

IN FOCUS

Differences in relative fitness among alternative mating tactics might be more apparent than real



Males of the striped mouse can follow alternative reproductive tactics, the fitness consequences of which might differ greatly between generations. Image by Ivana Schoepf.

Schradin, C. & Lindholm, A. (2011) Relative fitness of alternative male reproductive tactics in a mammal varies between years. *Journal of Animal Ecology*, **80**, 908–917.

Two theoretical frameworks guide research on multiple male phenotypes within natural populations. Each scheme recognizes that male polymorphisms vary in the degree to which genotype and environment influence trait expression. Consensus remains elusive, however, on whether average fitnesses must be equivalent and whether genetic differences need exist for polymorphism to persist over time. Schradin and Lindholm address these hypotheses in African four-striped mice with detailed parentage and body size data. Their results and interpretation call each framework's predictions into question, but reveal a common truth. Debate might be resolved if researchers agreed on which parameters to measure and compare.

Since Darwin (1874), controversy has simmered, and occasionally boiled, over whether polymorphic phenotypes must achieve equal fitness to persist within a population. Darwin said 'yes', as have most evolutionary geneticists, who added that such conditions maintain genetic polymorphism over time (Slatkin 1978). Yet more than 30 years of behavioural research on polymorphic male mating phenotypes continues to cast these hypotheses in doubt. Uncertainty arises from field data showing harem-holding males to be more successful at mating than smaller or weaker males. Dawkins (1980), to account for this observation, suggested that inferior male phenotypes might persist within populations if they make

'the best of a bad job,' gaining less fitness than highly successful males, but doing better than if they had failed to reproduce at all. Gross (1996) formalized Dawkins' parable with his Status-Dependent Selection (SDS) hypothesis, a now classic scheme suggesting that if individual male mating success depends on social status (usually body size) and if all individuals can assume the phenotype providing the greatest fitness given their current status (e.g. the 'bourgeois' strategy of game theory; Maynard Smith 1982; Taborsky 2008), then neither equal fitnesses nor genetic differences among male morphs are necessary for polymorphism to persist. Recent theoretical (Tomkins & Hazel 2007) and empirical studies (Oliviera, Taborsky & Brockmann 2008) appear to support this idea.

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Schradin & Lindholm (2011) provide new fuel for this debate. They describe the fitness consequences of three behaviourally flexible alternative mating tactics (Oliviera, Taborsky & Brockmann 2008) in four-striped mice (*Rhabdomys pumilio*, Fig. 1), a widespread annual rodent in southern Africa. Schradin and Lindholm document paternity and maternity in each of three years and examine the relationship between status (body mass) and fitness for all three male phenotypes, and at all three female densities, such detail is unprecedented in a single paper. Under high population density (2005), the results fit the 'theory of conditional strategies', wherein 'highly successful territorial males' sire 10-fold and 102-fold more progeny than roaming and philopatric males, respectively. Under intermediate population density (2007), the results accord with the 'theory of mixed (i.e. randomly expressed) strategies' wherein territorial and roaming tactics had similar fitness, although no philopatric males were observed. The authors also address the possibility that genetic differences underlie male phenotypes, by examining the male progeny of a single roamer and a single territorial male. The territorial phenotype appeared among 13/14 males, and 7/10 males in the roamer and territorial families, respectively. The authors consider these results consistent with the SDS hypothesis and with current descriptions of alternative mating tactics (Oliviera, Taborsky & Brockmann 2008), wherein male phenotypes are 'not genetically determined'.

Schradin and Lindholm's detailed results appear to support the two cornerstones of Status-Dependent Selection theory (unequal fitnesses and genetic monomorphism among morphs) and suggest that mixed strategies can exist; but their confirmation is not absolute. When population density was low (2003), only roamer males were present and no specific hypothesis was testable. The Status-Dependent Selection-predicted correlation between relative fitness and status was met in only 1/3 seasons, specifically when only one tactic was expressed within a generation (2003), and while males changed tactics readily (males guarded females when females were clumped, and searched for females when females were dispersed), male body mass covaried with fitness only when females were spatially dispersed. Schradin and Lindholm consider the distinction between conditional and mixed strategies 'not absolute', and propose that the term 'single strategy', independent of current fitness consequences, be used to describe polymorphisms in which males are not genetically distinct.

Do the results of Schradin and Lindholm support the Status-Dependent Selection Hypothesis? Practitioners of the evolutionary genetics approach to mating polymorphism (Shuster & Wade 2003) would likely say, 'no', but not because Schradin and Lindholm's methods lacked rigor. Instead, they would argue that the SDS hypothesis itself creates difficulties, because of the kind of data it requires. These difficulties concern how fitness is measured, how fitness is compared and how genetic differences among males are identified.

The first difficulty relates to how the 'best of bad job' and the SDS hypotheses (Dawkins 1980; Gross 1996) are framed.

Both schemes focus on the relative success of *mating* males, but as Darwin (1874) observed, unless the sex ratio is strongly female-biased, when some males gain disproportionate mating success, other males *must* be excluded from mating. Thus, when comparing the relative fitnesses of different male phenotypes, an evolutionary genetics approach requires that winner AND loser males be meticulously included in estimates of average fitness. If these 'zero-class' males are not counted, estimates of average fitness for each morph will be *too large*, estimates of the variance in fitness for each morph will be *too small* and relative fitnesses among morphs may *appear* distinct (as predicted by SDS) when in fact no significant differences exist (Shuster 2009).

How can the zero-class be measured? Success depends on the kinds of data collected, and because of their detail, those of Schradin and Lindholm are tantalizing indeed. Yet, unfortunate omissions exist, again because of a focus on mating males. Despite having documented maternity for most offspring (> 80%), Schradin and Lindholm present no data on the average success of females. Such data could verify that the average fitnesses of males and females are equal (because all offspring have a mother and a father; Fisher 1958). If the distribution of offspring among females can be accurately awarded among the different male morphs and *still* confirm equal average fitness between the sexes, then estimates of relative fitness among males are likely to be accurate (Wade & Shuster 2005), even when documentation of parentage is less than 100%.

The mean and variance in fitness for each male phenotype must next be estimated. Here, Schradin and Lindholm report average male fitness in terms of mate and offspring numbers, but neglect to report the distributions producing these summaries. Brevity is prized by journal editors, but including these distributions, here would have distinguished this already outstanding paper, by allowing direct reconstruction of the mean and variance in fitness for each male phenotype, and verifying whether non-mating males were included in the analysis (Shuster 2010). While Schradin and Lindholm note the existence of zero-class roamer and philopatric males, the authors state only that 40% of all offspring sired within male territories were *not* sired by the resident male (p. 14). These impressive results confirm that disproportionate territorial male success was indeed more apparent than real, but they obscure how extra-pair paternity may have inflated this average.

Relative fitnesses among the different male morphs must next be compared, and Schradin and Lindholm use ANCOVA and goodness of fit tests to show that 'relative fitnesses' among the three male phenotypes are distinct. The simultaneous comparison of male mass within morph across three years, at different female densities, is impressive and is among the most sophisticated tests of SDS predictions to date. However, these results too must be interpreted with caution for the reasons described above. While estimates of 'relative fitness' calculated without zero-class males are indeed 'relative', (absolute fitness for each mating male is divided by the average fitness for all mating males) such estimates will be biased

because exclusion of the zero class inflates average fitness overall. Moreover, while goodness of fit tests can reveal among-group differences in 'relative' fitness (i.e. that extreme mating success was more common among males of one phenotype than among males of a different phenotype), these differences are difficult to interpret in an evolutionary sense because they say nothing about how selection acts. Explicit partitioning of offspring numbers among the mating and non-mating males of each phenotype, followed by the comparisons of opportunities for sexual selection within and among morphs, as well as within and among years (e.g., DuVal & Kempnaers 2008; Krakauer *et al.* 2011), avoids these problems entirely.

Lastly, it is necessary to examine the relative fitnesses of the male morphs over time. While Schradin and Lindholm marshal an extraordinary amount of data over three separate years to conclude that relative fitness is unequal among morphs, the time frame for this conclusion is too short. Schradin and Lindholm found that the relative fitness of each morph differed within, and varied among, three generations. Far from confirming SDS theory, the observation of oscillations in relative fitness among morphs over this duration is similar to a pattern well-documented for male polymorphisms in salmon, lizards, ruffs, isopods and beetles, in which genetic differences among males are clear (Shuster 2010). This result in four-striped mice is consistent with negative frequency-dependent selection, the mechanism now thought to maintain polymorphisms of all kinds. Oscillations in male fitness appear to occur because fitness variance among males of one phenotype creates mating opportunities for males expressing a different phenotype (Shuster & Wade 1991).

What then about genetic differences among morphs? Abundant research on conditional phenotypes indicates that individual behavioural and developmental responses to environmental conditions, i.e., 'reaction norms', *do* have a genetic basis and *do* vary within populations like other quantitative traits (Milton, Ulane & Rutherford 2006). Schradin and Lindholm conclude that male phenotypes in this species are 'not genetically determined', yet while their $n = 2$ breeding experiment rejects a Mendelian hypothesis, it substantiates a quantitative genetic one. If male phenotype does represent an individual's reaction norm to conditions encountered during development, and if that male's progeny are reared in a different shared environment, then the disproportionate appearance of a *particular* phenotype among the male progeny indicates that quantitative genetic variation underlies male reaction norms in this species.

Schradin and Lindholm present truly fascinating results. The grain of their data is exceptionally fine. They describe yet another species in which male phenotypes are polymorphic in form, flexible in expression and variable in relative fitness. This is an excellent system to combine the rich history of behavioural research on male polymorphism, with the population and quantitative genetic tools that have proven so

powerful in describing other polymorphic species. However, it is still too soon to draw firm conclusions about how male polymorphism persists in four-striped mice. Evolutionary genetic methods applied to these data, and others like them, will help.

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