Status-dependence and morphological trade-offs in the expression of a sexually selected character in the mite, *Sancassania berlesei*

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Abstract

In the male dimorphic mite *Sancassania berlesei*, fighter males kill rivals with a pair of armoured legs whereas scrambler males are benign with unmodified legs. In an adaptive response mediated by colony pheromones, fighter expression increases at low colony density. Under the status-dependent evolutionarily stable strategy (ESS) model we expected heavier final instar nymphs to become fighters. This was supported in group reared nymphs. In individually reared nymphs fighter expression was experimentally suppressed using two concentrations of colony pheromone. Here, male morph expression again depended on tritonymphal body mass and contact is therefore unnecessary for individuals to judge their status. Fighter suppression was greater in the higher pheromone treatment, but morph determination remained status dependent. The weight and length of fighters was lower than scramblers of same-weight final instar nymphs, indicating a developmental trade-off, and a cost not recouped at the adult stage.

Introduction

Secondary sexual traits and behaviours can be expressed in a status-dependent manner. In its simplest form status dependence describes dichotomous states of trait expression in which high status individuals express one morphological trait or behaviour and low status individuals express an alternative behaviour (Forsyth & Alcock, 1990) or lack (Emlen, 1997a), or show reduced expression (Tomkins, 1999) of the morphological trait. Status dependence therefore involves discontinuous trait expression. Nevertheless continuous variation in condition will underlie status-dependent expression, such that among the individuals that express a trait, trait expression will vary with measures of condition, e.g. body size. The evolution of alternative reproductive phenotypes within a sex often represent a situation in which individuals make status-dependent, all-or-nothing, decisions over their investment in condition-dependent traits (Gross, 1996). In these species, the costs associated with secondary sexual trait expression are confined to a subset of the population.

The evolution of alternative reproductive tactics within a sex has been explained by three evolutionarily stable strategy (ESS) models (Maynard Smith, 1982; Gross, 1996). The conditional, or status-dependent ESS is the most commonly invoked of these models, explaining many of the dimorphisms seen in invertebrate systems and behavioural polymorphisms (Gross, 1996). Under the status-dependent ESS individuals adopt the tactic from which they will derive the greatest fitness return for their status (Gross, 1996). Status in this context is measured as competitive ability relative to others in the population, and is likely to correlate strongly with body size. This model therefore requires individual's to posses a developmental algorithm (set of decision rules) by which they can determine their status relative to others in the population. This algorithm is observed most readily in species in which there is a relationship between a dimorphic structure and body size, for example horn length in the Onthophagine dung beetles (Emlen, 1994; Moczek & Emlen, 1999), or forceps length in the

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European earwig (Tomkins, 1999). In these species a threshold body size exists across which individuals change their trait expression. In the context of the status-dependent ESS, this is the phenotypic consequence of the intersection of the fitness functions of the two morphs, where the fitness of one morph is exceeded by the fitness of the alternative (the ESS switch point).

The ESS switch point is a population parameter: theoretically it can change in time and space as the slopes and elevations of morph fitness change (Gross, 1996). Evidence for changes in the ESS switch point, manifest as divergent morph ratios, have been found between populations of the European earwig *Forficula auricularia* (Tomkins, 1999) and the dung beetle *Onthophagus taurus* (Moczek & Nijhout, 1999) and through selection in *O. acuminatus* (Emlen, 1996). Changes in morph ratio within populations over time have also been found in *O. acuminatus*, in relation to seasonal variation in diet (Emlen, 1997b). All these changes are relatively small. In this paper, we examine the developmental algorithm in a species in which fitness functions strongly depend on population parameters (Radwan, 1993a), resulting in radical shifts in male morph ratio between high and low density populations (Timms *et al.*, 1980, 1981; Radwan, 1993b, 1995).

Males of several species of acarid mites are dimorphic (Woodring, 1969a; Radwan, 1995, 2001); one of the morphs possess a weapon in the form of thickened and sharply terminated third pair of legs, which are used to kill other males (Woodring, 1969b; Radwan, 1993a; Radwan *et al.* 2000). In *Sancassania* (*syn. Caloglyphus*) *berlesei* such a strategy may enable fighters to gain sole access to females particularly in a small population, where it is possible to kill all rival males (Radwan, 1993a). In larger populations, however, monopolization is not possible and fighters (termed pleomorphs in Woodring, 1969a) achieve lower reproductive success (Radwan, 1993a) than scramblers (unarmed and nonaggressive phenotype termed bimorph in Woodring, 1969a). *Sancassania* males seem to match their phenotype to the environment in an adaptive fashion, as the expression of fighter phenotype is suppressed by pheromones from large colonies (Timms *et al.*, 1980). As a result, in small colonies all males assume the fighter phenotype, but in large, dense populations fighter morphs do not occur (Timms *et al.*, 1980; Radwan, 1993b, 1995). Here, we tested the hypothesis that the expression of the fighter morph is status dependent at intermediate densities at which the expression of both morphs occurs (Radwan, 1993b), i.e. within the range of densities that the alternative morph's fitness functions are likely to intersect. We tested this prediction using nymphal weights as a measure of body size and hence status. We hypothesized that large nymphs should be more likely to give rise to fighters because they have more resources to pay the physiological costs of developing thickened legs and because small individuals are unlikely to be successful fighters. We also weighed adult males after emergence to test for the cost of developing the thickened legs.

Methods

Mites were obtained from Department of Morphology, University of Vienna. The culture was originally derived from population collected from poultry litter. During experiments, the mites were maintained at 22 °C and >90% humidity buffered by KOH solution (153 g / 1 L H_2O), and fed a 3:1 mixture of powdered yeast and wheat germ.

The lifecycle of the mite follows through a series of mobile nymphal stages interceded by quiescent stages. The progression of development is therefore as follows; egg, larva, quiescent larva, protonymph, quiescent protonymph, tritonymph, quiescent tritonymph and adult. Morph determination takes place at the tritonymphal (preadult) stage (Woodring, 1969a). We weighed nymphs to the nearest 0.1 μg on *Sartorius supermicro* balance at the quiescent stage that lasts several hours; this facilitated handling and standardized their age.

Preliminary experiments determined the density of mites needed in a 2.5-cm diameter vial in order to yield substantial proportions of each morph. For example, the ratios in 2.5-cm diameter dishes were [fighters (pleomorphs) and scramblers (bimorphs), respectively: 10 larvae: 10 and 0; 20 larvae: 12 and 0; 30 larvae: 7 and 1; 40 larvae 12 and 4; 50 larvae: 11 and 8; females omitted].

Experiment 1: morph determination in a population

Following these preliminary findings, we therefore placed 60 quiescent larvae in each of three 2.5-cm diameter glass cells with bases made from a mixture of plaster of Paris and charcoal and provided with yeast and wheat germ *ad libitum*. We then weighed all mites at the quiescent tritonymphal stage and then placed them individually in 0.8-cm cells. After adults emerged we scored their morph.

Experiment 2: morph determination in isolation

In the second experiment, the larvae were housed individually in 0.8-cm diameter cells that were plugged with cotton-wool and were exposed to pheromones emanating from a large mite culture. Colony pheromones penetrate through the cotton wool plugs and suppress the expression of the fighter morph (Radwan, 2001). Using this method we could suppress expression of the fighter morph without the necessity of keeping mites in groups. This enabled us to make repeated measures of nymphs, and to determine whether conditional morph expression takes place when individuals are prevented from direct interaction with other mites. In a preliminary experiment with 3 cm^3 of mite / food mixture in 150 cm^3 desiccator we obtained eight fighters and

22 scramblers from individually isolated larvae, whereas all larvae reared in the desiccator without a large culture present emerged into fighters ($n = 21$ males).

The experiment started with the isolation of 320 quiescent larvae on two consecutive days. Each day, the larvae were divided equally between a high and low pheromone treatment. These treatments were achieved by rearing the mites in two desiccators each containing a large mite culture. The high pheromone treatment desiccator had a volume of 150 cm^3 and contained 2 cm^3 1:1 mites/food mixture (we decreased volume of mites compared with preliminary trial in order to obtain more fighters and thus avoid unbalanced data). The low pheromone treatment desiccator had a volume of 200 cm^3 and contained 1 cm^3 of approximately 1:1 food/mites mixture. As humidity within desiccators was buffered by KOH solution and the volume of mites was very small compared with the desiccator volume, the 25% difference in the latter should not affect our treatments in any other way than by changing the concentration of volatile substances emanating from mite cultures.

Cells were checked every 12 h for nymphs entering quiescent state, and later for emerging adults. We weighed two nymphal instars: quiescent protonymph and quiescent tritonymphs. Repeated weighing of subsets of both nymphal stages (in 4-h interval, blind) revealed that their weights were significantly repeatable (protonymphs: ANOVA, $F_{1,31} = 3.41$, $P < 0.01$, repeatability = 0.54; tritonymphs: $F_{1,21} = 66.54$, $P < 0.001$, repeatability = 0.97), although repeatability was much higher for tritonymphs. We also weighed adult mites 2 days after eclosion and then mounted them on slides in Berlese medium for body length measurement. We measured idiosoma length (body length without mouthparts), the measure that reflects overall body size well as evidenced by its tight correlation with body mass ($r > 0.7$, J. Radwan, unpublished data). Measurements were made under 40× magnification using micrometric screw.

Results

Experiment 1. Status dependence of mites in populations

In the first experiment (mites kept in groups of 60 individuals) we obtained 34 fighters and 20 scramblers (the ratios in cells 1–3 were 12:6, 9:5 and 13:9, respectively). Proportions of fighters did not differ significantly between the cells ($\chi^2_2 = 0.26$, n.s.).

Tritonymphs that emerged into fighters were heavier than those that emerged into scramblers (Fig. 1 and two-way ANOVA with block entered as a random factor, $F_{1,48} = 30.69$, $P < 0.05$). Blocks did not differ significantly in tritonymphal weight ($F_{2,48} = 4.82$, n.s.). The morph by block interaction was not significant ($F_{2,48} = 1.04$, n.s), confirming that the effects were consistent between cells.

Experiment 2. Condition dependence of mites in isolation

In the high pheromone treatment we obtained 41 (67%) fighters and 26 scramblers (16 and 15, respectively, on

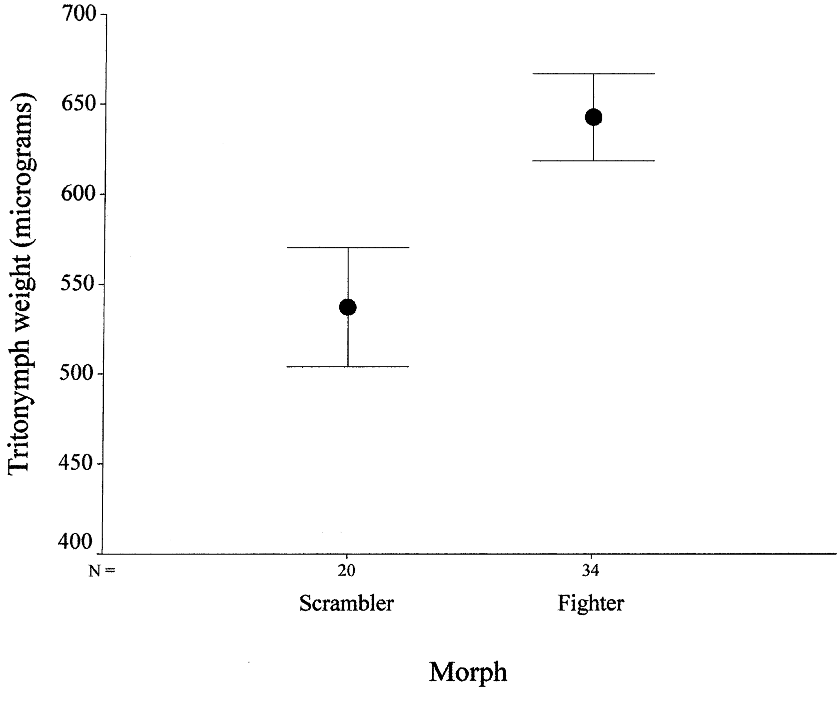

Fig. 1 Mean ± SE for the difference in tritonymph weight of male mites reared in groups of 60 per 4.4 cm^2 that eclosed into scrambler and fighter morphs.

day 1 and 25 and 11 on day 2; the difference between days was n.s., $\chi_1^2 = 2.23$, n.s.), and in the low pheromone treatment 56 (77%) fighters and 16 scramblers (31 and 6 on day 1 and 25 and 10 on day 2, the difference between days was n.s., $\chi_1^2 = 1.59$, n.s.). Suppression of fighter morph expression was significantly stronger in high pheromone treatment ($\chi_1^2 = 4.53$, $P < 0.05$). We also recorded seven intermorphs (i.e. males with one scrambler leg and one fighter leg).

The second experiment was analysed first to detect the effects of protonymph weight, and then of tritonymph weight. An ANOVA was performed with protonymph weight as the dependent variable and treatment and male morph as factors and block as a random factor, nonsignificant ($P > 0.15$) interactions were discarded sequentially from the model. There were no effects of treatment ($F_{1,135} = 0.018$, n.s.) on the weight of protonymphs, but there were highly significant effects of block ($F_{1,135} = 21.595$, $P < 0.001$). Protomymphs that produced fighters were on average heavier than those from which scramblers emerged (respective mean ± SD were 187.6 ± 24.9 and 181.4 ± 22.4 in block 1 and 170.1 ± 15.9 and 168.3 ± 15.8 in block 2), but the difference was not significant ($F_{1,135} = 1.061$, n.s.).

Slopes and intercepts of the regressions of tritonymph weight on protonymph weight were not statistically different between blocks within each treatment (low treatment, slope $F_{1,68} = 0.01$, n.s., intercept $F_{1,68} = 0.06$, $P = 0.081$; high treatment, slope $F_{1,63} = 0.14$, n.s., intercept $F_{1,63} = 0.104$, n.s.). For both treatments, the regression slope was significantly greater than 0 (high, $\beta = 2.36 \pm 0.46$, $F_{1,65} = 26.92$, $P < 0.001$, $r^2 = 0.29$; low, $\beta = 3.79 \pm 0.45$ $F_{1,70} = 71.28$, $P < 0.001$, $r^2 = 0.505$). Analysis of variance with tritonymph weight as the dependent variable, morph and treatment as factors and block as a random factor showed that the weight of tritonymphs that eclosed into fighters was significantly greater than those that developed into scramblers (Table 1, Fig. 2). The ANOVA results therefore suggest that male morph determination is associated with male weight in the last instar of growth, such that males achieving greater weight by the end of this period are more likely to develop into fighters.

The significant effect of treatment on male morph ratio is thought to reflect shifting ESS switch points, such that in the high pheromone treatment only males in the

Table 1 ANOVA with tritonymph mass as the dependent variable, treatment and morph as main effects and block as a random factor.

Source	d.f.	Mean square	*F*	*P*-value
Intercept	1	64244123.18*	493.75	0.029
Treatment	1	311.56†	0.102	0.804
Morph	1	225593.50‡	36890.93	0.003
Block	1	130114.08§	96.36	0.564
Treatment × morph	1	3614.85¶	2.099	0.385
Treatment × block	1	3065.87¶	1.781	0.409
Morph × block	1	6.11¶	0.004	0.962
Treatment × morph × block	1	1721.77**	0.209	0.648
Error	133	5245.469		

Error terms used: *MS block, †MS treatment × block, ‡MS morph × block, §(MS treatment × block) + (MS morph × block) – (MS treatment × morph × block), ¶MS treatment × morph × block, **MS error.

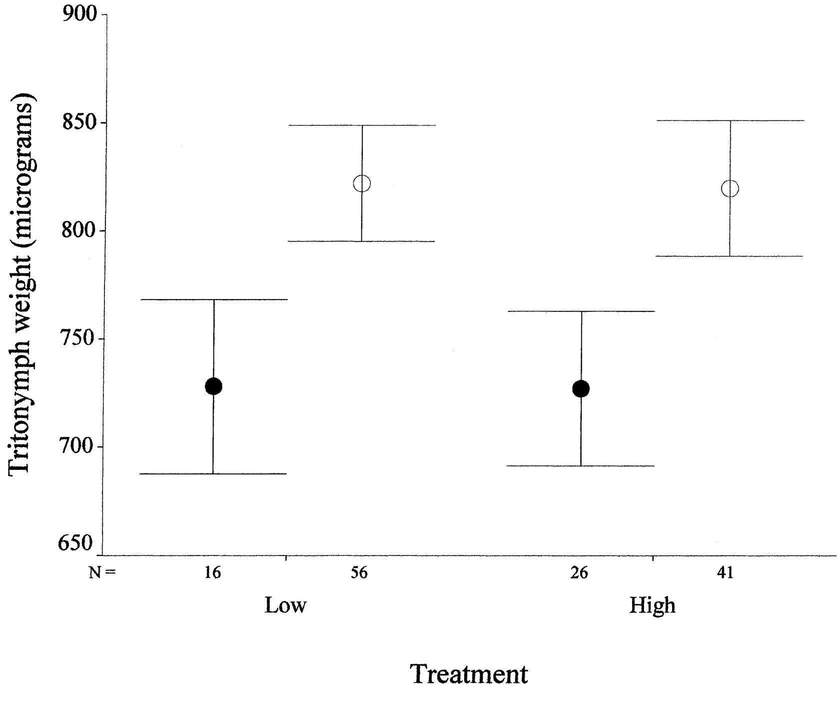

Fig. 2 Mean ± SE for the difference in tritonymph weight of male mites reared in isolation but in the presence of low and high colony pheromone concentrations, that eclosed into scrambler (●) and fighter morphs (○).

highest condition become fighters. Hence, the mean condition of fighters in the high pheromone treatment was expected to be higher than fighters in the low pheromone treatment, and the same was expected in scramblers as larger tritonymphs became scramblers in this treatment. These effects were estimated by comparing the mean weight of the morphs in each treatment (after differences in blocks had been removed by standardizing the data). The mean standardized tritonymph weight for scramblers on the low pheromone treatment (−0.606 ± 0.178) was actually higher, but not significantly than scramblers in the high pheromone treatment (−0.722 ± 0.157, $t_{40} = 0.455$, n.s.). The mean standardized tritonymph weight for fighters on the low pheromone treatment (0.238 ± 0.123) was lower as expected, but also not significantly than fighters in the high pheromone treatment (0.368 ± 0.153, $t_{95} = 0.667$, one-tailed $P = 0.253$).

Development time from quiescent larva to adult eclosion differed between blocks for fighters in the low pheromone treatment (Mann–Whitney $U = 229.5$, $P < 0.01$), therefore, we analysed differences between morphs separately for each block and treatment. In none of the treatments or blocks were there significant differences between fighters and scramblers in development time (Table 2, Mann–Whitney tests). Likewise, duration of tritonymphal stage (time from quiescent protonymph stage to adult eclosion) did not differ between fighters and scramblers (Table 2, Mann–Whitney test, n.s. in both blocks and within both treatments).

Somatic costs of producing the fighter phenotype

Male mites that adopted the fighter morph were heavier for their body length than males that adopted the scrambler phenotype (Table 3, Fig. 3). At morphological level, the difference in body plan of scramblers and fighters is primarily in the thickened legs, although other differences at anatomical level may be present. The fighter's somatic investment in their legs and other associated features of this phenotype such as muscles, can be estimated from the marginal means from the ANCOVA (fighter = 762.08 ± 1.0 μg; scrambler = 717.79 ± 1.0 μg) as 6% of their total body weight.

Table 2 Mean time (in days) for the development from a quiescent larva to adult for each morph, and from a quiescent tritonymph to adult. Ranges are given in brackets.

	Block 1		Block 2	
	Low pheromone	High pheromone	Low pheromone	High pheromone
Larva-adult				
Fighters	5.9 (5.5–6.5)	6.0 (5.5–6.5)	6.1 (5.5–6.5)	6.0 (5.5–6.5)
Scramblers	5.8 (5.5–6.0)	6.1 (6.0–6.5)	6.0 (5.5–6.5)	5.9 (5.5–6.6)
Protonymph – adult				
Fighters	3.3 (3.0–4.0)	3.5 (3.0–4.0)	3.4 (3.0–4.0)	3.4 (3.0–3.5)
Scramblers	3.3 (3.0–3.5)	3.4 (3.0–4.0)	3.4 (3.0–3.5)	3.3 (3.0–3.5)

Table 3 ANCOVA on log adult weight as a dependent variable with log adult size as a covariate, treatment and morph as main effects and block as a random factor.

Source	d.f.	Mean Square	*F*	*P*-value
Intercept	1	4.349E−03	676.185	0.000
Treatment	1	8.577E−06	1.333	0.250
Morph	1	5.445E−05	8.462	0.004
Block	1	1.122E−06	0.174	0.677
Log adult size	1	1.122E−03	174.420	0.000
Error	127	6.435E−06		

To investigate the allometric cost to male mites of producing the fighter phenotype, an ANCOVA of log adult weight was performed, with log tritonymph weight as the covariate, morph and treatment as factors and block as a random factor. The nonsignificant interactions were removed. There was a significant treatment by block interaction, the biological relevance of which is unclear. There were no differences in slope between the morphs in the relation between adult weight on tritonymph weight, however, there was a significant difference in the elevations of these slopes (Table 4). The different elevations mean that males that became scramblers were able to convert significantly more of their weight as a tritonymphs into weight as an adult, than those that became fighters (Fig. 4). The relationship between log tritonymph weight and log adult weight (both morphs) $\beta = 0.97 \pm 0.043$ (reduced major axis slope = 1.08) was not significantly different from one ($Z = 0.697$), demonstrating that the costs of adult development are borne equally by large and small males.

An ANCOVA was also performed to examine the effect on male body length of producing the fighter phenotype. The model was similar to that shown in Table 3 except that log adult size was used as the dependent variable, the results mirrored those in Table 4 in magnitude and direction: the effect of male morph ($F_{1,126} = 29{,}86$, $P < 0.001$) was significant showing that from a tritonymph of the same weight, fighter males eclose smaller than scrambler males.

Discussion

These experiments show that male morph determination in the Acarid mite *S. berlesei* is based on an algorithm that incorporates colony chemical cues and status. These experiments also show that the morphological structures of the fighter morph have costs in terms of the allocation of resources for competing morphological structures, in particular reduced body length and weight gain.

In a status-dependent male dimorphism, males are thought to adopt the tactic from which they will derive

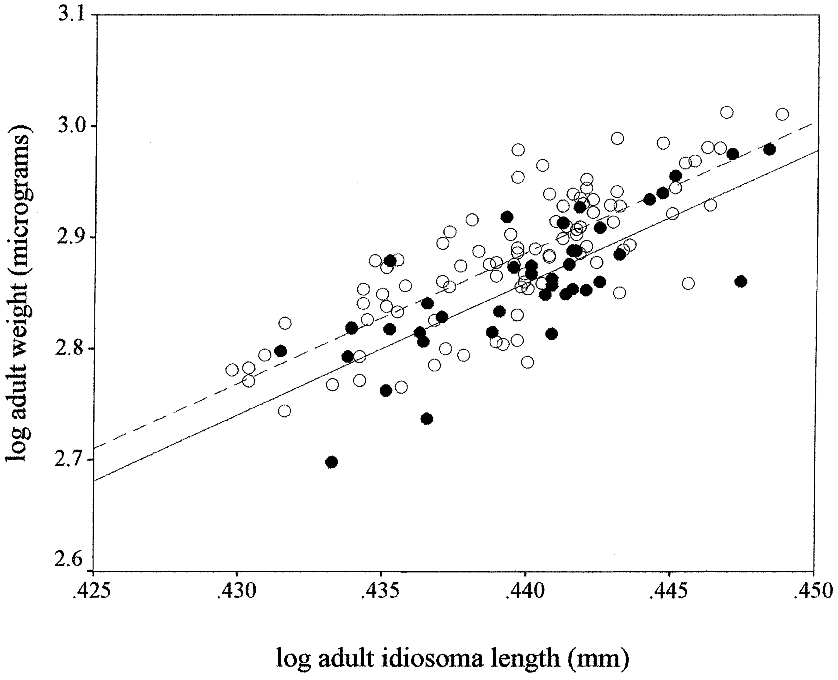

Fig. 3 The relationship between log adult size and log adult weight: for mites of the same body length, fighter males (dashed line, ○) are significantly (6%) heavier than scrambler males (solid line, ●).

Table 4 ANCOVA with log adult weight as the dependent variable, log tritonymph weight as the covariate, treatment and morph as main effects and block as a random factor.

Source	d.f.	Mean Square	*F*	*P*-value
Intercept	1	1.169E–03	2.098	0.150
Treatment	1	3.786E–04	0.048	0.862
Morph	1	2.581E–02	46.309	0.000
Block	1	7.641E–04	0.106	0.799
Log tritonymph weight	1	0.344	617.544	0.000
Treatment × block	1	7.986E–03	14.327	0.000
Error	129	5.574E–04		

the highest fitness benefit for their status (Gross, 1996). Individuals therefore have to have a decision rule, or algorithm, whereby they assess their status relative to other individuals in the population. In *S. berlesei* the morph determination is known to be influenced by chemical cues given off by the colony (Timms *et al.*, 1980), such that fighter morphs can be completely suppressed under conditions of high density or expressed by all males under conditions of low density (Timms *et al.*, 1981; Radwan, 1995). The adaptive significance of fighter expression in small colonies has been demonstrated in terms of a fitness advantage to fighters, in which males can kill all their rivals and dominate a number of females (Radwan, 1993a). Here, we investigated the algorithm involved in morph determination at densities that yield both morphs, both under conditions that allowed mites to interact directly with one another, and under conditions in which they were isolated. In both experiments the weight of the quiescent tritonymphs that became fighters was greater in comparison with those that became scramblers. These experiments show that direct social interaction and assessment is not necessary for individuals to judge their status for future morph determination.

The treatment with higher levels of colony pheromone did have fewer fighter males, this result is consistent with previous findings showing chemical suppression of this morph (Timms *et al.*, 1981; Radwan, 1993b). In the present study, we were able to test whether chemical suppression is a mechanism independent of that linking male morph and condition. It is conceivable that airborne chemicals emanating from colonies have a direct detrimental effect on males, decreasing their condition in much the same way as is the case for waste products contained in food (Radwan, 1991). Waste products can decrease male adult size in a degree comparable with that caused by restrictive diet, that in turn is known to suppress fighter morph expression. Under this scenario, chemicals emanating from colonies are predicted to cause a decrease in male condition whenever they are effective in suppressing the fighter morph. This was, however, not the case: increased fighter suppression in the high pheromone treatment could not be accounted for by the reduced tritonymph weight of males (Table 1). It is apparent therefore that the status-dependent morph determination is a mechanism that is independent of the morph suppression mechanism that arises from exposure to colony chemicals, which seems to act as a

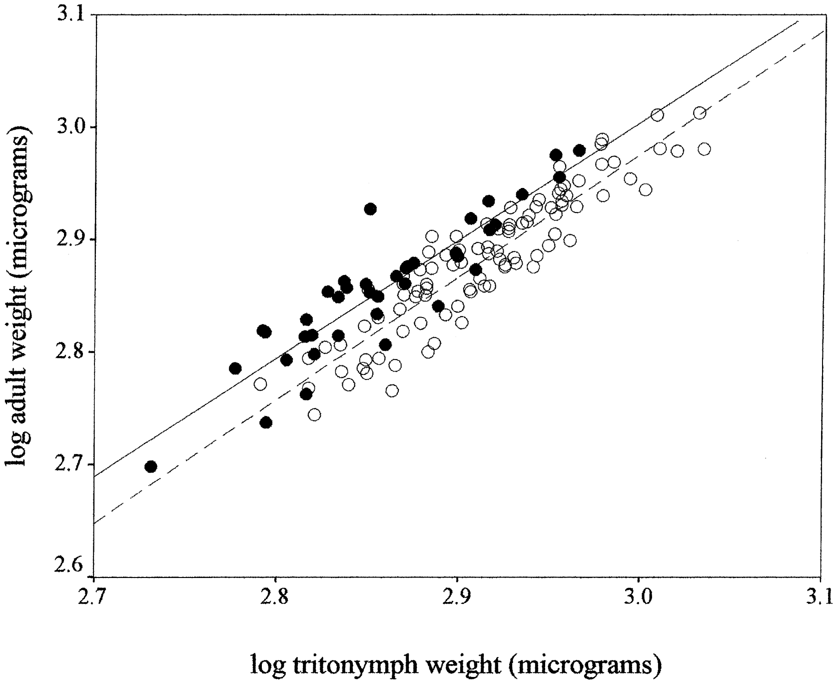

Fig. 4 The relationship between log tritonymph weight and log adult weight: the allometry of scrambler males (solid line, ●) is elevated above that for fighters (dashed line, ○).

cue to colony size rather than as a direct agent determining male condition.

Although weight was not influenced by treatment, we expected the changes in frequency of the fighter morph to arise because of a shift in the ESS switch point within the status-dependent algorithm. Evidence for this would have been higher tritonymph weight of both morphs in the high pheromone treatment compared with the low. The direction of this effect was in the expected direction only for fighters but was weak and nonsignificant. Around the population mean, small changes in switch point, can lead to large differences in morph frequency, hence these shifts will have only small effects on the means for each morph. Pheromonal manipulations leading to more extreme differences in morph proportions between treatments may be used in future to test this model in a more sensitive way.

Morph determination appeared to be unrelated to the weight of the protonymph, but was related to the weight of tritonymphs. The suggestion is therefore, that males that became fighters were absolutely heavier as quiescent tritonymphs, and achieved this in part through relatively greater weight gain as tritonymphs. This was not achieved through extended development time, as the duration of the tritonymphal stage (from quiescent protonymph to adult) did not differ between the morphs. However, tritonymph weights were significantly dependent on protonymph weights ($r^2 > 0.4$ in both treatments), and the lack of a significant effect of protonymph weight on male morph might result simply from higher measurement error (repeatability was only 0.54, compared with 0.97 for tritonymphs) and, consequently, lower statistical power.

The mass of the quiescent tritonymph represents condition in the sense that at this stage of the life-cycle the mite has a finite pool of resources to devote to competing life history and morphological traits (e.g. *sensu* Rowe & Houle, 1996). Our data show that the investment made in the thickened legs of the fighter males represents 6% of their body mass. This investment is associated with significant costs in terms of body length, a cost that is unlikely to be trivial as there is almost certainly an advantage to large size among fighter males. Developmental competition between morphological structures has been shown in a number of species, and has been proposed as a model for the development of same-sized bilateral traits (Klingenberg & Nijhout, 1998). In the context of male dimorphisms, Emlen and Nijhout (Nijhout & Emlen, 1998; Emlen, 2000, 2001) have elegantly demonstrated that when dimorphic structures such as the horns of male dung beetles develop, the other traits that arise from the same imaginal disc are reduced in size. For example, head horns reduce the size of other traits located on the head, e.g. eyes and mandibles, whereas thoracic horns reduce the size of elytra and wings (Nijhout & Emlen, 1998; Emlen, 2000, 2001). In *S. berlesei* however, the reduction in body length does not simply represent a redistribution of somatic resources as is the case in dung beetle horns. The significantly lower body weight of adult fighters, compared with scramblers that were tritonymphs of the same length, indicates that there are metabolic or other developmental costs of the production of the thickened legs. Similar low-level trade-offs have been documented in the investment between flight muscles and female fecundity in wing-dimorphic crickets (Roff, 1990; Roff & Fairbairn, 1991).

Moreover, males were weighed long enough after eclosion for them to have reached their stable adult weight, and hence the reduction in weight gain is an absolute cost that is not recouped. The honest signalling hypothesis suggests that larger males should pay relatively smaller costs for their secondary sexual traits than smaller males (e.g. Kotiaho, 2000). We found that the weight change between tritonymphs and adults was isometric, i.e. weight change was proportional to body length and we therefore have no evidence that larger males paid a smaller cost of producing the fighter phenotype. This is not entirely unexpected as there is unlikely to be a signalling or assessment function to the thickened legs, and in that sense there is no honest signalling context to the trait.

We have shown that the morph determination algorithm follows the status-dependent model in *S. berlesei*. This status dependence exists alongside the extraordinary variation in morph ratio that can occur in *S. berlesei* because of changes in chemical cues associated with population density. Large and small fighter males pay similar costs in terms of reduced length and weight gain in the transition from the tritonymph to adult life stages but fighters pay a higher cost than scramblers. The evolutionary significance of the size and weight 'costs' that we have detected and whether there are other associated negative effects on male life-history traits, that are perhaps more severe for smaller individuals, requires investigation.

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References

Emlen, D.J. 1994. Environmental control of horn length dimorphism in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Proc. R. Soc. Lond. B* **256**: 131–136.

Emlen, D.J. 1996. Artificial selection on horn body-length size allometry in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabidae). *Evolution* **50**: 1219–1230.

Emlen, D.J. 1997a. Alternative reproductive tactics and male dimorphism in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Behav. Ecol. Sociobiol.* **41**: 335–341.

Emlen, D.J. 1997b. Diet alters male horn allometry in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabeidae). *Proc. R. Soc. Lond. B* **264**: 567–574.

Emlen, D.J. 2000. Integrating development with evolution: a case study with beetle horns. *Bioscience* **50**: 403–418.

Emlen, D.J. 2001. Costs and the diversification of exaggerated animal structures. *Science* **23**: 291–1534.

Forsyth, A. & Alcock, J. 1990. Female mimicry and resource defence polygyny by males of a tropical rove beetle, *Leistotrophus versicolor* (Coleoptera: Staphylinidae). *Behav. Ecol. Socio. Biol.* **26**: 325–330.

Gross, M.R. 1996. Alternative reproductive tactics: diversity within sexes. *T.R.E.E.* **11**: 92–98.

Klingenberg, C.P. & Nijhout, H.F. 1998. Competition among growing organs and developmental control of morphological asymmetry. *Proc. R. Soc. Lond. B* **265**: 1135–1139.

Kotiaho, J.S. 2000. Testing the assumptions of conditional handicap theory: costs and condition dependence of a sexually selected trait. *Behav. Ecol. Sociobiol.* **48**: 188–194.

Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.

Moczek, A.P. & Emlen, D.J. 1999. Proximate determination of male horn dimorphism in the beetle Onthophagus taurus (Coleoptera: Scarabaeidae). *J. Evol. Biol.* **12**: 27–37.

Moczek, A.P. & Nijhout, H.F. 1999. The evolution of polyphenic development and its consequences: Rapid allometric divergence between exotic populations of the scarab beetle Onthophagus taurus. *Am. Zool.* **39**: 66–78.

Nijhout, H.F. & Emlen, D.J. 1998. Competition among body parts in the development and evolution of insect morphology. *P.N.A.S. USA* **95**: 3685–3689.

Radwan, J. 1991. The influence of a crowded environment on the size of males of *Caloglyphus berlesei* (Acari: Acaridae). *Internat. J. Acarol.* **18**: 67–68.

Radwan, J. 1993a. The adaptive significance of male polymorphism in the acarid mite *Caloglyphus berlesei. Behav. Ecol. Sociobiol.* **33**: 201–208.

Radwan, J. 1993b. Kin recognition in the acarid mite, *Caloglyphus berlesei* – negative evidence. *Anim. Behav.* **45**: 200–202.

Radwan, J. 1995. Male morph determination in two species of acarid mites. *Heredity* **74**: 669–673.

Radwan, J. 2001. Male morph determination in *Rhizoglyphus echinopus* (Acaridae). *Exp. App. Acarol.* **25**: 143–149.

Radwan, J., Czyz, M., Konior, M. & Kolodziejczyk, M. 2000. Aggressiveness in the two male morphs of the bulb mite, *Rhizoglyphus robini*. *Ethology* **106**: 53–62.

Roff, D.A. 1990. The evolution of flightlessness in insects. *Ecol. Mon.* **60**: 389–421.

Roff, D.A. & Fairbairn, D.J. 1991. Wing dimorphisms and the evolution of migratory polymorphisms among the insecta. *Am. Zool.* **31**: 243–251.

Rowe, L. & Houle, D. 1996. The lek paradox and the capture of genetic variance by condition dependent traits. *Proc. R. Soc. Lond. B* **263**: 1415–1421.

Timms, S., Ferro, D.N. & Waller, J.B. 1980. Suppression of production of pleomorphic males in *Sancassania berlesei* (Michael) (Acari: Acaridae). *Int. J. Acarol.* **6**: 91–96.

Timms, S., Ferro, D.N. & Emberson, R.M. 1981. Andropolymorphism and its heritability in *Sancassnia berlesei* (Michael) (Acari: Acaridae). *Acarologia* **22**: 391–398.

Tomkins, J.L. 1999. Environmental and genetic determinants of the male forceps length dimorphism in the European earwig *Forficula auricularia*. L. *Behav. Ecol. Sociobiol.* **47**: 1–8.

Woodring, J.P. 1969a. Environmental regulation of andropolymorphism in Tyroglyphids (Acari). In: *Proceedings of the Second International Congress of Acarology* (G.O. Evans, ed.), pp. 433–440. Academiai Kiado, Budapest.

Woodring, J.P. 1969b. Observations on the biology of six species of acarid mites. *Ann. Ent. Soc. Am.* **62**: 102–108.

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