

## BRIEF COMMUNICATIONS

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### STRUCTURAL COMPLEXITY OF THE ENVIRONMENT AFFECTS THE SURVIVAL OF ALTERNATIVE MALE REPRODUCTIVE TACTICS

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**Abstract.**—Alternative reproductive tactics in males are often associated with divergent phenotypes expressed as phenotypically plastic threshold traits. The evolution of threshold traits in these species has been modeled under the conditional evolutionarily stable strategy (ESS). Both strategic and genetic models predict that perturbations to the fitness trade-off between the male morphs will lead to a shift in the ESS switch point of the threshold. So far, demographic factors that influence the competitive ability of male morphs have been investigated and related to intraspecific population variation in male dimorphic thresholds. Here we reveal evidence for the theoretical prediction that abiotic features of the environment, in particular its structural complexity, are likely to influence the ESS threshold. In the male dimorphic mite *Sancassania berlesei*, we monitored the survival of aggressive fighter males and their benign scrambler counterparts in populations that differed in structural complexity. We found that, consistent with our prediction, the complex habitat favored fighter males, enabling them to kill a greater number of rival scramblers. We found no effect of habitat complexity on the survival of fighter males. These results demonstrate how abiotic as well as biotic aspects of the environment can be important in determining the frequencies of males adopting alternative tactics in different species or populations.

**Key words.**—Alternative reproductive tactics, evolutionarily stable strategy, polyphenism, sexual selection.

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Alternative reproductive tactics are often associated with a divergence in male morphology such that male phenotypes fall into two or more distinct morphs (Emlen 1994; Alcock 1995; Lank et al. 1995; Radwan 1995; Tomkins and Simmons 1996). Where the males in a population express different morphs as a consequence of environmental cues, rather than as a consequence of a polymorphism at a few loci, the conditional evolutionarily stable strategy (ESS) can be used as a tool to understand the evolution of male polyphenism (Hazel et al. 1990; Gross 1996). The genetic basis to the conditional ESS has been modeled as an environmentally determined threshold trait (Hazel et al. 1990, 2004). Such environmental threshold (ET) modeling provides a quantitative genetic and population genetic background for understanding the evolution of threshold traits in general. These models work on the basis that there is a fitness trade-off between the environments that yield the alternative morphologies, such that one morph has higher fitness in one environment and the other in the alternative environment (Hazel et al. 1990, 2004).

Under the same models, continuous environmental variation can lead to variance in body size, and size-dependent alternative tactics can arise as a consequence of a trade-off between morph fitness and status. This is the commonly observed basis to male dimorphisms in many species and has been termed the status-dependent ESS (Gross 1996). In such systems, larger males tend to guard females, while small males tend to avoid aggression (Forsyth and Alcock 1990;

Radwan 1993; Moczek 1999; Hunt and Simmons 2001). One aspect of key interest in understanding the evolution of threshold traits is how selection on alternative tactics gives rise to changes in the position of thresholds within a population (Radwan et al. 2002; Moczek and Nijhout 2003; Moczek 2004; Tomkins and Brown 2004; Tomkins et al. 2004; Unrug et al. 2004). Under the ET and ESS models, the position of the threshold is determined by the frequency of the environments in which each morph is favored, the magnitude of the fitness trade-off between morphs, and the genetic variance in the threshold (Hazel et al. 1990, 2004). Hence, assuming the availability of genetic variation for the threshold, Hazel et al.'s (1990) model predicts that perturbations to the fitness trade-off are likely to cause shifts in the threshold in a population. Similarly, Gross (1996) specifically predicted that changes in environmental (or demographic) factors that altered the fitness functions of the alternative tactics would lead to evolutionary changes in threshold position.

Demographic factors have been implicated in the divergence of male-dimorphic thresholds between populations of dung beetle *Onthophagus taurus* (Moczek 2004), earwig *Forficula auricularia* (Tomkins and Brown 2004), and mite *Sancassania berlesei* (Radwan et al. 2002). In the dung beetle, there was a correlation between increasing population density and increasing numbers of short-horned “minor” males and a shift in the dimorphic threshold to a larger body size (Moczek 2004). In the earwig, the opposite appears to be true, with higher population densities being associated with thresholds at relatively smaller body sizes and decreased numbers of the minor “brachylabic” phenotype (Tomkins and Brown 2004). The pattern in mites is similar to the dung beetle

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example, with experimental manipulations showing that fighter males have higher fitness in low-density conditions (Radwan 1993) and that there is a facultative, density-dependent shift in threshold. This density-dependence means that high population densities are characterized by many benign "scrambler" males and low-density populations are characterized by many aggressive "fighter" males (Radwan et al. 2002; Tomkins et al. 2004).

We are aware of no evidence that the abiotic environment has an influence on the relative fitness of male morphs in species with alternative reproductive tactics, despite the theoretical expectation that environmental factors should be important (Hazel et al. 1990; Gross 1996). Male dimorphisms are usually associated with intense male-male competition, and therefore research has tended to focus on demographic rather than purely environmental sources of variance in the fitness trade-off between morphs. This is despite the fact that many threshold traits, such as cryptic coloration (Hazel and West 1982) and predator defense (Lively 1986, 1999; Hazel et al. 1990; Lively et al. 2000) are modeled explicitly on the basis of environmental cues. We believe that environmental factors have been overlooked in their role in shaping the evolution of alternative reproductive tactics that are expressed as threshold traits. Important environmental factors are those that will increase the competitive ability of one morph over the other. Here, we test this specific prediction by manipulating the structural complexity of the environment of populations of the mite *Sancassania berlesei*.

*Sancassania berlesei* is an acarid mite often found in structurally complex subsoil structure. There are two male morphs: fighter males are characterized by thickened and sharply clawed third pairs of legs that they use to kill their rivals, whereas scambler males have unmodified legs and are benign. Previous research has shown that the dimorphism in *S. berlesei* is status dependent, with larger final instar nymphs eclosing into fighters (Radwan et al. 2002). As stated above, along with male size, there is also density sensitivity in the position of the threshold. Chemicals that emanate from high-density colonies appear to shift the threshold toward larger body sizes (Radwan et al. 2002; Tomkins et al. 2004). We hypothesized that structural complexity in the habitat of *S. berlesei* would increase the competitive advantage of fighter males over their benign scambler rivals, because fighters would readily be able to corner and kill their rivals. The ability of a single fighter to kill all rival males in small enclosed groups has been demonstrated to result in better than average survival for fighters; in contrast, in large, high-density, unstructured populations, where monopolization by fighters is not possible, fighters pay higher mortality costs of their aggressiveness (Radwan 1993). Thus, we predicted that in structurally complex habitats fighters would have the opportunity to monopolize females in semi-enclosed compartments, reducing the relative fitness of scambler.

#### MATERIALS AND METHODS

We used a culture of mites referred to as Balmerino in previous publications (Tomkins et al. 2004). These mites were collected from piles of chicken litter and have been acclimated to laboratory conditions for over 20 generations.

The culture of mite populations is described elsewhere (Radwan et al. 2002). We took 64 25-mm diameter by 25-mm deep vials that had plaster-of-paris bases and used these as arenas in which to rear the mites used in the experiments to adulthood. In such arenas male dimorphism is expressed in a status-dependent manner (Radwan et al. 2002). Twelve protonymph (second larval stage) mites were placed in each vial; ad libitum food was provided as three balls of dried yeast. This is enough food for the mites to complete their development to adulthood. At adulthood, the mites were placed into one of two types of experimental arena, at a ratio of six females, three fighters and three scambler in both. The simple habitat was a 25-mm diameter by 25-mm deep vial with a flat base of plaster of paris. The complex habitat was the same type of vial with a plaster base; however, these vials had 10 short (10-mm) sections of plastic drinking straws (about 3 mm in diameter) set vertically in the plaster. The plastic drinking straws created a habitat that was much more structurally complex for the mites, with tubular spaces inside the straws and irregular gaps between the straws. Both arenas were provided with the same amount of food, six balls of yeast. Yeast balls and mites were added to the experimental arena both inside and outside of the straws in the complex habitat.

Twenty populations of mites were set up for each habitat, and the survival of the male morphs and females was recorded once per day for the following seven days. We stopped recording survival at this time because the next generation of mites made it impossible to score the survival of the parental generation.

We used a repeated-measures analysis of variance to analyze the effect of habitat complexity on the survival of males of each morph and of females. Repeated-measures analysis was required because each population was surveyed on each of seven days, so the data for any one day were not independent of the previous day. Habitat was the main effect.

#### RESULTS

An important consideration for understanding the evolution of threshold traits is the fitness trade-off between the alternative tactics. The greater the trade-off, the more intense will be the stabilizing selection on a particular threshold position (Hazel et al. 1990). A repeated-measures general linear model was used to look at the effect that habitat complexity had on the differential survival of the male morphs, that is, the degree to which habitat influences the relative payoffs of one morph over the other. The data for males in this analysis conformed to the assumption of sphericity (Mauchly's  $W = 0.25$ ,  $df = 27$ ,  $P < 0.001$ ). The within-subjects analysis revealed a significant three-way (day  $\times$  habitat  $\times$  morph) interaction (Table 1); this shows that the rate at which males died differed according to the male morph and habitat. Figure 1a and 1b show this effect: the rate at which scambler died was greater than the rate at which fighters died in the complex habitat, but the difference was less marked in the simple habitat. There was a significant habitat  $\times$  morph interaction also (Table 2), showing that overall the survival of males depended on both factors. Because of the interactions we further examined the male morphs separately.

TABLE 1. Repeated-measures general linear model showing the within-subjects effects of day, habitat, and male morph on male survival.

Source	df	MS	<i>F</i>	<i>P</i>
Day	7	13.114	81.708	0.000
Day × habitat	7	0.299	1.864	0.073
Day × morph	7	1.242	7.738	0.000
Day × habitat × morph	7	0.396	2.470	0.017
Error (day)	532	0.161		

Repeated-measures general linear models were performed on the data for each male morph and for females. The data for fighter males conformed to the assumption of sphericity (Mauchly's  $W = 0.019$ ,  $df = 27$ ,  $P < 0.001$ ). The within-subjects effects (the changes across days, accounting for the repeated measures) showed that there was a significant decline in the number of fighters alive across the eight days ( $F_{7,266} = 28.93$ ,  $P < 0.001$ ; Fig. 1a). There was no difference between habitat types in the within-subjects slope of the decline (habitat × day interaction:  $F_{7,266} = 0.538$ ,  $P = 0.805$ ), and the decline was fitted best by a linear term ( $F_{1,38} = 67.7$ ,  $P < 0.001$ ). The between-subject effect of habitat type on the survival of fighter males was not significant ( $F_{1,38} = 1.40$ ,  $P = 0.244$ ; Fig. 1a). Fighter males therefore were not affected in terms of their survival by the structural complexity of their habitat.

For scambler males, the data also conformed to the assumption of sphericity (Mauchly's  $W = 0.017$ ,  $df = 27$ ,  $P < 0.001$ ). The within-subjects effects showed that there was a significant decline in the number of scambler males over the eight days of the experiment ( $F_{7,266} = 53.18$ ,  $P < 0.001$ ), but also that the rate of decline in the numbers of scambler males was different between the treatments (habitat × day interaction:  $F_{7,266} = 3.04$ ,  $P = 0.004$ ). This can be seen in Figure 1b as a greater decline in the complex habitat treatment than the simple habitat. The significance of the habitat × day interaction meant that the main between-subject effect of habitat ( $F_{1,38} = 3.52$ ,  $P = 0.068$ ) was not considered further.

We also surveyed the survival of females, even though there was no expectation for a difference in mortality due to environment. The data for females again conformed to the assumption of sphericity (Mauchly's  $W = 0.00$ ,  $df = 27$ ,  $P < 0.001$ ). The within-subjects effect revealed a significant decline in the number of surviving females across the days of the experiment ( $F_{7,266} = 22.6$ ,  $P < 0.001$ ; Fig. 1c) and also a significant difference between the treatments in the decline in female numbers (habitat × day interaction:  $F_{7,266} = 14.7$ ,  $P < 0.001$ ). The difference between the treatments is due to a greater decline in the number of females in the complex habitat. The significance of the habitat × day interaction meant that the main between-subject effect of habitat ( $F_{1,38} = 26.38$ ,  $P = 0.001$ ) was not considered further.

#### DISCUSSION

We tested the hypothesis that the fitness benefits that accrue to males pursuing alternative tactics can be altered by abiotic features of their environments. Our results suggest that the structural complexity of the environment in which the mites

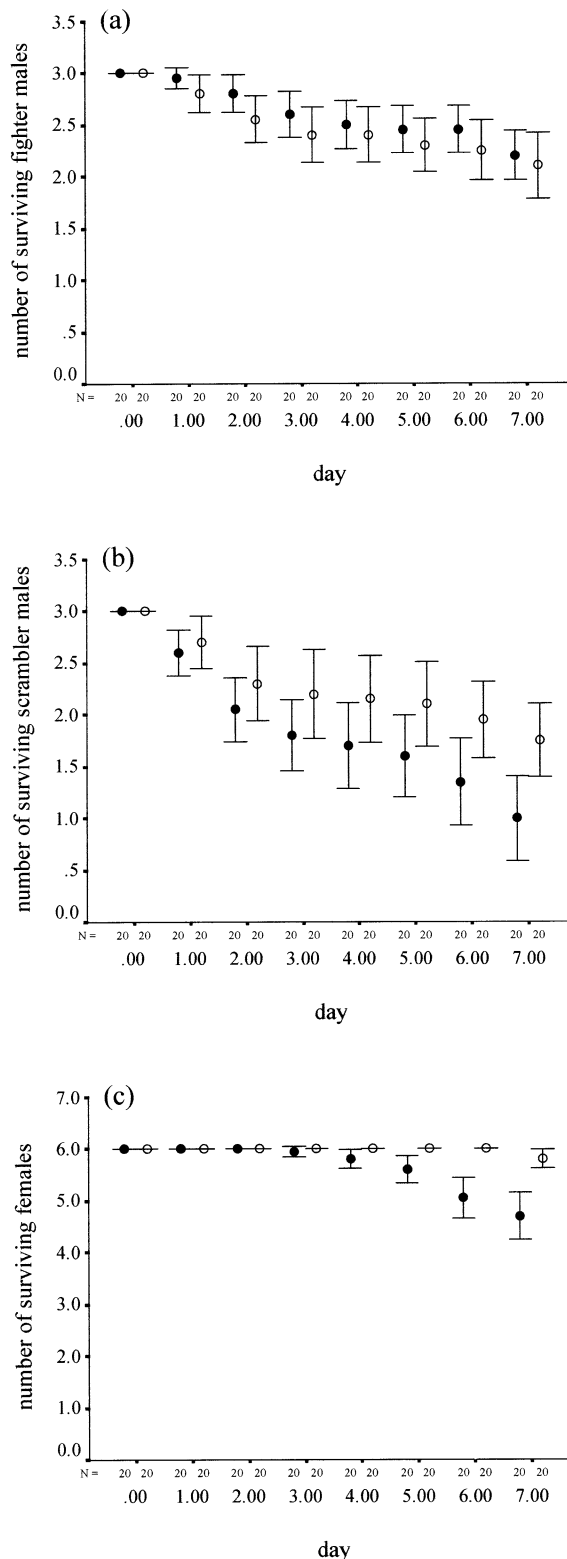


FIG. 1. Charts showing mean ( $\pm$ SE) number of surviving (a) fighters, (b) scambler, and (c) females over the experimental period of seven days, in complex (closed circles) and simple (open circles) habitats.

TABLE 2. Repeated-measures general linear model for the between-subjects effects of male morph and habitat on survival, adjusted for the daily repeated measures.

Source	df	MS	F	P
Intercept	1	3422.500	1527.251	0.000
Habitat	1	2.256	1.007	0.319
Morph	1	35.156	15.688	0.000
Habitat $\times$ morph	1	11.025	4.920	0.030
Error	76	2.241		

live does indeed influence morph fitness, with fighter males killing more rival scramblers when the habitat causes them to encounter one another in confined spaces.

We found no difference between the mortality of fighters in the habitats that differed in structural complexity; however, we did find that the scambler males were significantly more likely to be killed by a fighter male if they were in a structurally complex habitat. The mortality in both male morphs is likely to depend heavily on encounter rate with fighters and the potential for escape. One or both of these factors must differ between the morphs because even though fighters do kill one another, the structure of the habitat had little effect on fighter survival but did have a large effect on scambler mortality. With equal encounter rates, we would expect "cornering and killing" to have influenced fighter mortality in a way similar to scambler mortality. We did not find this, suggesting that the rate of lethal encounters increased more for scambler than fighters. Encounters between fighter males seem to have been rarer in the complex habitat than in the simple one. This hypothesis arises from the observation that, in the complex habitat, fighter males tended to control a ball of yeast and the females feeding on it; consequently fighters tended not to move around and would not have encountered one another once they were established on a resource patch. In contrast, scambler males, excluded from food and females by the improved ability of fighters to defend resource patches, were likely to have an increased encounter rate with fighters in their search for resources. Our observations could therefore be explained by the fact that scambler were more mobile than fighters in the complex environment and thus faced higher probability of encountering a fighter and getting killed. A lower encounter rate with other fighter males might make defending territory a less costly—and therefore more readily adopted—strategy for fighters in complex habitats. Thus, scambler might not have a choice but to increase female searching effort, inevitably resulting in trespass on the fighters' easily defended territories. It would be interesting to test specifically whether habitat structure increases territoriality of fighter males and/or increases the difference in motility between morphs.

Another consideration is the purely probabilistic effect of habitat structure on the chances of survival of both morphs. Radwan (1993) showed in a simple model that the relative encounter rate between fighters increases with population size. For example, in a population containing equal proportion of both morphs, at infinite population size the rate of encounter between a pair of fighters will be one-quarter of all possible encounters, whereas in a population containing two males (i.e., one fighter and one scambler) the proportion

will be zero. Consequently, fighter males tend to have a higher fitness at small population sizes, because under these conditions they can kill a significant proportion of rivals, but in large populations they are swamped by rivals (Radwan 1993). We found that fighters tended to survive longer than scambler in populations slightly larger than the small populations ( $n = 4$  males) investigated by Radwan (1993); an effect that was enhanced greatly by habitat structure. If structured environments keep the population partitioned into small subpopulations most of the time, this probabilistic consideration may have considerable effect. Hence, our data show that the relative fitness (measured as survival) both within and between morphs is affected by environmental complexity. Although we have not measured the magnitude of the status-dependent fitness trade-off between the morphs in this experiment, the effects that we have detected will directly influence the slopes and elevations of the fitness functions of the alternative tactics. Whether the structural complexity of the environment can predict shifts in the position of the threshold of this species remains to be experimentally determined.

The lower survival of scambler males in the complex habitat thus conformed to our expectation that, in a structured environment, scambler males would have decreased fitness. The effect in both treatments shows an initial decline in the first few days and then a period of stability until day 6 when it declines again. The fact that this is consistent in both habitats is intriguing, perhaps suggesting a behavioral pattern in fighting propensity or foraging activity that increased encounter rate early in the experiment. Indeed, an increased number of fights soon after group formation has previously been reported (Woodring 1969; Radwan 1993), although it has not been determined whether it is male age or experience that matters. Additionally, part of the initial decline is undoubtedly density related; the probability of encounters declining as more males are killed.

The difference in female survival over eight days in the two habitat types was unexpected, but was observed to be an artifact of the experimental arenas rather than a phenomenon with biological interest to the hypothesis under test. The survival of females was high, constant, and similar in the two habitats over the first three days of the experiment. This contrasts to the data for fighter and, particularly, scambler males in which there was an immediate decline in surviving males and a divergence between the habitat treatments. The mortality of the females was observed to be caused by them getting stuck to the side and base of the plastic straw in a moist morass of yeast. The female phenotype is such that the opisthoma is relatively much larger than males for a similar undercarriage of legs. Hence, females are much more liable to get trapped and stuck to smooth moist surfaces by surface tension. The plastic straws likely caused the deaths of the females in this habitat. The deaths of the females were different from those observed in males, where mortality could be readily attributed to fighters killing their rivals: mites have hydrostatic skeletons, and observations show that males that have been killed by a fighter can be distinguished because they leave behind a punctured and deflated corpse.

Our data clearly demonstrate that abiotic factors in the environment can readily influence the competitive ability of

males pursuing alternative reproductive tactics. The environmental factor we identified is perhaps less intuitive than interactions with other species, which may cause differential parasitism or predation in males adopting different behavioral roles, such as calling or being silent satellites (Cade 1979). The environmental effect we have documented is subtly different from the predator-induced polyphenisms that occur in a number of other systems (Lively et al. 2000). As far as we are aware, environmental complexity is not a cue to morph determination in the same way that predator presence can be. In the mite, chemicals related to population density appear to be the primary cue: these chemicals are evidently volatile and influence morph determination without direct contact (Radwan et al. 2002) and would likely pervade simple and complex habitats equally. Hence, it seems that morph determination is unlikely to be influenced by habitat structure.

Our findings emphasize how simple divergence in the abiotic environment can change the fitness returns of a particular behavior or phenotype even when other aspects of the species' biology are held constant. This has implications for population variation in tactic frequency in other systems in which both male dimorphic thresholds and genetic polymorphisms occur. For example, in the dung beetle *O. taurus*, in which minor males dig side tunnels and sneak copulations from guarded females (Moczek and Emlen 2000), it seems likely that soil characteristics would influence the ease with which these tunnels could be dug, a factor that might influence the fitness of minor males.

Our findings lend weight to the hypothesis that abiotic environmental factors, as well as the demographic ones already documented, are likely to influence the positions of dimorphic thresholds in species with alternative reproductive tactics. Indeed our results suggest that habitat structure is likely to be influential in the evolution of alternative male tactics. The demonstration that there is indeed a correlation between abiotic environmental conditions and the actual position of a threshold has yet to be made.

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