davies, 1987; Qvarnström & Forsgren, 1998; Wong & Candolin, 2005) so that total sexual selection operating on a male trait may be very different from that imposed by either mechanism in isolation. Consequently, a complete understanding of how sexual selection drives the evolution of male sexual traits can only come by studying the mechanisms of sexual selection both separately and in unison.

The notion that competitively superior males confer direct or indirect fitness benefits to females underpins much of our current thinking regarding sexual selection (Mead & Arnold, 2004; Andersson & Simmons, 2006; Kokko *et al.*, 2006). It has been suggested that one area where females can gain indirect benefits is to choose males that are successful in competition with other males (Berglund *et al.*, 1996; Wiley & Poston, 1996). Under these conditions we expect male–male competition and female mate choice to be reinforcing for the same male sexual trait(s). This certainly occurs (Berglund *et al.*, 1996), but is not universal (Moore, 1990; Qvarnström & Forsgren, 1998; Moore & Moore, 1999; Wong & Candolin, 2005). Indeed, one of the strongest areas of sexual selection research is examining how and when male and female interests diverge and result in sexual conflict (Parker, 1979; Arnqvist & Rowe, 2005). Male-driven sexual selection frequently imposes substantial costs on females (Chapman, 2001; Pitnick & Garcia-Gonzalez,

2002; Arnqvist & Rowe, 2005). Where such costs exist, it can be in a female's best interest to avoid mating with a dominant male (Moore *et al.*, 2001, 2003). Thus, there is no *a priori* reason to expect that the mechanisms of sexual selection will always operate in a similar manner (Arnold, 1983, 1985).

In this review, we evaluate the examples of the empirical evidence for the way that the mechanisms of sexual selection interact when they target the same trait(s). In contrast to previous reviews on this topic (Bradbury & Davies, 1987; Berglund *et al.*, 1996; Qvarnström & Forsgren, 1998; Wong & Candolin, 2005), which focused on whether the mechanisms overlap or not, we are illustrating how selection is typically measured and then examine the consequences that interactions between the different mechanisms of sexual selection will have for the evolution of male sexual traits. In particular, we emphasize how well-established analytical tools from quantitative genetics can be used to determine how the selection imposed by male–male competition and female mate choice combine to give the total strength and form of sexual selection operating on a male sexual trait(s). We conclude by discussing how approaches incorporating these insights may result in empirical progress in the study of how elaborate sexual traits evolve through sexual selection.

## Empirical evidence

Our primary aim in presenting case studies of examples of male–male competition and female mate choice operating within a species is to illustrate the value in examining the interaction between male–male competition and female mate choice. We hope to highlight the type of information we can gain and exploring possible general implications for the evolution of male sexual trait(s). There are many more comprehensive reviews of the literature on sexual selection, beginning with Andersson (1994) and leading to more recent and focused reviews by Neff & Pitcher (2005), Kokko *et al.* (2006), Ritchie (2007) and Kokko & Jennions (2008). We do not intend to replace these or the other reviews we have cited. Indeed, we restricted our examples in important ways. First, we focused exclusively on studies where sexual selection is clearly partitioned into male–male competition and female mate choice. Second, we only included those studies where the target of selection (i.e. the male sexual trait) is clearly identified. Showing mate choice or male–male competition occurs is necessary but not sufficient for the approach we hope to encourage. Third, we consider only those cases where the outcome of male–male competition and female mate choice are influenced by the same male trait. There are literally thousands of studies and species where male–male competition and female mate choice target different traits. These are not uninteresting, but require a different framework and different review, such as those cited

above. Finally, for convenience, we focus on male sexual traits, male–male competition and female mate choice. This is not a necessary assumption, but is used for heuristic purposes. We recognize that there can be ‘sex-role reversal’ and that the principles of intersexual and intrasexual selection are general. However, we adopt this convention as male–male competition and female mate choice are the most commonly studied. Our conclusions and generalizations should hold equally well for those species where females compete for mates and males discriminate among potential suitors.

One of the reasons for this review was the realization that within a population male–male competition and female mate choice can interact on different time-scales. This was made obvious to one of us when working on a territorial species where mate choice was restricted to males successful in gaining a territory (Moore, 1990) and then a species with dominance hierarchies where sometimes males gain mates by being dominant and sometimes by being preferred by females (Moore & Moore, 1999). Temporal separation or overlap of episodes of selection has implications for how each mechanism contributes to total sexual selection (Arnold & Wade, 1984a,b; Wade & Kalisz, 1989). Consequently, for each species we consider, we use available information on the mating system to classify the nature of the temporal interaction between mechanisms of selection. In particular, we classify the mechanisms of sexual selection as operating either simultaneously or sequentially within a population. In the former case, the two mechanisms occur contemporaneously, and the mating success of a given male within the population is influenced by either mechanism but not by both. Thus, the outcome of male–male competition is largely independent of female mate choice and vice versa. For example, in many mating systems with dominance hierarchies, male–male competition is ongoing and unsettled and mate choice sometimes occurs when dominant males are otherwise engaged (Moore & Moore, 1999). Thus, males can gain mating by either being dominant or by being attractive to females. In contrast, when the mechanisms of sexual selection act sequentially, mating success of a given male in the population is influenced by both male–male competition and female mate choice. One mechanism always precedes the other, which restricts the distribution of male traits(s) available for the later mechanism to operate. A classic example of this occurs in lekking species, where female mate choice typically follows an intense episode of male–male competition, settling the potential access to some males prior to the arrival of females (Moore, 1990; Höglund & Alatalo, 1995).

The case studies listed in Table 1 suggest a number of patterns in the sexual selection literature. First, body size is the trait most likely to influence the outcome of both male–male competition and female mate choice and these mechanisms are more likely to operate sequentially than simultaneously. It is not possible to determine,

however, if this pattern actually predominates in the majority of mating systems or if it is due to ascertainment bias: we may have a nonrandom sample of studies or differences in body size and sequential mechanisms of sexual selection may be more readily apparent or more tractable for researchers to study. Body size is certainly one of the traits commonly hypothesized to be important in sexual selection, even though body size is clearly important in many other contexts and influenced by natural selection as well.

Second, linear selection (Fig. 1) is the most common form of selection imposed by male–male competition and female mate choice and, in most cases, it is positive (i.e. selecting for greater trait elaboration). This is not altogether surprising given that linear selection is by far the easiest form of selection to detect statistically (Kingsolver *et al.*, 2001; Blows & Brooks, 2003). Moreover, experimental studies incorporating only two treatments (e.g. small vs. large males) are unable to detect nonlinear forms of selection: it is not a coincidence that when significant nonlinear selection is detected, it is in studies adopting an approach that explicitly measure selection gradients (Table 1). Therefore, determining if positive linear selection is actually the most common form of sexual selection operating on male sexual traits requires much greater emphasis to be placed on the role of both linear and nonlinear forms of sexual selection.

Third, in the majority of studies reviewed, the mechanisms of sexual selection are reinforcing with male–male competition imposing the same form and direction of selection as female mate choice. There were no generalizations regarding the exceptions. male–male competition and female mate choice can be different in form or of the same form but in opposite directions. Although we found no instances where male–male competition was nonlinear and female mate choice linear, we see no reason why this is not possible. If anything, our case studies illustrate that the potential exists for male–male competition and female mate choice to interact in a diversity of ways. The mechanisms of sexual selection were slightly more likely to be opposing when they occurred sequentially. This was not simply the result of more studies examining mating systems with sequential sexual selection: 20% of studies with sequential sexual selection suggest opposing mechanisms, whereas only about 10% of studies with simultaneous sexual selection revealed opposing mechanisms.

Finally, we found very few studies that have formally quantified linear and nonlinear selection gradients for both male–male competition and female mate choice. Even fewer have attempted to combine selection gradients across these mechanisms to estimate the strength and form of total sexual selection operating on male sexual traits. Consequently, before more robust generalizations on how total sexual selection shapes the evolution of male sexual traits can be made it is clear

**Table 1** Case studies where both mechanisms of sexual selection have been described and act on the same trait. In most of these, separate studies were performed to evaluate mate choice and male–male competition. We also suggest the most likely temporal time scale for the mechanisms based on the mating system of the species.

Species	Common name	Male trait	Time scale	Form of sexual selection*		Refs
				♂–♂ competition	♀ choice	
<b>Invertebrates</b>						
<i>Acheta domesticus</i>	House cricket	Body size	Sequential	Linear (+)	Linear (+)	[1]
<i>Anastrepha suspensa</i>	Caribbean fruit fly	Body size	Sequential	Linear (+)	Linear (+)	[2, 3]
<i>Aquarius remigis</i>	Water strider†,‡	Body size	Simultaneous	Linear (+)	Linear (–)	[4]
<i>Austropotamobius italicus</i>	Freshwater crayfish	Body size	Sequential	Linear (+)	Linear (+)	[5]
<i>Drosophila silvestris</i>	Picture-winged fly	Body size	Sequential	Linear (+)	Linear (–)	[6]
<i>Gryllus bimaculatus</i>	Field cricket	Body size	Sequential	Linear (+)	Linear (+)	[7–9]
<i>Gryllus integer</i>	Field cricket	Pheromones	Sequential	Linear (+)	Linear (+)	[10]
<i>Gromphadorhina portentosa</i>	Hissing cockroach	Body weight	Simultaneous	Linear (+)	Linear (+)	[11–13]
<i>Hapalogaster dentata</i>	Stone crab	Body size	Simultaneous	Linear (+)	Linear (+)	[14]
<i>Hygrolycosa rubrofasciata</i>	Wolf spider	Immuno-competence	Sequential	Linear (+)	Linear (+)	[15]
<i>Libella luctosa</i>	Pond dragonfly†,‡	Body size	Sequential	Linear (+)	Nonlinear (–)	[16]
		Wing patch size	Sequential	Linear (+)	Linear (+)	[16]
<i>Nauphoeta cinerea</i>	Lobster cockroach§	2MET	Simultaneous	Linear (+)	Linear (+)	[17]
		4E2M	Simultaneous	Linear (+)	Linear (+)	[17]
		3H2B	Simultaneous	Linear (–)	Linear (+)	[17]
<i>Prochyliza xanthostoma</i>	Carrion fly†	Body size	Sequential	Linear (+)	Linear (+)	[18]
		Head shape	Sequential	Linear (+)	Linear (–)	[18]
<i>Rhynchocinetes typus</i>	Rock shrimp	Body size	Simultaneous	Linear (+)	Linear (+)	[19, 20]
<i>Scatophaga stercoraria</i>	Yellow dungfly	Body size	Simultaneous	Linear (+)	Linear (+)	[21–25]
<i>Sigara falleni</i>	Water boatman†	Pala size	Sequential	Linear (–)	Linear (+)	[26, 27]
<i>Uca paradosumier</i>	Fiddler crab	Body size	Sequential	Linear (+)	Linear (+)	[28]
<b>Fish</b>						
<i>Coralliozetus angelica</i>	Angel blenny	Body size	Sequential	Linear (+)	Linear (+)	[29]
<i>Cottus gobio</i>	River bullhead	Body size	Simultaneous	Linear (+)	Linear (+)	[30]
<i>Danio rerio</i>	Zebrafish	Body size	Simultaneous	Linear (+)	Linear (+)	[31]
<i>Gasterosteus aculeatus</i>	Stickleback	Red colouration	Simultaneous	Linear (+)	Linear (+)	[32–36]
<i>Gobiusculus flavescens</i>	Two-spotted goby	Body size	Sequential	Linear (+)	Linear (+)	[37]
<i>Eviota prasina</i>	Green bubble goby	Dorsal fin	Sequential	Linear (+)	Linear (+)	[38]
<i>Oryzias latipes</i>	Japanese medaka	Body size	Simultaneous	Linear (+)	Linear (+)	[39]
<i>Padogobius martensi</i>	Freshwater goby	Body size	Sequential	Linear (+)	Linear (+)	[40]
<i>Pomatoschistus minutus</i>	Sand goby	Body size	Sequential	Linear (+)	Linear (+)	[41, 42]
<i>Rhodeus sericeus</i>	European bitterling	Body size	Sequential	Linear (+)	Linear (+)	[43]
<i>Salmo trutta</i>	Brown trout	Adipose fin length	Sequential	Linear (+)	Linear (+)	[44]
<i>Thalassoma bifasciatum</i>	Bluehead wrasse†	White band size	Simultaneous	Linear (+)	Linear (+)	[45]
<i>Xiphophorus helleri</i>	Green swordtail	Swordtail length	Simultaneous	Linear (+)	Linear (+)	[46]
<i>Xiphophorus nigrensis</i>	Panuco swordtail	Body size	Simultaneous	Linear (+)	Linear (+)	[47, 48]
<b>Amphibians</b>						
<i>Ambystoma tigrinum tigrinum</i>	Tiger salamander	Body size	Sequential	Linear (+)	Linear (+)	[49]
<i>Bufo americanus</i>	American toad	Body size	Simultaneous	Linear (+)	Linear (+)	[50, 51]
<i>Bufo woodhousei</i>	Woodhouse's toad	Call rate	Sequential	Linear (+)	Linear (+)	[52–54]
<i>Oligodon rubra</i>	Neotropical frog	Body size	Simultaneous	Nonlinear (+)	Nonlinear (–)	[55]
<i>Rana catesbeiana</i>	American bullfrog	Age	Simultaneous	Linear (+)	Linear (+)	[56]
		Body size	Simultaneous	Linear (+)	Linear (+)	[56]
<i>Uperoleia laevigata</i>	Smooth toadlet	Body size	Sequential	Linear (+)	Nonlinear (–)	[57–59]
<b>Reptiles</b>						
<i>Crotaphytus collaris</i>	Collared lizard	Colour	Sequential	Linear (+)	Linear (+)	[60]
<i>Uta stansburiana</i>	Side-blotched lizard	Body size	Sequential	Linear (+)	Linear (+)	[61, 62]
<b>Birds</b>						
<i>Callipepla squamata</i>	Scaled quail	Body size	Sequential	Linear (+)	Linear (+)	[63]
		Tarsus length	Sequential	Linear (+)	Linear (+)	[63]
<i>Euplectes ardens</i>	Red-collard widowbird†	Collar area	Sequential	Linear (+)	Linear (–)	[64, 65]
<i>Gallus gallus</i>	Red jungle fowl	Comb colour	Simultaneous	Linear (+)	Linear (+)	[66–68]
		Comb length	Simultaneous	Linear (+)	Linear (+)	[66–68]

Table 1 (Continued).

Species	Common name	Male trait	Time scale	Form of sexual selection*		Refs
				♂-♂ competition	♀ choice	
<i>Geothlypis trichas</i>	Yellow-throat	Size of facial mask	Sequential	Linear (+)	Linear (+)	[69]
<i>Junco hyemalis</i>	Dark-eyed junco	White in tail	Sequential	Linear (+)	Linear (+)	[70]
<i>Parus major</i>	Great tit	Song repertoire size	Sequential	Linear (+)	Linear (+)	[71, 72]
<i>Petronia petronia</i>	Rock sparrow	Size of throat patch	Sequential	Linear (+)	Linear (+)	[73]
<i>Phasianus colchicus</i>	Ring-necked pheasant	Ear tuft length	Simultaneous	Linear (+)	Linear (+)	[74–77]
Mammals						
<i>Loxodonta africana</i>	African elephant	Body size	Simultaneous	Linear (+)	Linear (+)	[78–80]
		Age	Simultaneous	Linear (+)	Linear (+)	[78–80]
<i>Mandrillus sphinx</i>	Mandrill	Red colouration	Sequential	Linear (+)	Linear (+)	[81]
<i>Microtus pennsylvanicus</i>	Meadow vole	Testosterone levels	Sequential	Linear (+)	Linear (+)	[82]
<i>Onychogalea fraenata</i>	Bridled wallaby	Body size	Simultaneous	Linear (+)	Linear (+)	[83]

References: 1. Savage *et al.* (2005), 2. Burk (1984), 3. Burk (1983), 4. Sih *et al.* (2002), 5. Gherardi *et al.* (2006), 6. Boake (1989), 7. Simmons (1988), 8. Simmons (1986a), 9. Simmons (1986b), 10. Kortet & Hedrick (2005), 11. Clark & Moore (1995a), 12. Clark & Moore (1995b), 13. Clark & Moore (1995c), 14. Sato & Goshima (2007), 15. Ahtiainen *et al.* (2006), 16. Moore (1990), 17. Moore & Moore (1999), 18. Bonduriansky & Rowe (2003), 19. Diaz & Thiel (2003), 20. Thiel & Correa (2004), 21. Borgia (1980), 22. Borgia (1981), 23. Parker (1970a), 24. Parker (1970b), 25. Sigurjonsdottir & Parker (1981), 26. Candolin (2004), 27. Candolin (2005), 28. Jaroensutasinee & Jaroensutasinee (2003), 29. Hastings (1988), 30. Bisazza & Marconato (1988), 31. Pyron (2003), 32. Bakker & Sevenster (1983), 33. Baube *et al.* (1995), 34. Rowland (1982), 35. Candolin (2000), 36. Candolin (1999), 37. Borg *et al.* (2006), 38. Sekiya & Karino (2004), 39. Howard *et al.* (1998), 40. Bisazza *et al.* (1989), 41. Forsgren *et al.* (1996), 42. Jarvenpaa & Lindstrom (2004), 43. Reichard *et al.* (2005), 44. Petersson *et al.* (1999), 45. Warner & Schultz (1992), 46. Benson & Basolo (2006), 47. Morris *et al.* (1992), 48. Ryan *et al.* (1990), 49. Howard *et al.* (1997), 50. Gatz (1981), 51. Howard (1988), 52. Sullivan (1983), 53. Sullivan (1982), 54. Sullivan (1987), 55. Bourne (1993), 56. Howard (1978), 57. Robertson (1986a), 58. Robertson (1986b), 59. Robertson (1990), 60. Baird *et al.* (1997), 61. Calsbeek & Sinervo (2002a), 62. Calsbeek & Sinervo (2002b), 63. Hagelin (2002), 64. Pryke *et al.* (2001a), 65. Pryke *et al.* (2001b), 66. Zuk *et al.* (1990a), 67. Zuk *et al.* (1990b), 68. Ligon *et al.* (1990), 69. Tarof *et al.* (2005), 70. McGlothlin *et al.* (2005), 71. Krebs *et al.* (1978), 72. Baker *et al.* (1986), 73. Griggio *et al.* (2007), 74. Mateos & Carranza (1997a), 75. Mateos & Carranza (1997b), 76. Mateos & Carranza (1999), 77. Mateos (1998), 78. Moss (1983), 79. Poole (1989), 80. Rasmussen & Schulte (1998), 81. Setchell (2005), 82. Spritzer *et al.* (2005), 83. Sigg & Goldizen (2006).

\*Sexual selection is defined as linear or nonlinear based on Fig. 1. Nonlinear (+) indicates disruptive selection and nonlinear (–) indicates stabilizing selection.

†Studies where formal selection gradients are calculated.

‡Studies where the episodes of selection are combined in an attempt to estimate total sexual selection.

§The target of selection in *Nauphoeta cinerea* is the male sex pheromone, consisting of three components: 2MET, 2-methylthiazolidine; 4E2M, 4-ethyl-2-methoxyphenol; and 3H2B, 3-hydroxy-2-butanone.

that more quantitative studies of sexual selection and its underlying mechanisms are needed. As we demonstrate below, the use of formal selection analysis to estimate linear and nonlinear selection gradients and to combine them across episodes of sexual selection is central to this process.

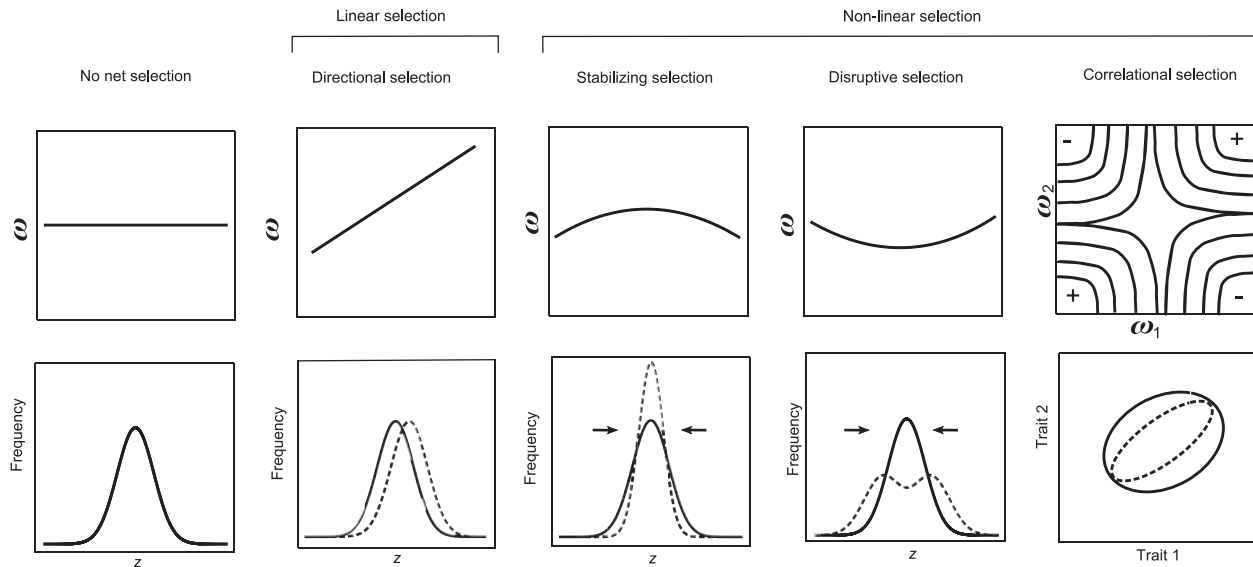
## Estimating total sexual selection

Estimating the strength and form of total sexual selection is a two stage process: sexual selection must first be estimated independently for each mechanism and then combined to gain a measure of total sexual selection. However, to determine both the independent and cumulative effects of the mechanisms of sexual selection, and to allow direct comparisons across studies, we need a standardized approach. Quantitative genetic theory, and in particular the concept of the standardized selection gradient, provides a comprehensive framework to measure (Lande & Arnold, 1983; Manley, 1985; Endler, 1986; Phillips & Arnold, 1989) and combine (Arnold & Wade,

1984a,b; Wade & Kalisz, 1989) the mechanisms of sexual selection. While this framework has existed for well over two decades, our review clearly demonstrates that the majority of sexual selection researchers are not embracing these techniques. Our aim is therefore to provide an overview of these techniques, illustrating the usefulness for studies integrating multiple mechanisms of sexual selection, in the attempt to better direct future studies towards a holistic view of sexual selection.

## Quantifying the strength and form of sexual selection

There is no shortage of techniques for documenting the strength and form of sexual selection (Brodie *et al.*, 1995). The most popular is the multiple-regression-based approach of Lande & Arnold (1983). We can illustrate this approach with a simple example of male–male competition acting on three different morphological traits: body size ( $X_1$ ), patch size ( $X_2$ ) and tail length ( $X_3$ ). Individual fitness ( $W$ ) is measured as subordinate or



**Fig. 1** The different forms of sexual selection. Selection is the relationship between phenotype ( $z$ ) and fitness ( $\omega$ ) (top) and produces an immediate change in the phenotypic distribution within a generation (bottom: solid lines before selection, dashed lines after selection). Traditionally, the form of selection has been classified by its impact on the phenotypic distribution. (a) Illustrates the example of *no net selection* resulting in an unchanged phenotypic distribution, (b) *directional selection*, in this case positive which results in an increase in the trait mean. The opposite would be true for negative directional selection, (c) *stabilizing selection* where individuals with an intermediate trait value have a higher fitness which results in a decrease in the variance of the trait, (d) *disruptive selection* where individuals with extreme trait value have higher fitness which results in an increase in the trait variance and (e) *correlational selection* acting on the joint expression of a pair of traits, illustrated by a saddle-shaped contour plot with regions of highest fitness represented by '+'. Correlational selection changes the covariance between traits. Phillips & Arnold (1989) propose only two broad categories of selection: *linear* selection that produces a change in the phenotypic mean and *nonlinear* selection that produces a change in all other moments of the phenotypic distribution. Thus, (b) constitutes linear selection, while (c), (d) and (e) all represent forms of nonlinear selection.

dominant status (0 and 1 respectively), although this fitness measure is not necessarily restricted to being a discrete variable (Brodie & Janzen, 1996). Standardizing trait values [ $z_i = \frac{(x_i - \mu_i)}{\sigma_i}$ ], and converting individual fitness to relative fitness ( $\omega = \frac{W}{\bar{W}}$ ), we can use multiple regression to calculate linear selection gradients:

$$\omega = \alpha + \beta z_1 + \beta z_2 + \beta z_3 + \epsilon, \quad (1)$$

where  $\alpha$  is the regression intercept,  $\beta$ s represent the partial regression coefficients and  $\epsilon$  is the random error component. The partial regression coefficients are the standardized linear selection gradients and estimate the contribution of a particular trait to fitness while holding the effects of the other traits constant.  $\beta$  therefore represents the direction of the steepest uphill slope from the population mean on the individual fitness surface (Lande & Arnold, 1983).

Nonlinear forms of selection can then be estimated by running a separate regression that includes quadratic ( $z_i^2$ ) and cross-product ( $z_i z_j$ ) terms:

$$\omega = \alpha + \beta z_1 + \beta z_2 + \beta z_3 + \frac{\gamma}{2} z_1^2 + \frac{\gamma}{2} z_2^2 + \frac{\gamma}{2} z_3^2 + \gamma z_1 z_2 + \gamma z_1 z_3 + \gamma z_2 z_3 + \epsilon. \quad (2)$$

The linear terms ( $\beta$ ) are not interpreted from this equation. Instead, we use this equation with higher order terms to determine how selection affects the variances and covariances of traits when the effects of linear selection are removed (Lande & Arnold, 1983). The  $\gamma$  coefficients associated with the squared terms reflect the direct effects of nonlinear selection on the trait variances, or the curvature of the fitness surface along the individual traits axes ( $z_1$ – $z_3$ ) (Lande & Arnold, 1983; Phillips & Arnold, 1989; Brodie *et al.*, 1995). A negative  $\gamma$  is an indicative of convex selection (i.e. curved downward) and a positive  $\gamma$  is an indicative of concave selection (i.e. curved upwards). The  $\gamma$  coefficients associated with the cross-products represent the direct effects of correlational selection on the covariance between two traits, or selection for traits to become positively (positive  $\gamma$ ) or negatively (negative  $\gamma$ ) correlated.

While the interpretation of linear selection operating on phenotypic traits is relatively straightforward, the interpretation of nonlinear selection can be troublesome as the number of individual traits being examined increases. If only a few traits show nonlinear forms of selection, the multiple-regression approach provides an adequate description and quantification (Hunt *et al.*, 2007). However, with a large number of traits and several significant nonlinear terms, interpreting the  $\gamma$

coefficients individually may underestimate the strength of nonlinear selection (Blows & Brooks, 2003). Phillips & Arnold (1989) showed that how the interpretation of nonlinear selection can be improved through the use of canonical analysis to locate the major axes of nonlinear selection by diagonalizing the  $\gamma$  matrix (i.e. characterizing the matrix by determining the eigenvectors and eigenvalues; see Blows (2007) for a general overview of matrix diagonalization and its applications in evolutionary biology). This produces two matrices: the  $\mathbf{M}$  matrix where the columns are the eigenvectors derived from this characterization and the  $\Lambda$  matrix, which contains the eigenvalues ( $\lambda$ ) along the diagonal and zeros for all the off-diagonal values and which describes the curvature of the fitness surface. The sign and magnitude of the eigenvalues ( $\lambda$ ) therefore provide a description of nonlinear selection acting on the major axes. If all  $\lambda$  are negative, then the fitness surface is convex, suggesting a multivariate peak. If all  $\lambda$  are positive, then the fitness surface is concave suggesting a multivariate bowl. If there is a mixture of both positive and negative values of  $\lambda$ , then the fitness surface is a saddle. The larger the magnitude of  $\lambda$ , the more curved the surface. This curvature may also have a linear component, described by  $\theta$ , and can be calculated as  $\mathbf{M}^T\beta$ , where  $T$  is the transposition of  $\mathbf{M}$ . (Phillips & Arnold, 1989).  $\theta$  therefore represents the slope of the fitness surface along each of the major axes.

Each column in  $\mathbf{M}$  represents a linear equation describing that axis, therefore the original trait values can be substituted into this equation to derive a  $\mathbf{y}$ -score that places the original trait values into canonical space for each individual included in the analysis. These scores provide a simple way of calculating  $\theta$  and  $\lambda$  for each of the major axes, along with their standard errors and significance values (Phillips & Arnold, 1989). With multiple regression using  $\omega$  as the dependent variable and the  $\mathbf{y}$ -scores and their quadratic terms ( $\mathbf{y}_{ii}$ ) as the independent variables the coefficients of the linear and quadratic terms provide both  $\theta$  and  $\lambda$ :

$$\omega = \theta y_1 + \theta y_2 + \theta y_3 + \frac{1}{2}(\lambda y_1^2 + \lambda y_2^2 + \lambda y_3^2) + \varepsilon. \quad (3)$$

An advantage of this approach is that standard errors of the coefficients are also produced, facilitating tests of significance.

It is important to note that the majority of analyses of multivariate selection, including the approaches outlined above, are inherently correlational in nature. As such, estimated selection gradients have the potential to be heavily biased by unmeasured traits (Mitchell-Olds & Shaw, 1987). Moreover, because these analyses are applied to phenotypic data, environmentally induced covariances between traits and fitness can lead to biased estimates of selection and misleading predictions about evolutionary change (Rausher, 1992; Stinchcombe *et al.*,

2002). Consequently, selection gradients obtained from such analyses should always be interpreted with a moderate degree of caution. If possible, such as in species with pedigreed populations, calculating selection on breeding values provide a more conservative estimate of evolutionary responses (Rausher, 1992). Regardless, as suggested by Endler (1986), selection analyses are always best backed up with manipulative studies (e.g. Brooks *et al.*, 2005; Bentson *et al.*, 2006).

### Combining episodes of sexual selection

Whenever the selection imposed by male–male competition and female mate choice is not identical in sign or form, total sexual selection will differ in strength from that imposed by either of these mechanisms operating in isolation (Fig. 2). The potential also exists for total sexual selection to be different in form to either mechanism (Fig. 2). This asymmetry exists because the selection gradients across these individual mechanisms (or episodes of selection) combine to give the total selection gradient for a given phenotypic trait (Arnold & Wade, 1984a,b). The extent of this asymmetry, however, depends critically on whether male–male competition and female mate choice occur simultaneously or sequentially. Simultaneous and sequential episodes of selection have differential effects on total sexual selection because of the way they influence the phenotypic distribution of male traits available for selection to operate. While both types of interaction will influence the overall strength and form of total sexual selection, they have the potential to do so in very different ways.

Arnold & Wade (1984a,b) demonstrate that, assuming the phenotypic variance–covariance matrix ( $\mathbf{P}$ ) is unaffected by selection, the selection gradients across successive episodes of selection sum to give the total selection gradient for a given trait:

$$\beta_{\text{total}} = \beta_1 + \beta_2 + \beta_3 + \dots \beta_n. \quad (4)$$

However, the assumption that  $\mathbf{P}$  remains constant is unlikely to be valid (Wade & Kalisz, 1989). Furthermore, this additive partitioning assumes that the episodes of selection occur sequentially. However, as we have already illustrated, the mechanisms of sexual selection could also occur simultaneously within the population. Thus, combining episodes of selection to estimate total sexual selection requires that we have the information on when and how male–male competition and female mate choice operate on individuals, as well as their effect on the phenotypic distribution of trait(s) that are the target of sexual selection.

When the mechanisms of sexual selection occur simultaneously, both male–male competition and female mate choice select from the same distribution of male traits, such as a system where dominance hierarchies are formed but some males outside the hierarchy also gain matings

through mate choice. Thus, male–male competition does not limit the distribution of male traits available for female mate choice to operate (or vice versa). Instead, the population is subdivided so that a proportion of males obtain mates by competing with other males, while the other proportion gains reproductive success as a result of differential attractiveness to females. This requires us to consider whether the mechanisms of sexual selection result in soft or hard selection.

Under soft selection, the proportion of gametes contributed to the next generation from each subpopulation (e.g. dominant or attractive males) is directly related to the proportion of individuals from the total population found in that subpopulation, whereas under hard selection the proportion of gametes contributed by each subpopulation is dependent on the fitness of the individuals in the subpopulation relative to the mean fitness of the total population (Christiansen, 1975). Accordingly, soft and hard selections differ in the weighting of subpopulations when calculating the total selection gradient (Via & Lande, 1985). Under a regime of soft selection, the total selection gradient will be the sum of the partial selection gradients for male–male competition ( $\beta_A$ ) and female mate choice ( $\beta_B$ ) weighted by the relative proportion of the population experiencing one or the other mechanism of sexual selection:

$$\beta_{\text{total}} = f_A \beta_A + f_B \beta_B, \quad (5)$$

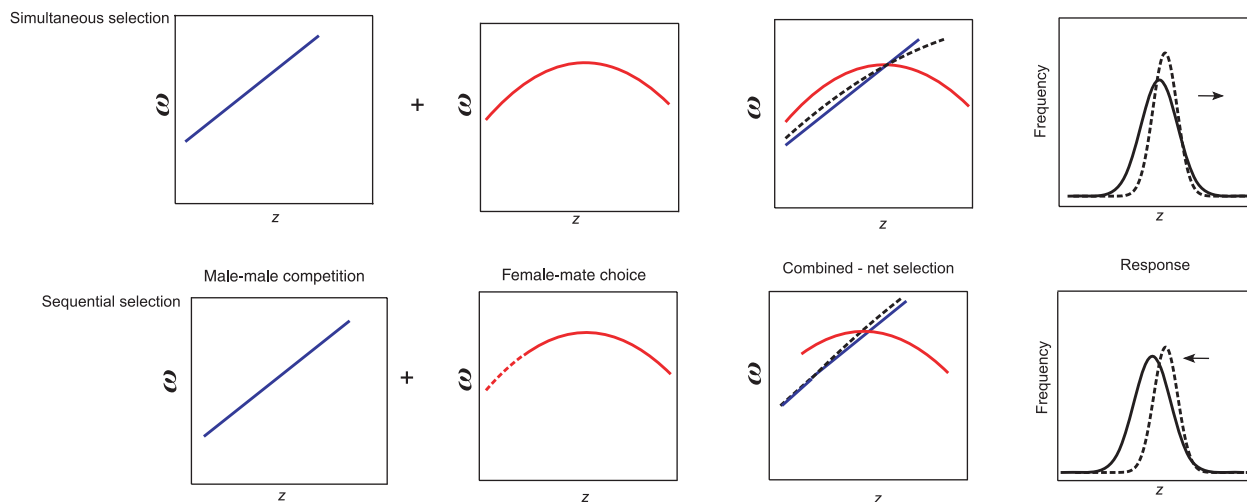
where  $f_A$  is the proportion of the population where success in male–male competition determines mating success,  $f_B$  is the proportion of the population where attractiveness determines mating success, and  $f_A + f_B = 1$ .

Under hard selection, the selection arising within individual mechanisms of sexual selection are weighted by mean fitness as well as the proportion of the population experiencing one or the other mechanism to give the total selection gradient:

$$\beta_{\text{total}} = [f_A \left( \frac{W_A}{\bar{W}} \right) \beta_A] + [f_B \left( \frac{W_B}{\bar{W}} \right) \beta_B], \quad (6)$$

where  $W_A$  is the mean fitness of males competing for mating success through dominance in subpopulation A, and  $W_B$  is the mean fitness males competing through differential attractiveness in subpopulation B, and  $\bar{W}$  is the grand mean fitness or the mean fitness over the entire population calculated as  $\bar{W} = f_A W_A + f_B W_B$ . The weightings again sum to one.

In contrast, when the mechanisms of sexual selection occur sequentially, as might occur in lekking or territorial species where males fight for access to hot spots and then females arrive and discriminate among the successful males, male–male competition influences the phenotypic distribution available for female mate choice to operate (Fig. 2). If this occurs, male–male competition and female mate choice will no



**Fig. 2** The operation of simultaneous (top) and sequential (bottom) sexual selection. In both cases, male–male competition (blue line;  $\beta = 1.67$ ) exerts positive linear selection on a male sexual trait ( $z$ ) and female mate choice (red curve;  $\gamma = -0.15$ ) exerts stabilizing selection on the same trait. We illustrate simultaneous sexual selection using a model of soft selection where the proportion of the population gaining mating success through male–male competition in 0.7 and the proportion gaining mating success through female mate choice is 0.3. More weight is therefore given to the selection gradient for male–male competition. Total sexual selection (dashed line) is a weak form of stabilizing selection, which has slightly increased the trait mean and reduced its variance. In our example of sequential sexual selection, female mate choice follows an episode of male–male competition and males that are unsuccessful in this episode are not available when female choice operates (dashed section of the red curve). We assume that this reduces the trait variance by 0.15 and therefore weight the female mate choice gradient by this weighting factor ( $a_m$  in text). Total sexual selection is largely linear in form, which increases the trait mean and slightly reduces its variance.



longer be independent and their partial regression gradients do not sum to give the total selection gradient unless weighted accordingly. With sequential mechanisms of sexual selection, the total selection gradient can be made additive by weighting each successive episode of selection by the cumulative change that occurs in  $\mathbf{P}$  due to selection. The total selection gradient with  $m$  episodes of linear selection is calculated as:

$$\beta_{\text{total}} = \beta_1 + a_1\beta_2 + a_2\beta_3 + \dots + a_{m-1}\beta_m, \quad (7)$$

where the weighting factor,  $a_m$ , is the product of the inverse of the original  $\mathbf{P}$  before any selection ( $\mathbf{P}_0^{-1}$ ) and  $\mathbf{P}$  before selection in a given episode ( $\mathbf{P}_{m-1}$ , which is equivalent to  $\mathbf{P}$  after selection in the preceding episode) or  $a_{m-1} = \mathbf{P}_0^{-1}\mathbf{P}_m$ .

Alterations in  $\mathbf{P}$  can either enhance or diminish the operation of female mate choice. Thus, following the annotation used in eqn 5, the total sexual selection gradient is:

$$\beta_{\text{total}} = \beta_A + (a\beta_B), \quad (8)$$

where  $a$  is the product of the inverse of  $\mathbf{P}$  before male–male competition and  $\mathbf{P}$  after male–male competition (but before female mate choice).

### The evolutionary consequences of combining mechanisms of sexual selection

The way in which male–male competition and female mate choice interact and combine alters the strength and form of total sexual selection and therefore has important consequences for the evolution of male sexual traits. To illustrate this point, we present a number of hypothetical scenarios in Fig. 3 where total sexual selection operating on a male sexual trait is very different from that imposed by either male–male competition or female mate choice. These are just a few of the large number of outcomes that are theoretically possible.

If the selection gradients for male–male competition and female mate choice differ in strength but are of the same sign and form (Fig. 3a–c), sexual selection will be reinforcing. Total sexual selection will always be of the same form and sign as each of the individual mechanisms. In contrast, if the selection gradients differ in sign but are of the same form (Fig. 3d–f), sexual selection will be opposing. Total selection will be the same form and sign as the strongest selection gradient but different from the weaker selection gradient. In all instances, however, the strength of the total selection gradient will depend on how the selection gradients combine. The same will be true when the selection gradients for male–male competition and female mate choice differ in form (Fig. 2).

Collectively, a consideration of the form and sign of individual mechanisms of sexual selection has important implications for the evolution of the male

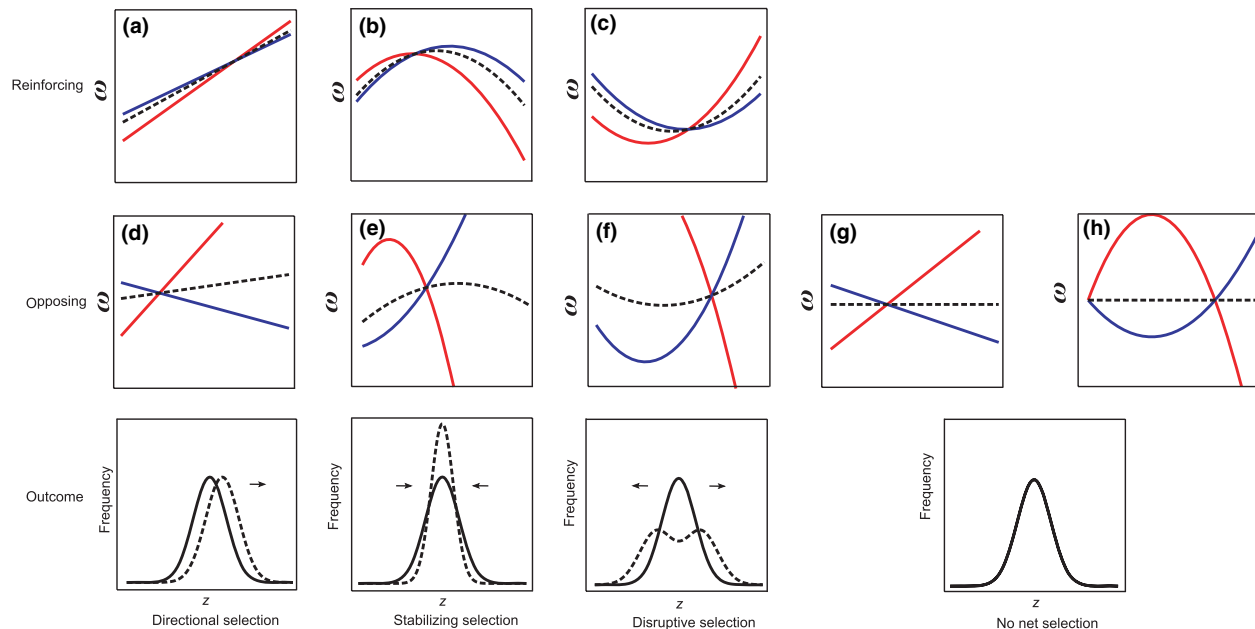
sexual trait that is the target of selection. It is almost impossible to predict the total strength of sexual selection operating on a male sexual trait without detailed knowledge of selection imposed by male–male competition and female mate choice and how each mechanism must be weighted based on their interaction. Total sexual selection can be enhanced or diminished compared to selection imposed by either mechanism alone (Fig. 3). Studying a single mechanism of sexual selection therefore can be very misleading. The diversity of possible outcomes for total sexual selection when the mechanisms of sexual selection vary in strength, sign and form places even greater emphasis on the need to understand total sexual selection when understanding how male sexual traits evolve.

A potentially interesting, yet largely unexplored, example of opposing sexual selection will occur when the weighted selection gradients for male–male competition and female mate choice are equal in strength (after weighting) but opposite in sign (Fig. 3g,h). When this occurs, the total strength of sexual selection operating on the male sexual trait will be zero. Thus, despite strong selection imposed by both mechanisms of sexual selection, total sexual selection is balancing and the phenotypic distribution of the male trait will remain unchanged. This will act to preserve the levels of genetic variance in the male trait and may therefore represent one of the (now many) resolutions to the longstanding ‘lek paradox’ (Moore & Moore, 1999).

Finally, it can be difficult to measure both mechanisms of sexual selection independently. It is often easier to measure male–male competition while controlling for female mate choice than to measure female mate choice controlling for male–male competition (Halliday, 1983). This is particularly true when the mechanisms of sexual selection are simultaneous rather than sequential. However, because the two mechanisms ultimately combine to give a measure of total sexual selection, it may be possible to measure the total sexual selection and one of the two mechanisms. The relative importance of the remaining mechanism can then be determined by simple subtraction.

### Caveats

We have provided a simple classification of temporal aspects of sexual selection. We are aware, however, that ‘real-world’ biology can be considerably more complex. For example, our classification of the studies listed in Table 1 as having sequential or simultaneous mechanisms of sexual selection should be viewed as hypotheses. While we are confident of this classification for our own studies (e.g. Moore, 1990; Moore & Moore, 1999) we urge others to examine their own study species and determine how well this classification fits.



**Fig. 3** A number of hypothetical scenarios illustrating the outcome for total sexual selection (bottom, dashed lines) when male–male competition (blue lines) and female mate choice (red lines) are subject to different forms of reinforcing (top) and opposing (middle) selection. In all cases, we have used the simplest case scenario of simultaneous sexual selection under a model of soft selection. As in Fig. 2, the proportion of males achieving mating success through male–male competition is 0.7 and through female mate choice is 0.3. Figures (a–c) represent examples of reinforcing sexual selection when male–male competition ( $\beta = 1$ ,  $\gamma = -0.15$ ,  $\gamma = 0.15$ ) and female mate choice ( $\beta = 1.5$ ,  $\gamma = -0.20$ ,  $\gamma = 0.20$ ) are linear, stabilizing and disruptive in form respectively. In each case, total sexual selection is of the same form as both mechanisms of sexual selection but different in strength. Figures (d–f) represent examples when male–male competition ( $\beta = -0.57$ ,  $\gamma = 0.21$ ,  $\gamma = 0.36$ ) and female mate choice ( $\beta = 2.33$ ,  $\gamma = -0.83$ ,  $\gamma = -0.50$ ) are opposing in direction and/or form and the outcome for total sexual selection is linear, stabilizing and disruptive respectively. Here, total sexual selection is the same form as the strongest selection gradient and different to the weaker selection gradient. Figures (g, h) represent examples when male–male competition ( $\beta = -0.71$ ,  $\gamma = 0.21$ ) and female mate choice ( $\beta = 1.67$ ,  $\gamma = -0.50$ ) are opposing and equal strength (after weighting). In both cases, total sexual is zero.

It is also possible (if not probable) that our classification is simplistic. We have assumed that male–male competition and female mate choice have at least some independent elements. This may not always be true. In several species, females incite male–male competition, blurring the line between intra- and inter-sexual selection (Cox & LeBoeuf, 1977; Semple, 1998; Pizzari, 2001). In other species, success in male–male competition is enhanced by female mate choice (Sorenson & Derrickson, 1994). In this case, the temporal order is reversed (but note that in Sorenson & Derrickson, 1994, different traits influenced mate choice and male–male competition as is the case in so many studies). We believe that our classification is robust, and fits many species, but ultimately this is an empirical question and we hope that this review stimulates others to question the nature of the interrelationship between inter- and intrasexual mechanisms of sexual selection. Regardless of the classification, however, it should be possible to examine both total sexual selection and at least one of the mechanisms, allowing the remaining mechanism to be derived by subtraction.

## Conclusions and future directions

There is no longer much debate that sexual selection from both male–male competition and female mate choice has been a potent force driving the evolution of elaborate male sexual traits. For a variety of reasons, however, most empirical studies examine the individual mechanisms of sexual selection in relative isolation. Our review demonstrates how this approach can give a misleading view of the total strength and form of sexual selection operating on a male sexual trait. Whenever male–male competition and female mate choice interact the potential exists for the total strength and form of sexual selection acting on a male sexual trait to differ substantially from that imposed by either mechanism. Consequently, a complete understanding of how male sexual traits evolve requires studying both of these mechanisms.

The most important challenges facing researchers studying the evolution of male sexual traits are empirical. Our examples from the sexual selection literature (Table 1) highlight a number of important

areas that may improve future empirical research on this topic. An obvious first step is more studies that quantify both linear and nonlinear forms of sexual selection. This will require the transition from empirical studies that use experimental designs with dichotomous treatments (e.g. large vs. small males) to those where formal selection analysis across a range of phenotypes can be implemented. Such an approach is favoured because the selection gradients are directly comparable across studies, and can be combined across episodes of selection to provide an estimate of the total strength and form of sexual selection operating on a male sexual trait.

Empirical studies should also attempt to quantify and combine selection gradients across all biologically relevant episodes of selection. We recognize that females may sometimes compete with each other (Gwynne, 1991) and males may express mate choice (Bonduriansky, 2001). The principles we outline apply equally to these interactions, as well as to any interaction(s) that may occur between pre- and post-copulatory mechanisms of sexual selection. Several empirical studies have shown that pre- and post-copulatory mechanisms of sexual selection can both be reinforcing (e.g. precopulatory mate choice and differential allocation, Head *et al.*, 2006; female preferences for manipulative traits, Cordero & Eberhard, 2003) or opposing (e.g. precopulatory male-male competition and sperm competition, Danielsson, 2001), but none have combined these sequential episodes of selection to gain insight on how total sexual selection operates. Even less is known about the interaction between the different mechanisms of post-copulatory sexual selection.

There is also a need for more empirical studies that examine a variety of sexual traits other than body size. Body size may not be characteristic of most sexual traits. Sexual selection typically favours large body size (Blanckenhorn *et al.*, 2000) although there are notable exceptions. However, body size also influences fitness in a diversity of life-history stages, at various spatial and temporal scales and according to sex (Blanckenhorn *et al.*, 2000). Limits to body size evolution may be myriad. More promising are studies of characters that are limited in expression to the adult stage and have little relevance outside of courtship and mating (i.e. secondary sexual characters). Darwin's (1859, 1871) classic view was that sexual selection explained the evolution of secondary sexual characters. It is possible that secondary sexual characters are more likely to experience opposing mechanisms of sexual selection. This can begin to be addressed by studying how male-male competition is affected by secondary sexual traits thought to be important in mate choice. Such traits are often surprisingly important in male contests (Baird *et al.*, 1997).

Finally, we can do no better than to quote Lande & Arnold (1985, p. 662):

It remains a major empirical question to determine whether in species with extreme sexual dimorphism female mate choice acts in the same direction as other selective forces such as natural selection or intermale combat. This question can be approached by measuring phenotypic selective forces within a generation within a population, in the field or in the laboratory, without studying the inheritance of the characters. (Lande & Arnold, 1983)

We hope that our review stimulates more studies that adopt this quantitative approach to provide a more holistic view of sexual selection.

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