

Make love and war - Quantifying discrete male polymorphic reproductive ratios

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Abstract

Fighters primarily develop at low population densities; Though the proportion of males becoming fighters at any given density may change over time. This change is likely to be due to condition-dependence. Data is presented to illuminate these matters and a model is developed linking fighter development to the costs of being a fighter (in terms of survival) and the benefits of being a fighter (in terms of fecundity).

1 Introduction

Phenotypic plasticity is the property of a genotype to produce different phenotypes when exposed to different environments. Plasticity is therefore a description of the reaction norm of a genotype, which is the function defined in environment / phenotype space relating environmental input to phenotypic output. A wide range of forms of phenotypic variation exists. There may be a single phenotype (this is when development is said to be 'channeled') or there can be continuous or discontinuous variation (Lloyd, 1984). In a channeled phenotype, development is buffered against a variation of the genotype and against variation of the environment (Waddington, 1952). Developmental conversion occurs when environmental signals influence the development of an animal into different types (Lloyd, 1984). Here the development is directed in one or several discrete ways, which can bring changes in many traits of an organism. *Sancassania berlesei*, an acarid mite, provides an example of such a developmental conversion, which is seen to be triggered by an environmental signal (Woodring, 1969; Timms et al., 1980, 1981a,b; Radwan, 1992, 1993), where it has been shown that a different phenotype develops at low population densities. Developmental conversions can also be found in the larval stages of *Nemoria arizonaria* which develop mimesis of pussy willows or twigs (Greene, 1989). Here the environmental trigger is the tannin concentration, which regulates if the caterpillars develop into mimics of pussy willows or twigs.

Between the extremes of channelling (single phenotype) and developmental conversion (phenotype is discrete and depends on the environment), organisms can show a variety of forms of phenotypic plasticity. Here the different traits of an organism can differ in the extent of a variation. This phenotypic modulation

does not have to be adaptive (Smith-Gill, 1983). Variations in growth can also occur because of nutritional differences, but the response to different food levels may be itself adaptive.

A discrete phenotype can exhibit not only different morphologies but also differences in behaviour and life-history strategies. Polymorphism in one sex has been found in many taxa, including arthropods, fish, lizards and birds. It can show itself in differences in morphology, behaviour, physiology as well as and/or life-history (Gadgil, 1972; Gross, 1996). Examples of the taxa displaying polymorphism in one sex are the amphipods *Jassa marmorata* and *Jassa falcata* (Borowsky, 1985; Conlan, 1989), the beetle *Onthophagus acuminatus* (Emlen, 1999), the bird *Philomachus pugnax* (Lank et al., 1995) and some species of mites (notably from the family Acaridae)(Evans et al., 1961) (See figure 1). Andropolymporphism (a species having two or more male phenotypes)

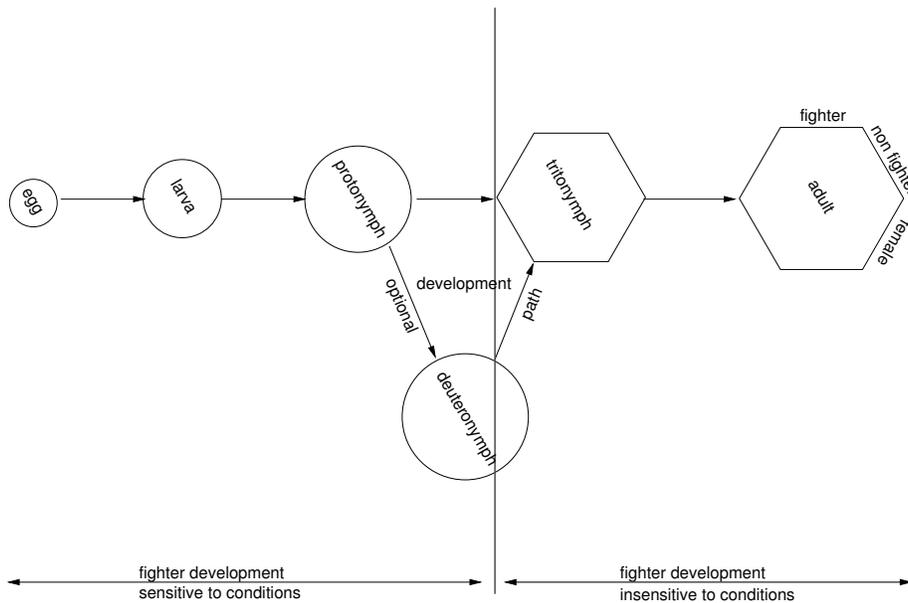


Figure 1: Life-cycle of *S. berlesei*. Development goes from egg to larva to a protonymph, a tritonymph to the adult. Under adverse conditions, optionally, another life stage develops, the deuteronymph or hypopus. This stage is non feeding and is the (mostly) long distance dispersal stage of the species. The grey area marks the region where environmental conditions have an effect on the development of fighters/non-fighters. In the white area environmental conditions have no effect on morph determination.

in mites can generally be found in the Astigmata (Zakhvatkin, 1959; Hughes, 1976; Timms et al., 1981a,b).

Besides the detailed description of andropolymporphism, the detailed study of the evolution of alternate male strategies has not received much attention

(Gross, 1996; Kurdziel and Knowles, 2002) and has been mostly empirical (Schroeder et al., 1996; Radwan and Klimas, 2001; Cremer and Heinze, 2002; Kurdziel and Knowles, 2002).

Using *S. berlesei* (an andropolymorphic mite with two distinct phenotypes, a so-called "fighter" and a "non-fighter") as a model organism this study will be a quantitative investigation of the costs and benefits of developing into each morph. *S. berlesei*'s morph determination shows an environmental influence as found by Timms et al. (1980), Radwan (1995) and Ballard (1997). At low population density fighters develop, and they cannot be found at higher population densities (Radwan, 1995). Ballard (1997) suggested that with increasing density the fighter finds less time for mate interactions but is overwhelmed by fight interactions indicating a density-dependence.

The influence of density is likely important, as animals have to interact (mate, fight) and a larger area results in fewer interactions, as the animals meet fewer times. A fighter has to fight and kill (therefore meet) another male to "cash-in" on his advantage to be able to kill other males. Lapsley (1999) found fighters in a large coupled arena, although the numbers of mites exceeded the numbers where fighters would usually be found. The animals have to be in close proximity (or densely packed) to react in the way described here. So we interpreted this as a density-dependent effect, rather than a population size effect. As experiments reported in this study use the same size vials, population density is directly proportional to population size.

The development of fighters at low densities is environmentally conditioned. Timms et al. (1980) investigated the cues and found that a chemical found in large colonies acted as a suppressor of fighter development. Timms et al. (1980) also researched if food texture or the ether extract taken from a mite population had an influence on fighter development. In both cases no influence on fighter development was found.

If fighters only develop at low densities, one must ask why this may have evolved. For it to be adaptive, the costs must be lower than the benefits at low densities and vice versa at high densities. Costs and benefits are both levied in fitness terms, so fighters should expect to achieve a higher reproductive success than non-fighters at low densities, with the reverse at high densities. A fighter in a low density situation only has to kill its (few) competitors and can then subsequently monopolise the females. This is facilitated by fighters developing faster than non-fighters (Radwan, 1995). Conversely at high densities, fighters should have a lower reproductive success, perhaps because they spend more time fighting than mating and competitors are too common to enable them to monopolise females. One therefore expects a relationship between population density and fighter fitness, as suggested by (Radwan, 1993).

Timms et al. (1980) conducted experiments in 1979 and found significant differences between fighters and non-fighters. The investigation established that populations of fighter males of *S. berlesei* live longer than non-fighter males, and fighter males produce more young earlier than non-fighter males, although there is no difference in egg numbers laid by females of each type.

Woodring (1969) and Nesbitt (1993) discovered small subtle polymorphisms.

Fighters and non-fighters may vary (apparently discontinuously) in size and shape, though Nesbitt (1993) found no difference in their ability to feed, mate and move in many morphs of various *Sancassania* species.

Normally fighters only develop if they are reared from pre-tritonymph individuals. The normal procedure to obtain fighters is to pick pre-tritonymph larvae from a stock culture and allow them to develop in isolation or at low densities.

In previous studies it was assumed that the time or stage to the tritonymph state had no influence on the percentage of fighters developing at certain densities, and that only two discrete states existed. Individuals may "switch" onto the fighter developmental pathway if they experience the necessary environment early in development, but after the tritonymph stage, regardless of the environment, fighter development is not possible. A relationship between stage or time and morph determination was assumed to be non-existent.

1.1 Investigating the occurrence, costs and benefits of the fighter morph

In this chapter an investigation of the incidence, costs and benefits of developing into a fighter will be made, lower densities were investigated in more detail and it is demonstrated with a model of reproductive success, why it might be beneficial for a mite of the species *S. berlesei* to become a fighter not only when it is possible to totally monopolise its opposition (as in densities one or two pairs), but also when the densities are a bit higher or if the mite faces fighting opposition. Uniquely to this study, we will relate the information obtained by empirical methods to a quantitative model incorporating the costs and benefits of being one or the other morph.

Therefore the following questions will be asked:

1. Is there a threshold density above which fighters do not develop any more, or is the relationship continuous?
2. Is density the only cue for fighter morph determination?
3. Does the switch in the developmental path of the mite occur at a discrete point in time?
4. Can we measure the benefits of being a fighter in terms of fecundity;
5. and the costs in terms of survival?

1.1.1 Density-dependent morph determination

At low population density, fighters develop and cannot be found in higher population densities (Radwan, 1995). This relationship could be continuous or discontinuous. If discontinuous, there could be a threshold density below which all males become fighters. If continuous the probability of becoming a fighter could vary smoothly as density changes, with no 'stepwise' threshold.

1.1.2 Condition-dependent morph determination

As well as the density being a determinant of the probability of becoming a fighter, Radwan (1995) found an influence of environment, notably food availability. Poorly fed males were less likely to become fighters.

1.1.3 Fighter fecundity in all environmental conditions

In order to assess the costs and benefits of developing into a fighter, information on the fecundity of the different morphs under different conditions is required. First, the fecundity of the two morphs with females which are either virgin or non-virgin (but sperm depleted) is assessed. *S. berlessei* disperses as hypopi (a non-feeding additional life-stage, that develops in adverse conditions, and is *S. berlessei*'s dispersal stage) on beetles, so fighters developed at low densities in a newly colonised patch are likely to encounter virgin females. Fighters, when they develop at high densities, would be more likely to encounter non-virgin females. On the other hand females at a new patch at low densities will be more likely to encounter fighters and at high density more likely non-fighters. At high densities per capita food availability is reduced. Females mating with fighters and non-fighters might encounter animals with different pre-tritonymph life-history. As the individual life-history up to deuteronymph stage may occur on a different patch from where the animals actually mate, it is possible, that animals with a low food life-history (up to dispersal stage) arrive at a high food site, if emigrating from previous even worse conditions. Although hypopi arise in adverse conditions (Ballard, 1997), this does not mean that they experienced bad conditions before they became hypopi. This means hypopi could have grown up as eggs and larvae with sufficient conditions, and somewhere in their protonymph stage bad conditions arose, which would have turned them into hypopi. Therefore a variety of different feeding conditions can arise at new patches.

1.1.4 Survival probabilities of fighters and non-fighters

If a fighter is in an environment solely with non-fighters, he can kill the non-fighters and will himself encounter no hostilities. But if a fighter is together with other fighters he will obviously encounter fighters himself. As fighters actively seek out other males and initiate fights (personal observation) one would expect that the probability of survival of a fighter with other fighters present sinks when compared to a non-fighter, as non-fighters try to evade fights if engaged in them.

2 Methods

Data analysis was conducted in S-Plus 2000, besides the GLMM (General[ised] Linear Mixed Model) analyses, which was calculated in Genstat using the iterative reweighted restricted maximum likelihood method (IRREML). GLMMs

are generalised linear models with normally distributed random effects in the linear predictor. Non-linear regression models were tested and compared with residual least squares. General (or generalised) linear models (GLM) were used where appropriate and further details about the form of GLM employed are given when the test results are given. The residuals were checked for non-violation of normality of the residuals vs the fitted values and heteroscedacity.

2.0.5 Percentage of fighters developing from isolated individuals at egg stage

To establish any time or stage dependence in the morph determination, 100 eggs and 100 larvae were picked from a 1996 stock culture and placed in 20mm wide and 50mm high plastic vials. The vials were lined with Plaster of Paris ($\text{CaSO}_4 \cdot \frac{1}{2} \text{H}_2\text{O}$) which was dampened to maintain humidity. Food was supplied in the form of a small ball of yeast.

The tubes were placed in a 24 degrees Celsius incubator and left for seven days. After this time the number of males (fighters and non-fighters) and females were counted.

2.0.6 Density-dependent morph determination

An experiment was conducted in 1998 with the standard conditions and equipment described earlier. Two hundred and ten vials were set up with larvae isolated at pre-tritonymph stage and fed one ball of yeast per day. The density of animals in these tubes was 1, 2, 5, 10. After a week the number of developed fighters were noted.

2.0.7 Condition-dependent morph determination

An experiment was conducted to consider the number of fighters developing at different levels of food, differing times and amount of food supplied at varying densities. Food was supplied in two different regimes, low and high food, whereby low food consisted of a grain of yeast per day and high food of five balls of yeast per day.

The food was given either from the beginning of the experiment, or after a five day delay. Pre-tritonymph larvae were selected from tubes, which had been taken from the stock cultures. These larvae were then separated into the experimental tubes. The number of fighters, non-fighters and females was recorded. The total number of tubes was 40.

2.0.8 Fighter fecundity in a good quality, resource stable environment

To estimate the fecundities and survival probabilities of fighters and non-fighters an experiment was conducted in which fighters were brought together at differing densities with non-fighters and females. The number of animals and their phenotype was recorded. During the day of the experiment at hourly intervals

the number of matings and fights between fighters and non-fighters was noted. The animals were put together at the densities 5, 10, 20 and 50. Fighters, non-fighters and females were added according to table 1. Detailed information was taken on densities 5 and 10 (see section 1.1.1), where the advantages for fighters should slowly tail. To get a strong signal on high extreme combinations detailed information was collected at densities 20 and 50, where the advantage of being a fighter should not be non-existent. Fighters and their reactions in densities <5 were frequently observed in other experiments, so were not tested here due to time restrictions.

$\delta =$	5	10	20	50
	$1_f, 4_{nf}, 5_{fe} \cdot 2$	$1_f, 9_{nf}, 10_{fe}$	-	$1_f, 49_{nf}, 50_{fe}$
	$2_f, 3_{nf}, 5_{fe} \cdot 2$	$2_f, 8_{nf}, 10_{fe}$	-	-
	$3_f, 2_{nf}, 5_{fe} \cdot 2$	-	-	-
	$4_f, 1_{nf}, 5_{fe} \cdot 2$	-	-	-
	$5_f, 0_{nf}, 5_{fe} \cdot 2$	$5_f, 5_{nf}, 10_{fe}$	-	-
	-	$7_f, 3_{nf}, 10_{fe}$	-	-
	-	$10_f, 0_{nf}, 10_{fe}$	-	-
	-	-	$20_f, 0_{nf}, 20_{fe}$	-
	-	-	-	$50_f, 0_{nf}, 50_{fe}$

Table 1: Experimental setup: δ =density; f = fighter; nf = non-fighter; fe = female; $x_T = x$ animal(s) of type T. $\cdot 2 =$ two repetitions. Experiment unbalanced due to time/laboratory restrictions. To gain equal sized fighters, non-fighters and females and to account for deaths over 400 tubes had to be reared simultaneously, which was the maximum possible to handle. Therefore point estimates were taken.

2.0.9 Fighter fecundity in all environmental conditions

Animals were taken as larvae from a culture of about 1000 animals which was itself taken from the stock cultures, to match experimental conditions of a previous experiment which looked at general life-history parameters, (described in the next chapter). Non-virgin females were produced by rearing them as larvae and by then bringing them together for one day with about ten males, fighters and non-fighters in equal proportions. After one day the females were isolated, until no more eggs had been laid. Rearing larvae, in isolation produced virgin females. Rearing larvae in isolation produced non-fighters and fighters. Sixty four animals were reared using a crossed experiment using the factors described in table 5. Animals were raised on the designated pattern and where kept on the designed feeding regime (high and low food). After the animals had been reared the males and females were paired, resulting in a total amount of tubes of 32. The eggs laid by the females were counted after five days, this being the peak of female productivity under optimal conditions .

2.0.10 Survival probabilities of fighters and non-fighters

To establish if the survival probabilities of fighters at different levels of densities and fighter densities the surviving animals were recorded in the experiment described in section 2.0.9 and with the experimental setup of table 1. survival probabilities were recorded (see section 2.0.9).

3 Results

3.0.11 Percentage of fighters developing from isolated individuals at egg stage

Out of 100 animals isolated at egg stage 93 developed into adults. Out of these 93 adults, 52 developed into males. Out of these 52 males, 39 developed into fighters. From 100 animals isolated as larvae at pre-tritonymph stage 96 developed into adults. Forty-seven of these 96 adults became males. 37 of these males were fighters. Therefore 75% of males developed into fighters when individuals were isolated at egg stage compared to 79 % when isolated at pre-tritonymph post egg stage. This difference in percentages is not significant ($\chi^2 = 0.025, df = 1, p = 1$).

One can therefore have some confidence that the development switch, when it is possible to become a fighter given the necessary environmental indications, occurs at a discrete time, namely within the tritonymph stage. It is therefore not important at which stage the animal is isolated, given it is before the tritonymph stage.

3.0.12 Density-dependent morph determination

The results with number of vials, mean and SE are given in table 2.

density	N	$\bar{x}(P_f)$	$SE(P_f)$
1	59	0.72	0.053
2	59	0.27	0.034
5	20	0.14	0.035
10	70	0.02	0.005
$\sum N$	208		

Table 2: Mean percentage $\bar{x}(P_f)$ and standard error $SE(P_f)$ of the probability of developing into a fighter for *S. berlessei* isolated at pre-tritonymph stage at density 1 2 5 10 in year 1998.

A non-linear regression was performed and a relationship between fighter morph determination and density in high food conditions was found ($RSS = 16.9, SE = 0.032, t = 20.96$).

The relationship is represented in equation 1 where δ is density and P_f is the probability of developing into a fighter.

$$P_f = \frac{0.69}{\delta} \quad (1)$$

Equation 1 is graphically demonstrated in figure 2.

3.0.13 Condition-dependent morph determination

δ	N	high food <i>Mean</i> \pm <i>SE</i>	N	low food <i>Mean</i> \pm <i>SE</i>
1	3	0.667 \pm NA	5	0.400 \pm NA
2	2	0.500 \pm 0.500	3	0.333 \pm 0.167
3	1	0.000 \pm NA	3	0.444 \pm 0.111
4	2	0.125 \pm 0.125		
5	2	0.200 \pm 0.000	1	0.000 \pm NA
6			2	0.250 \pm 0.083
7	2	0.143 \pm 0.000		
9			1	0.111 \pm NA
10	1	0.200 \pm NA		
12			1	0.167 \pm NA
13			1	0.154 \pm NA
14	2	0.250 \pm 0.03		
17			1	0.175 \pm NA
21	1	0.240 \pm NA		
$\sum N$	16		18	

Table 3: Number, mean and SE of the probability of becoming a fighter at two different levels of food at different densities δ . NA=Non available.

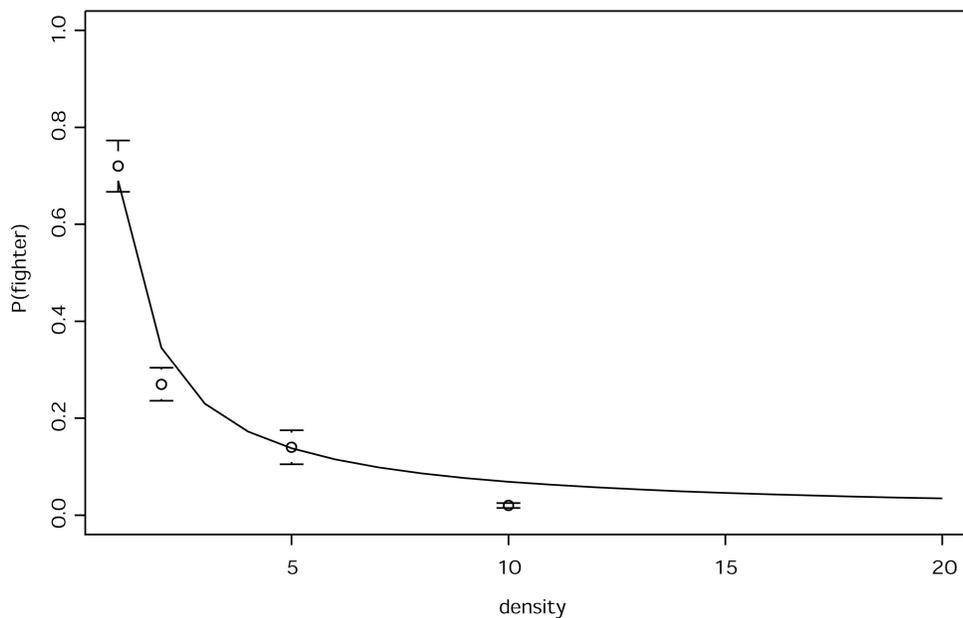


Figure 2: Relationship as calculated by a non-linear regression between the probability of developing into a fighter [$P(\text{fighter})$] vs culture density and data points with standard error bars.

The results are summarised in table 3. Six tubes did not complete the experiment, because of premature death of the animals. An analysis of deviance table of a generalised linear model with Poisson error and identity link function (table 4) shows a significant effect of food, density and the interaction of density with food. Males in high densities with low food supply had a lower probability of becoming a fighter than with high food provisioning.

3.0.14 Fighter fecundity in all environmental conditions

Results are presented in table 5. Animals supplied with food at a low rate and animals experiencing a five-day window without food after birth had a higher mortality. A total of eight vials did not complete the experiment (six tubes with non-fighters and two with fighters). This is not significant ($\chi^2 = 2.16, df = 1, p = 0.106$). Nevertheless a vial in each category completed the test.

A Gaussian GLM was performed and the residuals checked for non-violation of normality of the residuals and heteroscedacity. The model:

	df	$p(Chi)$
<i>food</i>	33	0.023
δ	32	0.046
<i>food</i> : δ	31	0.0015

Table 4: Analysis of deviance table of generalised linear model with Poisson error and identity link function on number of fighters developed on different levels of food and densities δ .

		fed at birth		fed after 5 days after birth		
		NF	F	NF	F	
low food	V	52 \pm NA	64 \pm 19.79	V	0 \pm NA	81 \pm 33.94
		n=1	n=2		n=1	n=2
	NV	91 \pm NA	55 \pm 21.21	NV	101 \pm NA	56 \pm 79.19
		n=1	n=2		n=1	n=2
high food	V	32 \pm 45.25	124 \pm 4.24	V	150 \pm 14.14	125 \pm 21.92
		n=2	n=2		n=2	n=2
	NV	34 \pm NA	105 \pm 115.96	NV	60 \pm NA	34.5 \pm 40.30
		n=1	n=2		n=1	n=2

Table 5: Mean \pm standard deviation and number of vials (n) for number of eggs laid by virgin (V) and non-virgin (NV) females on day of first egg-laying, fed on high and low food which was provided at start or after five days and mated with fighters (F) and non-fighters (NF). NA= Non applicable.

$$N_{eggs} \propto \text{Type of male}$$

was the minimum adequate model.

Females fertilised by fighters, pooled over all conditions, laid more eggs ($\bar{x} \approx 80.56$) than non-fighters ($\bar{x} \approx 65$) (Gaussian GLM, $n=32$, $p < 0.02$).

3.0.15 Fighter fecundity in a good quality, resource stable environment

As *S. berlesei* exhibits sperm competition (Radwan, 1991) the order of matings is relevant. In an experiment comparing reproductive success of males mating first or second with a female, Radwan (1991) estimates that 86% of eggs are fertilised by the second and last mating. However this percentage dropped to 56% when the last mating was more than six hours after the previous mating.

Mate guarding does not exist in *S. berlesei* (Radwan, 1991). Therefore, it seems that one option for *S. berlesei* to eliminate sperm competition would be to kill other fighters and non-fighters as fast as possible and postpone mating for not more than six hours. This pattern could not be recognised in the laboratory where after introduction of fighters and non-fighters into a test tube, both

attempt to start mating nearly instantaneously. In fact the number of matings obtained by fighters is much greater than that of non-fighters. The non-fighters achieve very few matings with fighters presence, except in tubes where they significantly outnumber the fighter(s) (corrected for initial fighter/non-fighter numbers and eliminating trials with no non-fighters in them) (one-sided Wilcoxon rank-sum test, $n=13$, $m=18$, $p < 0.05$) (see table 6).

	Median	n	NA's
<i>fighters</i>	0.37	18	0
<i>non - fighters</i>	0.001	13	5

Table 6: Median of hourly per capita mating success obtained by fighters and non-fighters over all densities as calculated by animal numbers by female fecundity and divided by hours. NA's= not available; no non-fighters in the vial initially.

For simplicity and in order to trace the effect of density-dependence on survival and fighter reproductive success, it is assumed in the following model, that the animals present after one week obtain most of the reproductive success (as the last mating gains most of the fertilisations), and that, whilst both phenotypes are alive, they achieve the same amount of matings (and order of matings). There was no difference in the fecundity of females fertilised by fighters and non-fighters, when the feeding regime (high food) was the same and animals with both feeding times were pooled (two-sided Wilcoxon rank-sum test, $n=8$, $m=6$, $p \gg 0.05$, see table 5). Therefore, when three fighters and two non-fighters are in a population, fighters should gain 60% of all matings and therefore the reproductive success of the non-fighters would be 40%. After one week the cuticle of the males is sufficiently hardened so that fighting does not result in any further deaths (Timms et al., 1980), so that changes in the proportion of fighters and non-fighters in the starting cohort are unlikely due to fighting after this time period.

	<i>Value</i>	<i>SE</i>	<i>t - value</i>
<i>c</i>	8.23	0.714	11.52
<i>θ</i>	26.14	1.43	18.25

Table 7: Result of non linear regression for female fecundity per day per density pooled over all feeding regimes, with value, SE and t-value and residual standard error of 18.55 on 961 df.

The relationship between fecundity (mean egg female⁻¹ day⁻¹) and density was fitted with a non linear regression (see table 7 and equation 2), where $c = 8.23$, $\theta=26.14$, δ =pair density, y =number of eggs females laid by female per day pooled over all feeding regimes, to get the effect of density-dependence in

all conditions.

$$y = c + \frac{\theta}{\delta} \quad (2)$$

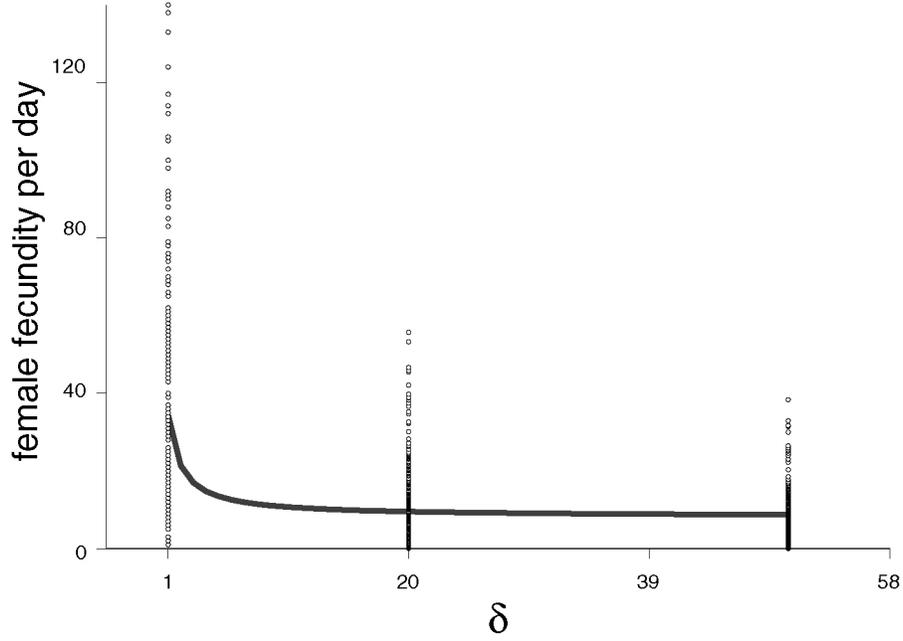


Figure 3: Non linear regression and data for female fecundity per day pooled over all feeding regimes vs δ =density in pairs.

Although females are able to lay in excess of 80 eggs per day if reared in isolation and with excess food, the data was collected from mites reared on high and low food sources and the fit therefore represents the mean of eggs produced over all nutritional conditions on all days.

The proportion of fighters, Φ_F in a total population is:

$$\Phi_F = \frac{N_F}{N_{NF} + N_F} \quad (3)$$

where N_F is the number of fighters and N_{NF} is the number of non-fighters.

From this one can estimate the number of eggs a fighter can achieve in competition with non-fighters:

$$N_{F,eggs} = \frac{(\Phi_F) \cdot (c + \frac{\theta}{N_{F\epsilon}})}{N_F} \quad (4)$$

where, $N_{F,eggs}$ = fighter paternity, N_F = number of fighters, N_{NF} = number of non-fighters, N_{Fe} = number of females, $c = 8.23$, $\theta=26.14$ (after equation 2).

Equation 4 shows the number of eggs one fighter can achieve per day if in competition with other fighters and non-fighters. Using the data from table 9 and the numbers of fighters, non-fighters and females from table 1, one can calculate the $N_{F,eggs}$ initially and after the time period of one week, when fighters cannot kill other males of its own cohort. The initial estimate of fighter paternity arises from the initial densities (and so is an estimate of paternity if no non-fighters are killed by the fighters). The final estimate of fighter paternity represents the paternity that occurs after fighting-related mortality (which occurs in the first days prior to hardening of the cuticle). Comparison of the two measures estimates the fecundity benefits due to fighting.

The result of the above calculations can be found in figure 4 and 5 and table 8.

<i>t</i>	<i>Median</i>	<i>n</i>
0	2.6	18
1 week	6.0755	18

Table 8: Median fighter fecundity (eggs female⁻¹ day⁻¹ over densities 5, 10, 20, 50 at start of experiment; therefore without the influence of any fights) and after one week after cuticle hardening when fighting ceases to be efficient to kill other males through cuticle hardening and therefore the effect of fighting ceases to exist.

The difference in eggs per fighter per female after all fights have completed is significantly greater than the number of eggs that could have been achieved, had no fights taken place (Wilcoxon rank sum test, n=18, p<0.0001). Fighters that kill other non-fighters have, therefore, an advantage by killing off other males and "snatching" their matings.

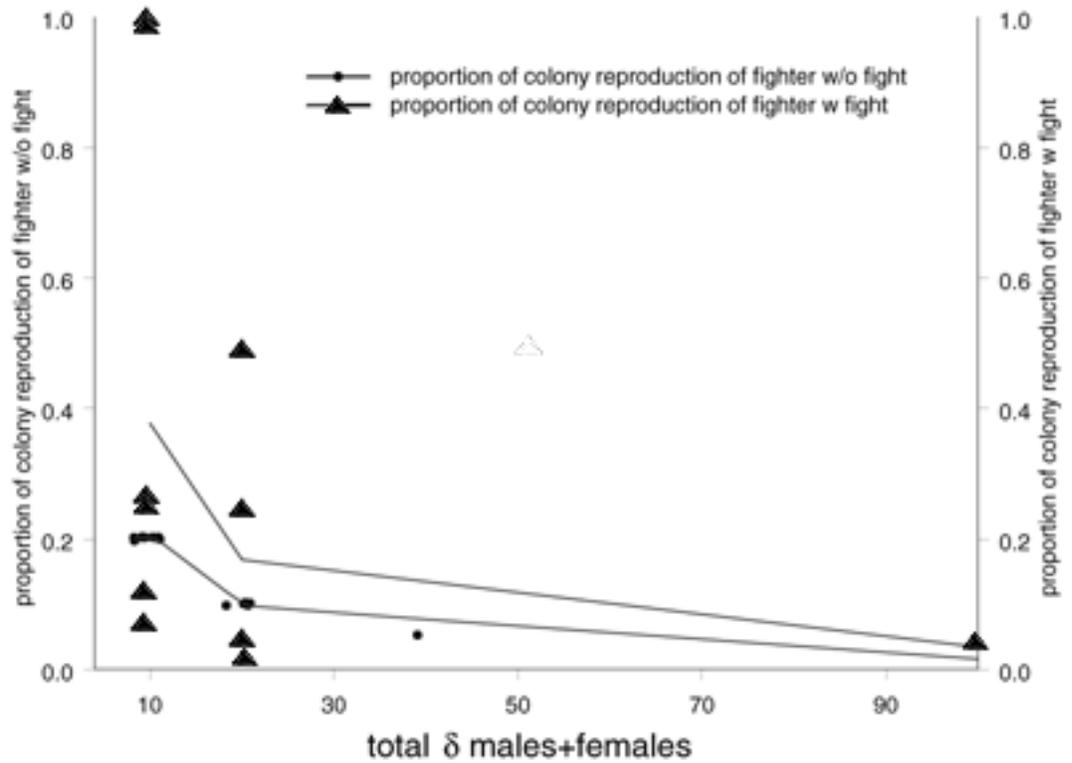


Figure 4: Proportion of colony reproduction of fighters per day vs total animal density δ initial at experiment start (initial = expected reproductive success, by frequency w/o fights, lower line) and after one week post cuticle hardening when fighting is not successful anymore (= gained reproductive effort with fights, upper line). w = with, w/o = without. Fighters gain an increase in overall colony reproductive success through fighting.

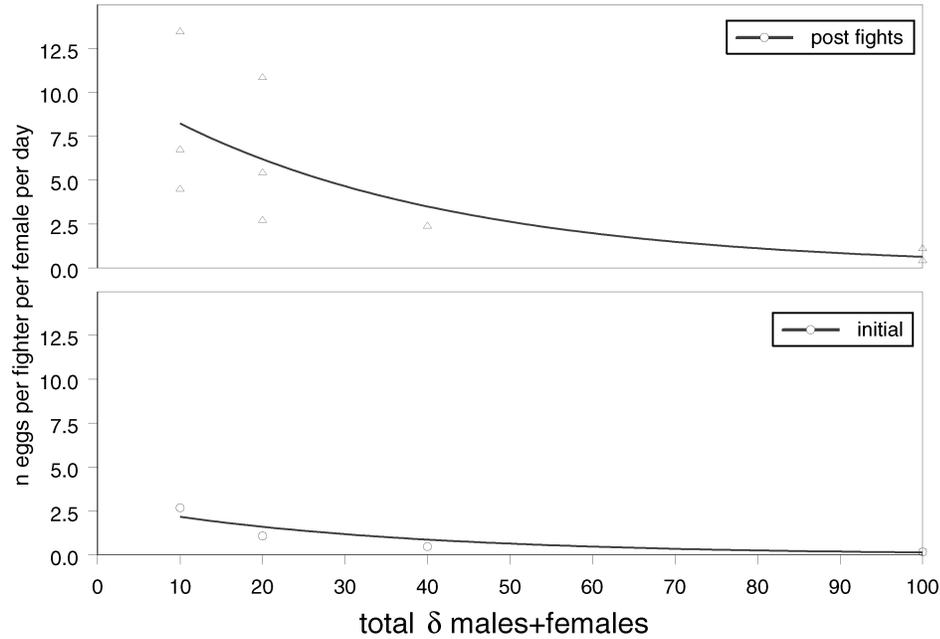


Figure 5: Fighter fecundity (eggs female⁻¹ day⁻¹ vs total animal density δ initial at experiment start (initial = expected reproductive success, by frequency w/o fights) and after one week post cuticle hardening when fighting is not successful anymore (post fights=all fighting took place). Each fighter has a higher chance of achieving more reproductive success through fighting.

3.0.16 Survival probabilities of fighters and non-fighters

This experiment investigated survival of fighters and non-fighters over a period of a week within colonies of different densities (see table 9).

A generalised linear model with Binomial error was conducted with the proportion of surviving fighters as response and the log transformed values of the initial numbers of fighters and non-fighters as independent variables. The minimal adequate model for describing the influence of the above parameters, after evaluating all model combinations, was found to be the model with the log transformed number of fighters as a single term (Binomial GLM, $term = \log(n \text{ of fighters})$, $df=11$, $p(\chi^2)=0.03$).

A non-fighter's chances of survival seems to rise when the proportion of fighters to non-fighters becomes smaller and density increases. In lower densities

δ	<i>fighters</i>				<i>non – fighters</i>			
	Median	n	Mean	SE	Median	n	Mean	SE
5	0.550	10	0.605	0.082	0.000	8	0.1875	0.131
10	0.200	5	0.488	0.021	0.1667	4	0.1667	0.095
20	0.200	1	0.200	-	-	-	-	-
50	0.58	2	0.58	0.420	0.408	1	0.408	-

Table 9: Mean and SE and Median and n of the percentage of surviving males vs pair density δ over five days until cuticle hardening takes place and fights do not result in killings anymore.

fighters managed to kill off all non-fighters (table 9), while in a density of 50 with one fighter present, only half of the non-fighters were killed within a week. Fighters together have a higher percentage of survival over all pair densities (1-50) and fighter densities than non-fighters (Wilcoxon rank-sum test, $n=13$, $m=18$, $p < 0.0016$). Fighters have a survival probability of 55% while non-fighters have a survival probability of only 20% over all densities. Generally one would expect fighters having a higher risk of getting killed as they are actively seeking confrontation, but their armour and aggression seems to be sufficient to compensate for this.

4 Discussion

In a changing environment, phenotypic plasticity leads to changing phenotypes (Meyers and Bull, 2002). This phenotypic variation can be found within single individuals (Levins, 1968), among individuals in the population at one time (Ballare et al., 1990) or over generations (Gibson et al., 1992). With its density-dependent morph determination *S. berlesei* seems to react to changes in population density caused by intrinsic (e.g. population oscillations through migration) and extrinsic factors (e.g. temporal and spatial variation - food). In a finely grained heterogenous environment (spatially or temporally) it seems to be best for the male to delay the decision if to become a fighter as long as possible. Presumably the shorter the time period is between the decision time to become a fighter or not and the time when the actual adult male emerges, the better a male is prepared for the situation he encounters. The fighter morph determination decision is possible up to the deuteronymph stage and is, as has been shown above, highly influenced by environmental conditions. Long distance dispersal, when it occurs, is via the deuteronymph (hypopus) and phoresy. Given this, the tritonymph (the stage after the proto- or deuteronymph) may well develop on a different patch, at different population densities, than its natal patch. Conditions then may well predict the conditions it will experience as an adult. It therefore makes sense to delay the decision regarding which morph to become, as long as possible. Presumably development pathways preclude a decision at the time of the last molt, so that the decision cannot be made later

in the development stages.

There is an exponential-like decline in the probability of becoming a fighter with density, rather than a step like threshold. The reasons lie most likely in a reduced fecundity for fighters in higher densities and a system inherent condition-dependence. This condition-dependence seems to be tightly coupled with the density-dependence, or simply the higher density leads to a lower level of food for all animals. Therefore the lower fighter numbers at lower densities with low food are responding to previous low food conditions, such as might occur at the time they hatched. Therefore the condition-dependence is a potential mechanism for delayed density-dependence to occur. However, even a well-fed isolated male will not develop into a fighter if olfactory clues from dense cultures are introduced to them (Timms et al., 1980). Therefore there is some true density-dependence and the condition-dependence is not the only mechanism of density-dependence.

Condition-dependence on *S. berlesei* was found by Radwan (1995). Feeding the mites on filter paper led to the same number of fighters when reared alone as well fed fighters at $density = 24$. Fighters on filter paper simply have very little to invest in extra legs. It is more astounding that actually two fighters developed out of 41 with a very low amount of food. This also explains why here even under low food conditions (a minute amount of yeast, which still is more nourishing than filter paper) at very low densities, fighters developed with about 40% probability.

Condition-dependence seems to be of major importance in male polymorphism and has recently also been found in *J. marmorata* (Kurdziel and Knowles, 2002). This seems to be highly likely, as in *S. berlesei* as in *J. marmorata* and *J. falcata* the fighting or aggressive morph needs to build up extra body mass. Fighters in *S. berlesei* have to develop extra leg mass and *J. marmorata* and *J. falcata* have larger extra morphs, which need more bio mass to build up. Interestingly there is also a condition-dependence in *Ontophagus spec.* where the dominant phenotype has to develop extra horns (Emlen, 1999). It seems to be therefore a major prerequisite that, for an andropoly-morph to develop, the conditions have to be at least reasonable for the build up of extra body mass. It seems to be also necessary that the trade-off between the extra-body mass and reproductive benefits have to be overcome in the first instance, before one looks at general reproductive trade-offs, or the condition-dependent trade-off has to be considered much more strongly.

The fighter "gambles" on being the winner of all fights. This results in the gains being very high compared to a non-fighter as he not only gains a higher percentage of all matings and a higher egg number than a non-fighter in the same condition, but more eggs in an initial low density population. This can be more important than in an already established population, as these eggs are the genetic founders of all future generations. A fighter could potentially gain a higher percentage of the overall female fecundity than a non-fighter, dependent on both ratio and density. At density five he could gain 100% more fecundity than a non-fighter dropping to about 50% at higher densities. A fighter could therefore achieve (also in higher densities) more fecundity, as a result of killing

other rivals. The variance at lower densities (due to the random outcome of fights) seems to be substantial, as the mite might be killed at emergence or he might win all fights. Only in very high densities, the probability of gaining a high percentage of the overall colony reproductive success sinks, as there are simply too many competitors being either fighters or non-fighters. This seems to be therefore an adaptation to the extremes and a fitness to reduced variance seems unlikely, as fighters do develop at low densities. There is also an inherent relationship between population-size and variance. Given that the numbers relate to independent Bernoulli trials, the variance one Bernoulli trial (become a fighter with probability 0.9) is higher than in 100 Bernoulli trials according to the law of large numbers (in repeated, independent trials with the same probability p of success in each trial, the percentage of successes is increasingly likely to be close to the chance of success as the number of trials increases). Therefore the risks, but also the potential gain is much higher for a fighter in lower densities, while in higher densities, there is as much benefits and potential costs are reduced and the fighter's fitness will converge on the average for a male.

By actively changing the relation between himself and other individuals the fighter increases the variance and the chance to gain up to 100% of all reproductive success, if he kills off all competition. This seems to be the reason, why fighters are also relatively often present at densities > 2 . Sperm competition favouring the last to mate therefore promotes a polymorphism that kills all other males and is highly aggressive. This can be seen as a form of advanced more effective mate guarding, as it can be found for example in wasps (Field and Keller, 1993) and in birds (Westneat, 1993).

The overall results show that the effects initiating the density-dependence as mentioned in Radwan (1991) are not necessarily the only influencing factors. Radwan (1991) discusses that fighters would gain fewer matings through increased time spent fighting and that this would be the trade-off in the fighter morph determination. While this might be the case, a very high influence on the trade-off of being a fighter in high densities seems to be, that the reproductive success gained will be very low through simple frequency-dependence, the chance of being killed and a reduced female fecundity at higher densities.

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