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Environmental and genetic determinants of the male forceps length dimorphism in the European earwig *Forficula auricularia* L.

Received: 18 November 1998 / Received in revised form: 14 May 1999 / Accepted: 25 July 1999

Abstract Male dimorphisms are particularly conspicuous examples of alternative reproductive strategies. The male forceps length dimorphism in the European earwig *Forficula auricularia* has long been considered an example of a status- (body size) dependent male dimorphism. In this paper, I test three hypotheses relating to the dimorphism of *F. auricularia*. First, that the dimorphism is status dependent and determined by nutrition. Second, that the dimorphism is a density-dependent adaptation. Third, that there is a genetic basis to population differences in morph frequency seen in the field. These hypotheses were tested by rearing two populations in a split-family rearing design with two diets and two densities. Populations of male earwigs reared in the common garden differed in forceps length and relative forceps length. The populations also differed in the morph frequencies, with 40 versus 26% long-forceped males. These results confirm the notion that there is a genotype-by-environment interaction that determines the morph frequency in a population. There were only minor effects of density on male forceps length and no influence of density on the male dimorphism. In accordance with the hypothesis that the morphs are status-dependent alternatives, large-forceped males only arose on the high-protein diet that produced earwigs of a large body size. However, not all large males produced the long-forceped phenotype. I put forward an extension of the status-dependent dimorphism model that may account for the pattern of forceps dimorphism in this species.

Key words Dermaptera · Male dimorphism · Alternative strategies

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Introduction

Game theory has shown us that there may be more than one solution to a given ecological problem and, thus, that we need not expect all individuals within a population to overcome such problems in the same way (Maynard Smith 1982). Where the problem is one of reproductive success, competition between males for females may lead to the evolution of alternative male mating strategies through differences both in behaviour (Alcock 1997; Emlen 1997) and morphology (Eberhard 1982; Gross 1982; Shuster and Wade 1991; Emlen 1994; Alcock 1996b; Cook et al. 1997). There are three principal ways in which alternative mating strategies are thought to coexist. First, as a frequency-dependent genetic polymorphism with alternative strategies, existing as two or more evolutionarily stable strategies (ESSs) in which the strategies have, on average, equal pay-offs (Maynard Smith 1982; Gross 1996). Second, a mixed strategy where different tactics are employed either probabilistically or at different stages of the life cycle, but where there is no genetic polymorphism (Maynard Smith 1982; Gross 1996). Third, a conditional or status-dependent (Maynard Smith 1982; Gross 1996) mating strategy can evolve in a genetically homogeneous population where facultative alternatives are exploited to optimise reproductive success under different circumstances. This is the most common example of alternative reproductive tactics within the sexes (Gross 1996; Roff 1996).

Gross (1996) has presented a graphical model to explain the evolution of status-dependent dimorphisms. This model demonstrates how the fitness functions of the alternative tactics and their elevations determine both the status (e.g. body size) at which one tactic gives way to another, and also how this in turn influences the ratio of one morph to another in the population (Gross 1996). This model highlights two critical questions about male dimorphisms: (1) what determines the morph frequency in the population, and (2) what determines the morph of an individual?

The determination of morph frequencies has received relatively little empirical attention (Eberhard 1982; Radwan 1995; Alcock 1996a; Roff 1996; Cook et al. 1997; Hews et al. 1997). In the status-dependent model, morph frequencies are determined by the position of the switchpoint between the two morphs in relation to the body size distribution of the population. If the elevation of the fitness function of one morph increases relative to the other morph, the resulting shift in the switchpoints will alter the frequency of the morphs in the population (Gross 1996). The number of competitors or mates may influence the elevation of the fitness function of a particular morph in relation to its alternative. For example, the male dimorphism in the acarid mite *Caloglyphus berlesei* is determined by population density: the fighter males only appear at low densities at which they can kill rivals and dominate females (Radwan 1993). Similarly male dimorphisms across fig wasp species covary with brood size (Cook et al. 1997). In small broods, all males are winged and disperse in search of females, while in large broods, all males are apterous and fight for matings within their natal fruit. At intermediate brood sizes, males tend to be dimorphic (Cook et al. 1997). Evidence for genetic differences between populations in the frequencies of morphs that are status dependent has yet to be demonstrated.

The forceps length of the male European earwig *Forficula auricularia* shows dimorphic variability: small males have short forceps which scale isometrically with body size, while large males tend to have long forceps that are positively allometric (Tomkins and Simmons 1996). This forceps length dimorphism has long been regarded as an example of a conditional or status-dependent dimorphism (Diakonov 1925; Kuhl 1928; Eberhard 1982; Eberhard and Gutierrez 1991). This interpretation stems from early experiments in which only short-forceped (brachylabic) males were reared from sires of both morphs (Diakonov 1925) and in which long-forceped (macrolabic) males originated only among well-fed nymphs (Kuhl 1928). Nevertheless, more recently, Lamb (1976) found that when earwigs were reared on high-protein diets, males reached body sizes in excess of those in the field, and within most families there were no macrolabic males. These findings, although based on a small sample size, imply that the basis of the dimorphism may be genetic rather than conditional. Furthermore, forceps length in brachylabic *F. auricularia* has recently been demonstrated to have a significant heritable component (Tomkins and Simmons 1999). A final feature of this dimorphism is the extremely high variation in morph frequency between populations. This difference is most exaggerated between island and mainland populations, with islands supporting frequencies of macrolabics as high as 35% (Tomkins and Simmons 1996), whereas the mainland may have as few as 2% (Huxley 1927). Differences in morph frequencies also occur between islands that are geographically close (Tomkins and Simmons 1996).

Here I describe the results of an experimental manipulation of diet and density testing three hypotheses concerning the male forceps length dimorphism in *F. auricularia*. The first hypothesis is that the dimorphism is status dependent, with the prediction that there is a critical body size at which the brachylabic morph gives way to the macrolabic morph. The second hypothesis is that rearing density influences the forceps length dimorphism: the high density of earwigs on the Farne Islands and the high proportion of macrolabic males in these populations have lead me to expect that increasing density results in an increase in the frequency of the macrolabic morph. The final hypothesis is that the difference in morph frequencies observed between populations in the field has a genetic basis. The latter hypothesis predicts consistent differences in morph frequency even when earwigs are reared under common-garden conditions (i.e. two populations reared in the same environment).

Methods

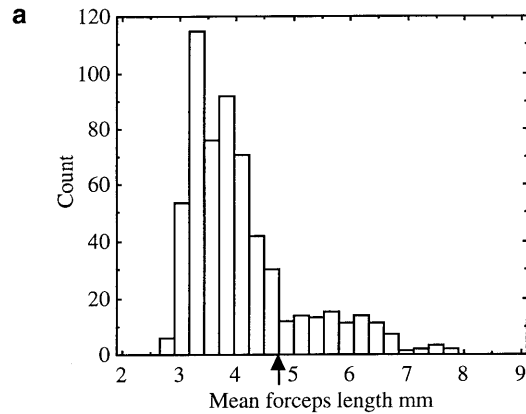
On the 3 April 1996, approximately 150 clutches of *F. auricularia* eggs and the females attending them were collected from burrows beneath stones and driftwood on Brownsman Island and West Wideopen Island of the Farnes group in Northumberland, UK. Each female and her eggs were placed into a depression in a soil-filled 50-mm-diameter Petri dish, and the Petri dish lids were replaced and secured with an elastic band. The females had returned to tending their eggs when they were checked after a few hours. The Petri dishes with females and their eggs were taken to the laboratory and kept at 15°C. Most broods hatched on the 10 April±1 day.

In a split-family rearing design, first-instar nymphs were placed into two diet and density treatments. The densities were either one or eight per 50-mm-diameter Petri dish; the eight earwigs were always from the same brood. The diets on which the nymphs were reared was either a low-protein diet of porridge oats (11.8% protein, 8.7% fat, 7.2% plant fibre), or a high-protein diet of Aquarian goldfish flake (40% protein, 11.5% fat, 0.6% plant fibre). Food and water were provided ad libitum and old food and frass were removed from the dishes on a weekly basis. From the broods collected, 45 families from West Wideopen, and 57 from Brownsman Island were put into the experimental treatments. There was a mean of 32 earwigs per family from West Wideopen and 34.3 per family from Brownsman. Offspring mortality was high (up to 67%) in the low-diet high-density treatments. Only 47 families (32 from Brownsman and 15 from West Wideopen) of the original 102 had offspring that survived to be measured in each of the treatments; these 47 families contributed 633 offspring (see Table 2). Slight differences in sample size are due to earwigs being eaten by their siblings before they could be measured; often forceps were measurable, but the pronotum was completely eaten.

Petri dishes containing fourth-instar nymphs were checked every day for eclosed adults. Adults in the high-density treatments were removed on the day of eclosion and their left and right forceps lengths and pronotum width were measured. Forceps were measured from where their base terminates at right angles into the body in a straight line across the curve to the tip. The tip of the left wing was then cut off to show that they had been measured and they were returned to their original Petri dish. The date of eclosion was recorded in the low-density treatments and earwigs were measured later. All measurements were made using the same Prior ZS2500 stereo microscope on earwigs that had been anaesthetised with CO₂.

Models have been developed for establishing the body size threshold across which male phenotypes change in male dimorphic (Eberhard and Gutierrez 1991; Emlen 1996). Unfortunately, a

Brownsman



West Wideopen

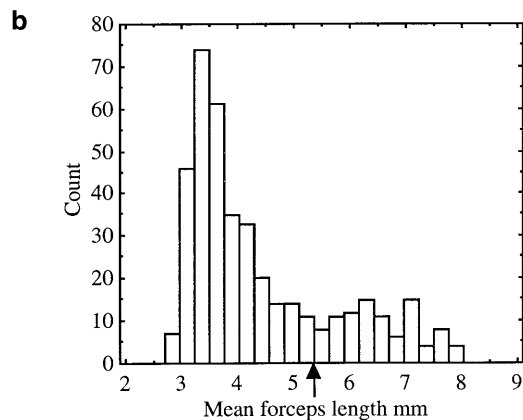


Fig. 1a, b Frequency histograms of male forceps length. The arrow indicates the boundary between macrolabic and brachylabic males

meaningful estimation of a switchpoint body size (threshold) using Eberhard and Gutierrez's (1991) model is prohibited by the extensive overlaps between the morphs, resulting in many individuals being assigned to the wrong morph. Emlen's (1996) model for beetle horns does not follow the shape of the earwig data. A

more sensitive approach is to look at forceps length and shape rather than body size (Tomkins and Simmons 1996). Therefore to discriminate between the morphs, I constructed a frequency histogram of forceps length containing 20 bins for each population. I reason that the lowest value between the two peaks (Fig. 1a,b) delimits the different forceps morphologies, and assigned this bin and all those larger than it to the macrolabic morph.

The data were analysed separately for each trait using a nested analysis of variance. The effects were fixed, except for "family" which I treated as a random effect since families are random representatives of the populations from which they come. "Diet", "density" and "island" were analysed as main effects and families were nested within island to facilitate a comparison between families within the islands.

Results

Pronotum width

There were no significant effects of the density treatment on pronotum width (Tables 1, 2), there were also no significant interactions between density and island or with families within islands (Table 1). Pronotum width was significantly greater in high-protein treatments (Tables 1, 2), and the non-significant interaction between island and diet demonstrates that both populations showed the same response to diet. There was a significant interaction between diet and families within islands (Table 1) and a highly significant interaction between diet and density (Table 1). The latter interaction is the result of males on the low-protein diet growing larger at the higher density, probably because the low diet was unavoidably supplemented by cannibalism and the exuviae of other earwigs. The islands differed significantly in pronotum width, Brownsman males being larger in all treatments, and there was a significant effect of family within islands on pronotum width.

Forceps length

Male forceps length was not significantly influenced by rearing density, and both islands showed this pattern

Table 1 Sources of variation in adult pronotum width and forceps length for two Farne Island populations of the European earwig. Families were split between the diet and density treatments

Source	Pronotum width			Forceps length			Relative forceps length		
	<i>df</i>	MS	<i>F</i>	<i>df</i>	MS	<i>F</i>	<i>df</i>	MS	<i>F</i>
Density	1,58	0.017	1.966	1,57	0.585	0.866	1,57	0.089	0.659
Diet	1,52	7.428	546.506****	1,52	21.350	210.657****	1,51	20.500	107.082****
Island	1,46	0.170	4.818*	1,48	9.945	8.074**	1,48	3.942	14.898***
Family (island)	45,39	0.038	2.444*	45,38	1.284	1.124	45,38	0.277	1.263
Family×density (island)	45,488	0.009	1.171	45,482	0.687	1.150	45,484	0.139	1.186
Family×diet (island)	45,488	0.014	1.835**	45,482	1.070	1.791**	45,484	0.201	1.712**
Density×diet	1,488	0.122	15.597****	45,482	0.635	1.064	1,484	0.001	0.009
Island×density	1,54	0.003	0.296	1,54	0.008	0.012	1,54	0.011	0.079
Island×diet	1,51	0.002	0.1269	1,51	8.855	8.675**	1,51	2.222	11.574**
Error	488	0.008		484	0.597		482	0.117	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$

Table 2 Pronotum widths and forceps lengths (mm) and relative forceps lengths, of male earwigs from the Brownsman and West Wideopen populations reared at different densities and diets

	High density				Low density			
	<i>n</i>	High protein	<i>n</i>	Low protein	<i>n</i>	High protein	<i>n</i>	Low protein
Pronotum width								
Brownsman	116	2.05±0.01	86	1.81±0.01	133	2.06±0.01	100	1.75±0.01
West Wideopen	59	1.90±0.01	37	1.76±0.02	60	2.01±0.01	42	1.72±0.01
Forceps length								
Brownsman	116	4.51±0.08	85	3.44±0.03	132	4.58±0.01	97	3.31±0.02
West Wideopen	59	4.97±0.16	37	3.41±0.03	60	5.26±0.18	43	3.28±0.02
Relative forceps length								
Brownsman	116	2.19±0.04	85	1.89±0.01	131	2.21±0.04	97	1.88±0.01
West Wideopen	59	2.49±0.07	37	1.94±0.02	60	2.60±0.08	42	1.91±0.02

since there was no interaction with island. Families within islands similarly showed no significant variance in forceps length in response to the density treatment. Forceps length was significantly longer in the high-protein treatments (Tables 1, 2), and families within islands showed significant variance in forceps length in response to diet (Table 1). Unlike pronotum width, for forceps length there was no significant interaction between diet and density. There was a significant interaction between diet and island (Table 1): males from the West Wideopen population developed longer forceps on the high-protein diet than males from the Brownsman population. Indeed, there was a significant difference between the forceps lengths of the males from the two islands; despite their smaller body size (see below), males from West Wideopen had significantly longer forceps (Tables 1, 2).

Relative forceps length

Relative forceps length, measured as forceps length/pronotum width, provides an indicator of the investment in forceps relative to body size, made by earwigs in response to the treatments. Relative forceps length followed the same pattern as forceps length for all of the effects. Diet significantly increased the relative length of forceps, and the relative forceps length of the West Wideopen males was longer than that of the Brownsman males. There was also a significant interaction between family and diet, within islands, on relative forceps length. The significant interaction between island and diet reflects the relatively longer forceps of macrolabial males from the West Wideopen population (see below).

Forceps length dimorphism

Only in the high-protein diet treatments were macrolabial males present (Fig. 2) and further analysis is conducted only on these treatment groups. Figure 2 demonstrates that although macrolabial males only appear in the popu-

lations after a certain size, there is nevertheless extensive overlap between the body sizes of the morphs.

The forceps length at the divergence between the morphs is longer for West Wideopen, reflecting the population differences in forceps length (Fig. 1: West Wideopen 5.29 mm, Brownsman 4.74 mm). There were no significant differences between the high- and low-density treatments (reared on high diets) in the proportions of the morphs (West Wideopen: high density macrolabial:brachylabial=20:39, low density 28:32, $\chi^2=1.519$, NS; Brownsman: high density macrolabial:brachylabial=28:116, low density 42:136, $\chi^2=0.581$, NS). There was a significantly higher frequency of macrolabials (high diets, high and low densities combined) in the West Wideopen population macrolabial:brachylabial: West Wideopen 48:71 (40:60%); Brownsman 65:187 (26:74%); $\chi^2=7.39$, $df=1$, $P=0.006$). To determine whether the morphs on the two islands differed in their relative forceps lengths, a two-factor ANOVA was performed on morph and island, the critical result being the interaction term between morph and island. Macrolabial males from the West Wideopen population did have relatively longer forceps (morph×island: $F_{1,620}=58.6$, $P<0.0001$; Fig. 3).

Discussion

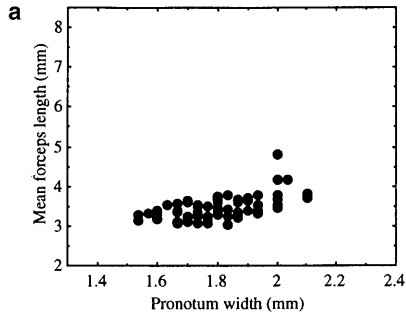
I investigated the male forceps length dimorphism in the European earwig *F. auricularia* by rearing earwigs from two populations in a split-family rearing design in a common garden. The results demonstrate that only earwigs reared on the high-protein diet produced macrolabial forceps and the hypothesis that the dimorphism is a facultative response to rearing density is not supported. The status-dependent dimorphism model (Gross 1996) is supported by these results.

There were significant family effects on pronotum width, and significant diet×family interaction terms for pronotum width, forceps length and relative forceps length. These terms demonstrate that families differ in their responses to diet, i.e. in some families, traits were larger in the high-protein diet than in the low, while in

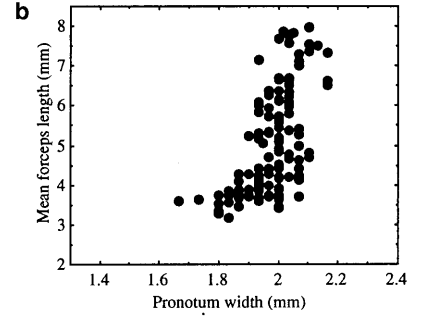
Fig. 2 Scatter plots of mean male forceps length on pronotum width for West Wideopen Island (a–d) and Brownsman Island (e–h), reared at high (a, b, e, f) and low densities (c, d, g, h) and on diets of high (b, d, f, h) and low protein (a, c, e, g)

West Wideopen males

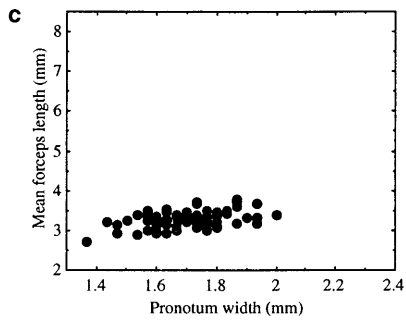
High density, low diet



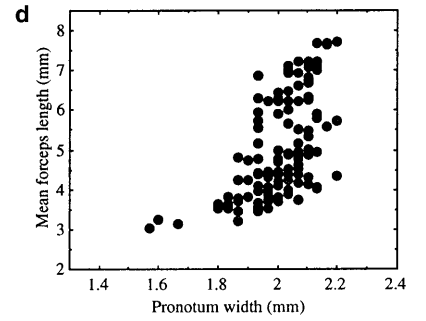
High density, high diet



Low density, low diet

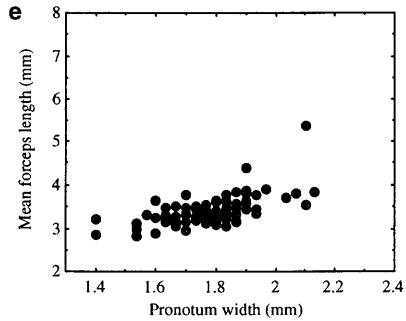


Low density, high diet

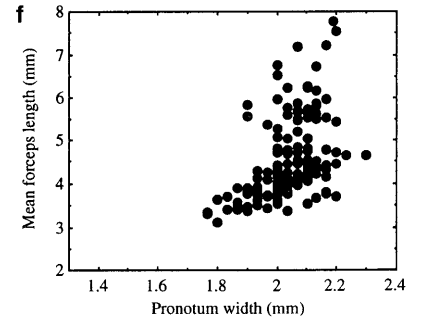


Brownsman males

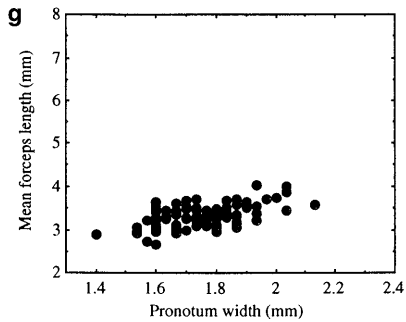
High density, low diet



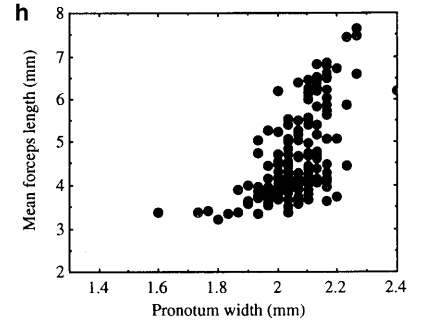
High density, high diet



Low density, low diet



Low density, high diet



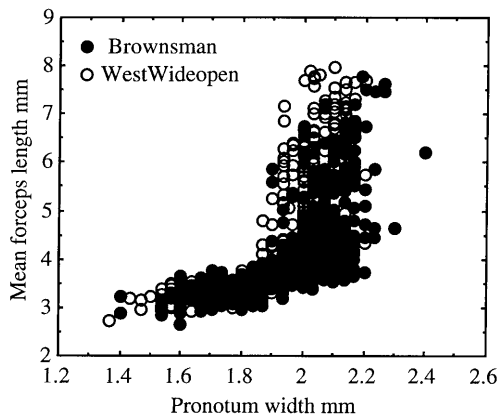


Fig. 3 Male forceps length on pronotum width for males from all treatments and both populations, demonstrating the earlier production of macrolabics in the West Wideopen population and their longer forceps

others, the converse was true. This could reflect heritable variation in the ability to assimilate food. Alternatively this apparent genotype by environment interaction may be the result of common environmental effects, since the earwigs reared at high densities were related and shared the same environment. Indeed a post hoc test on individuals that were reared alone (excluding all density effects) shows that in this group there was no family×diet interaction (pronotum width: $F_{45,241}=1.393$, $P=0.061$; forceps length: $F_{45,238}=1.083$, $P=0.344$; relative forceps length: $F_{45,236}=1.102$, $P=0.316$). The powers of these interaction tests were all <0.96 and it seems, therefore, that it was the common environment that was driving the significant family×diet interactions. It is worth noting that high density was achieved with groups of kin: whether or not this is a significant confounding variable is not clear. Although clearly confounded in this experiment, heritable variation in these traits has been shown for an Italian population of *F. auricularia* (Tomkins and Simmons 1999).

In neither population was forceps length tightly related to body size; rather, the response to manipulations of diet quality is complicated by the presence of earwigs that are very large bodied but have brachylablic forceps. This overlap is unexpected in a dimorphic trait that is status dependent. Previous workers have also reported an overlap in body size across the male morphs of *F. auricularia* (Diakonov 1925; Huxley 1927; Kuhl 1928; Tomkins and Simmons 1996). The overlaps previously reported could have arisen from sampling different populations or years, or from the error involved in measuring body length (Diakonov 1925), a variable trait. Here, by rearing earwigs on controlled diets and measuring pronotum width, a fixed trait, I have demonstrated that the overlap in body size of the morphs is a consistent feature of the dimorphism in this species.

This overlap in the morphs contrasts with the current status-dependent dimorphism model (Gross 1996) and requires explanation, a number of which are possible.

First, there may be a genetic polymorphism, with some individuals genetically incapable of becoming macrolablic (Briceno and Eberhard 1987; Radwan 1995). Second, all males may be able to express the macrolablic phenotype, but there may be genetic variance in the threshold body size at which they switch phenotypes. Third, the overlap could be accounted for by a mixed strategy in which morphs arise from a probabilistic switch after a given body size has been reached; the probability of switching being 40% in the West Wideopen population and 26% in the Brownsman population. If there is a genetic polymorphism or genetic variance among males for the switchpoint body size, we would expect to find familial propensities towards one morph or another. If, however morphs are assigned probabilistically, as in a mixed strategy, there should be no such pattern. A post hoc test to discriminate between these hypothesis showed that there were no significant differences between broods in the proportions of the morphs (West Wideopen: $F_{1,38}=1.07$, NS; Brownsman: $F_{1,53}=1.27$, NS). Although this suggests that there is no obvious genetic basis for some large males remaining brachylablic, it cannot verify the occurrence of a mixed strategy, in particular because broods may have been fathered by more than one male. There is also a fourth possibility: that errors in male self-assessment may generate the overlap. The exact nature of the genotypic control of the dimorphism requires further experimental investigation.

Finally, not expecting to find overlaps between morphs may be an interpretational problem. The current model of Gross (1996) does not incorporate variance about the fitness functions, and this results in two characteristics of interpretation of the model. First, the fitness functions are characterised by lines and the threshold between morphs as a switchpoint (implying little overlap between the morphs). Second, the point where the fitness functions intersect is a point of equal fitness for both morphs (Gross 1996). In reality, variance that may be associated with the fitness functions has implications for the switchpoint and the point of equal fitness. Variance is likely to be normally distributed around the fitness functions and so there will be an optimal switchpoint at the intersection of the lines; however reduced selection may allow substantial variance around this optimal point. The result of weak selection around a switchpoint will be a range of body sizes over which individuals have the potential to achieve equal fitness whichever morph they become (Fig. 4).

The degree of overlap in body size between morphs will be determined by two factors, first, the degree to which the slopes differ (the more similar the slopes of the fitness functions, the broader the switch zone) and, second, the variation around the fitness functions. The slopes of the fitness functions will be determined by the size dependence of the pay-offs of the particular strategies. For example in *F. auricularia*, macrolablic males with larger forceps are more likely to win fights (Radesäter and Halldórsdóttir 1993), and brachylablic males

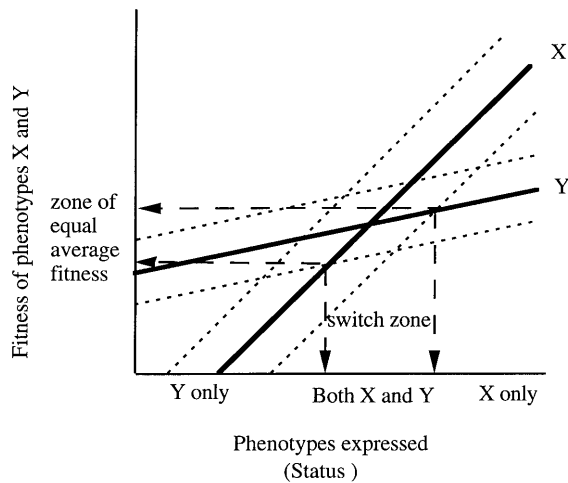


Fig. 4 Variance around the fitness functions of X and Y create a range of statuses across which phenotypes become more likely to switch from Y to X. This corresponds to a zone of equal fitness of the phenotypes; this zone is bounded by the point at which the SE of one fitness function crosses the mean of the other fitness function. In the switch zone, both phenotypes may be expressed creating an overlap in status between the morphs. Low-status individuals should all have the Y phenotype, while high-status individuals should all have the X phenotype

with larger forceps are known to be preferred by females (Tomkins and Simmons 1998): the fitness functions of both brachylabic and macrolabic males are likely to have a positive slope. The variance around the fitness functions is likely to reflect the intensity of the selection on the dimorphic trait, which in turn selects for smaller errors of self-assessment and reduced genetic variance in the threshold at which males switch phenotypes. This extension to the status-dependent model could explain the overlaps seen in the morphs of other species, notably the rhinoceros beetles *Chalcosoma caucasus* and *C. atlas* (Kawano 1995a, 1995b), as well as other earwig species (Eberhard and Gutierrez 1991; Tomkins and Simmons 1996).

The differences in morph frequencies that were found to occur between field samples from the two populations (Tomkins and Simmons 1996) were also observed in the common-garden experiment. These differences in morph frequency, in addition to the nutritional determination of the morph, indicate that morph frequencies are the result of a genotype by environment interaction (Roff 1996). This between-island difference is strong evidence for additive genetic variance in the threshold at which males switch morphs (Roff 1996) even though there was no such pattern apparent within families. Evidence for genetic variation in threshold traits is not scarce (Roff 1996). However, I believe this to be the first evidence that a status-dependent male dimorphism has a threshold that is genetically determined and has shifted *relative* to the mean population size, resulting in a change in morph frequency. This relative shift in switch zones is likely to be the consequence of directional selection: although pronotum width is on average smaller in the West Wide-

open population, male forceps are absolutely longer, a difference that is particularly exaggerated in macrolabics (Table 2). Artificial selection for relative horn length in the dung beetle *Onthophagus acuminatus* resulted in a shift in the switchpoint (Emlen 1996). However, although the switch changed to a lower body size, the mean body size of the population also decreased. This analysis does not reveal whether the position of the switchpoint changed relative to the mean body size of the selected population (Emlen 1996) and evidence for a change in morph frequency is not presented. The increase in relative horn height in the “up-selected” population results from the population switching at an absolutely smaller size and horn length remaining the same. Selection acting to change a switchpoint from one position to another will act most intensely on those individuals whose status (body size) lies between the old and new points of equilibrium. Emlen’s (1996) experiment selected for relative horn length equally across all individuals and perhaps is unrealistic in this respect.

In conclusion, it appears that in accordance with early studies (Diakonov 1925; Kuhl 1928), macrolabic males only arise when nutritional conditions for the nymph are favourable and a large body size is reached. Nevertheless, many males within the size class capable of producing forceps of the macrolabic morphology did not. The origin of this overlap between the morphs was unrelated to rearing density, but may reflect a body size at which both morphs have equal fitness. Finally, different morph ratios between populations that were reared under common-garden conditions indicate that there is a genotype \times environment interaction determining the frequencies of the male morphs. This in itself suggests that there is additive genetic variance within populations for the body size at which males switch phenotypes (Roff 1996) and differences in morph frequency observed in the field populations are likely to be the result of switchpoint evolution.

Acknowledgements I thank John Hunt, Janne Kotiaho, Armin Moczek and Leigh Simmons for their help with this manuscript and for useful discussions of the data. The constructive advice of Douglas Emlen, Jacek Radwan and Allen Moore improved the manuscript. Tom Heyes helped maintain the earwigs. The practical work was carried out while I was supported by a BBSRC studentship; I am currently supported by a fellowship from the University of Western Australia. This work complies with the current laws of the United Kingdom.

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Communicated by D.T. Gwynne