COMMENT

Comment: On the consequences of sexual selection for fisheries-induced evolution

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Abstract

It is becoming increasingly recognized that fishing (and other forms of nonrandom harvesting) can have profound evolutionary consequences for life history traits. A recent and welcome publication provided the first description of how sexual selection might influence the outcome of fisheries-induced evolution (FIE). One of the main conclusions was that if sexual selection generates a positive relationship between body size and reproductive success, increased fishing pressure on large individuals causes stronger selection for smaller body size. Here, we re-evaluate the sexual selection interpretation of the relationship between body size and reproductive success, and suggest it may in fact be representative of a more general case of pure natural selection. The consequences of sexual selection on FIE are likely to be complicated and dynamic, and we provide additional perspectives to these new and exciting results. Selection differentials and trait variance are considered, with density-dependent and genetic effects on the strength and the direction of sexual selection given particular attention. We hope that our additional views on the role of sexual selection in FIE will encourage more theoretical and empirical work into this important application of evolutionary biology.

It is becoming increasingly recognized that fishing (and other forms of nonrandom harvesting) can have profound evolutionary consequences on life history traits (Stokes et al. 1993; Law 2000; Conover and Munch 2002). Such anthropogenic interference can cause important changes to populations' body size, age and growth profiles, and may alter their reproductive potential and viability (Dieckmann and Heino 2007; Jørgensen et al. 2007; Kuparinen and Merilä 2007). Fisheries-induced evolution (FIE) has been invoked to explain the rapid population viability declines seen in many heavily harvested populations (Conover 2000; Hutchings 2000), and has lead to calls for an 'evolutionary enlightened management' approach (Ashley et al. 2003; Jørgensen et al. 2007).

In recent years, evidence has also accumulated for a role of sexual selection in the dynamics of populations of conservation importance (Caro 1998; Legendre et al. 1999; Moller and Legendre 2001; Côté 2003; Doherty et al. 2003; Kokko and Rankin 2006), highlighting the necessity of integrating mating systems and animal behavior into the treatment of conservation issues (Rowe and Hutchings 2003; Quader 2005; Rowe et al. 2007). Most evaluations of the conservation risks faced by exploited populations fail to acknowledge the strength and the importance of sexual selection, relying largely on temporal and spatial estimates of abundance alone.

Recently however, Hutchings and Rowe (2008) made a valuable first step towards integrating sexual selection into our understanding of the consequences of exploitation, by providing the first description of how sexual selection might influence the outcomes of FIE.

The response of a trait's mean to selection (R) is the product of its heritability (h^2) and the selection differential

(S) acting upon it ($R = h^2S$). S is the difference between the mean of reproducing individuals and that of the total population prior to selection. S is usually calculated under the null assumption that the degree of reproductive success of an individual is independent of the trait in question. But if harvesting is selective with respect to traits that influence reproductive success, then independence between S and reproductive success is lost. The actual response to selection then depends on how the mean and variance of these traits affect reproductive success. Sexually selected characters are a class of traits that display positive relationships with reproductive success, and selection on these traits is often much greater than that on traits, which are under natural selection only (Kingsolver et al. 2001). If harvesting is nonrandom with respect to sexually selected traits, then fisheries-induced selection may have a disproportionate effect on any evolutionary response.

Hutchings and Rowe (2008) compared S's under the assumption that body size causes greater reproductive success in large individuals, and is therefore under sexual selection, with the null case where body size has no influence on reproductive success. Among other important results, they observed that increased fishing pressure on large individuals causes stronger selection for smaller body size when there is a positive relationship between body size and reproductive success. Based on these observations, the authors suggested that the evolutionary outcomes of selective fishing might be influenced by sexual selection (on body size).

Here, we suggest that Hutchings and Rowe's (2008) findings may in fact be representative of the general case of pure natural selection, and that the consequences of sexual selection on FIE may therefore be even more complicated than this first treatment suggests. In particular, we re-evaluate the sexual selection interpretation of the relationship between body size and reproductive success and provide additional perspectives to Hutchings and Rowe's (2008) new and exciting results. Although we raise some uncertainties regarding the respective role of natural versus sexual selection, the fundamental message conveyed by the authors, namely that FIE of traits linked to reproductive success may lead to unanticipated consequences, remains clear.

In their simulations, Hutchings and Rowe (2008) modeled sexual selection as an exponential gain in reproductive success with increasing body size. However, such an increase in reproductive success might not necessarily be brought about by sexual selection: similar fitness curves are also expected under pure natural selection. For females in particular, fecundity (e.g., egg number) usually follows an allometric relationship with body length (Bagenal and Tesch 1978; Stearns 1992). Likewise, while repro-

ductive success in males may be independent of body size in random mating, nonbroadcast spawners that face little sperm limitation risk, examples of such species are scarce. Male fecundity (i.e., ejaculate volume) often scales naturally with body size (Trippel and Morgan 1994; Wootton 1998; McIntyre and Hutchings 2003). Thus, in both males and females, we may reasonably expect, a priori, a positive association between reproductive success and body size. Table 1 provides a (nonexhaustive) synopsis of the causes of relationships between body size and reproductive success in both sexes, and the mode(s) of selection that create them.

If Hutchings and Rowe's (2008) 'sexual selection' case is the general expectation under most natural selection situations, then what are the consequences for FIE of true sexual selection? In agreement with Hutchings and Rowe's (2008) general thesis, we believe that sexual selection will, in most cases and with everything else being equal, result in stronger FIE towards smaller body size. However, for sexual selection to operate (in the traditional sense of males competing to fertilize females), variance in reproductive success ought to be higher in males than in females, such that some males sire a disproportionate amount of offspring. In turn, if body size is a sexually selected trait, sexual dimorphism should exist in the fitness functions of body size (Gross and Sargent 1985), except under the narrow condition where the magnitude of fecundity selection on female body size exactly matches the strength of sexual selection on male body size. Given that sexual selection is usually stronger than natural selection (Kingsolver et al. 2001), we expect the slope of reproductive success on male body size to be greater than that of females'. Therefore, owing to the disparity between the sexes in the magnitude of S (with $S_{\male} > S_{\female}$), we suspect that the evolutionary decline in body size will usually be much greater than that predicted by Hutchings and Rowe, as their model assumed no sex differences. Their findings with respect to sexual selection may therefore be rather conservative.

We also note that sexually selected characters have a distinctly different genetic architecture and variance structure when compared to nonsexually selected traits. Sexual traits tend to have much higher levels of both phenotypic (V_P) and genetic (V_G) variance than nonsexual traits (measured as the coefficient of variation, CV = standard deviation/mean), while not differing markedly in their heritabilities ($h^2 = V_G/V_P$) (Pomiankowski and Moller 1995). Hutchings and Rowe (2008) did not highlight these fundamental variance differences, yet their simulations clearly showed that they have important ramifications for FIE: populations with higher trait CVs suffered from stronger selection against larger individuals. So if body size is under both sexual and natural selection for

Table 1. A summary of potential relationships between body size and reproductive success in males and females, and the mode(s) of selection acting upon them.

Sex	Correlation	Example(s)	Published examples	Mode of selection
♀	$r > 0$	Fecundity increases with size	Bagenal and Tesch 1978; Wootton 1998; Thorpe et al., 1984; Morita & Takashima, 1998; Stearns 1992; Heinimaa & Heinimaa, 2004	NS
		Parental care increases with size		NS, SS
		Larger individuals = higher genetic quality		NS, SS
♀	$r = 0$	?		–
♀	$r < 0$	Senescence	Brown-Borg et al. 1996; Metcalfe & Monaghan, 2001	?
♂	$r > 0$	Broadcast spawning		NS, SS
		Fecundity/fertility increases with size	Trippel and Morgan 1994; Wootton 1998; McIntyre and Hutchings 2003;	NS
		Parental care increases with size	Bisazza & Marconato, 1988; Cote & Hunte, 1989; Wiegmann & Baylis, 1995	NS, SS
		Larger individuals = higher genetic quality	Mangel and Stamps, 2001	NS, SS
		Male dominance	Fleming & Gross, 1994, Foote et al., 1997; Garant et al., 2001, Wedekind et al., 2001; Wedekind et al., 2002, Wedekind & Müller, 2004; Jacob et al., 2007	SS
♂	$r = 0$	Female mate choice	see Barbosa and Magurran, 2006	SS
		Random mating		–
		Nonbroadcasting spawning		–
		No sperm limitation		–
♂	$r < 0$	Senescence	Brown-Borg et al. 1996; Metcalfe & Monaghan, 2001	?

NS, natural selection; SS, sexual selection.

increased size, then the sex differences in selection differentials and trait variance (i.e., $S_\male > S_\female$, and $CV_\male > CV_\female$) would be expected to lead to greater evolution towards smaller size in the presence of size-selective harvesting, compared to the case of no fishing.

While both we and Hutchings and Rowe (2008) favor the conclusion that sexual selection likely causes greater FIE towards smaller individuals, we also urge caution with this generalization. Sexual selection is notoriously complex, and its strength depends on numerous population- and individual-based mechanisms or factors. With all else being equal, sexual selection is likely to be strong (Kingsolver et al. 2001; Svensson and Gosden 2007). However, harvesting may elicit a cascade of effects that renders sexual selection ineffective or difficult to predict. For instance, fertilization success (Rowe et al. 2004) and the ability of dominant males to monopolize females are likely to decline with decreasing density, and sexual selection consequently becomes relaxed (Eshel 1979; Shuster and Wade 2003; Kokko and Rankin 2006). Thus, if fishing reduces population density, the effects of sexual selection may become small. Yet, if the spatial clustering of reproducing individuals tends to increase with decreasing population densities (Salthaug and Aanes 2003), the strength of sexual selection may actually increase in populations exposed to exploitation. Moreover, if body size is sexually dimorphic, then size-dependent harvesting creates asymmetries in the capture rates of each sex and

leads to biased operational sex ratios, which in turn may affect the outcome of sexual selection. Thus, density-dependent and population-level effects appear to have crucial influences on the strength and even the direction of sexual selection (Kokko and Rankin 2006). Hence, they should be incorporated when analyzing the interaction between sexual selection and FIE.

Indirect genetic effects and covariances must also be considered when evaluating the potential consequences of FIE and the interplay between FIE and sexual selection. If body size is genetically correlated to (major components of) individual quality, such as longevity (Brown-Borg et al. 1996), fecundity or fertility (Stearns 1992; Trippel and Morgan 1994; McIntyre and Hutchings 2003), size-selective harvesting may lead to a decrease in not only body size, but also individual reproductive success and hence the overall viability and persistence probability of the population. Moreover, if sexually selected traits are genetically correlated with female mate preferences [sensu Fisher (1958), Lande (1981)], any evolution of male traits will be accompanied by co-evolution of female sexual behavior.

We hope that our clarification of some of the assumptions and consequences of Hutchings and Rowe's (2008) welcome contribution, and our additional perspectives on the role of sexual selection in FIE will encourage more theoretical and empirical work into this important application of evolutionary biology.

Acknowledgements

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