Functional Ecology 1994
8, 458–463

Size-dependent predation by *Dugesia lugubris* (Turbellaria) on *Physa acuta* (Gastropoda): experiments and model

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Summary

1. We investigated experimentally predation by the flatworm *Dugesia lugubris* on the snail *Physa acuta* in relation to predator body length and to prey morphology [shell length (SL) and aperture width (AW)].

2. SL and AW correlate strongly in the field, but display significant and independent variance among populations. In the laboratory, predation by *Dugesia* resulted in large and significant selection differentials on both SL and AW. Analysis of partial effects suggests that selection on AW was indirect, and mediated through its strong correlation with SL.

3. The probability P_{ij} for a snail of size category i (SL) to be preyed upon by a flatworm of size category j was fitted with a Poisson-probability distribution, the mean of which increased linearly with predator size (j). Despite the low number of parameters, the fit was excellent ($r^2 = 0{\cdot}96$). We offer brief biological interpretations of this relationship with reference to optimal foraging theory.

4. The largest size class of *Dugesia* (>2 cm) did not prey on snails larger than 7 mm shell length. This size threshold might offer *Physa* a refuge against flatworm predation and thereby allow coexistence in the field.

5. Our results are further discussed with respect to previous field and laboratory observations on *P. acuta* life-history patterns, in particular its phenotypic variance in adult body size.

Key-words: Life-history theory, predator–prey interactions, selection (direct, indirect)

Functional Ecology (1994) **8,** 458–463

Introduction

Body size is one of the most important variables in structuring populations because vital rates (fecundity, growth, survival) frequently depend on it—often more so than on age (e.g. Peters 1983; Sauer & Slade 1987; Ebenman & Persson 1988). Such dependences are bound to affect the evolution of life histories (Stearns 1992; Perrin & Sibly 1993); a size-dependent mortality, in particular, strongly influences optimal resource-allocation patterns (Perrin, Sibly & Nichols 1993). This implies that any proper interpretation of observed life-history patterns requires precise information about the size dependence of mortality in natural conditions.

While documenting the life-history patterns of the freshwater gastropod *Physa acuta* (Drap.) in laboratory conditions, Perrin (1986) reported that the snails under study grew to adult sizes which were much larger than optimal under these conditions. The fitness cost was high: individuals reproducing earlier, at a smaller size, benefited from both a better survival at maturity and a higher lifelong fecundity, which resulted in a strong negative correlation between fitness and adult size. In accordance with our argument above, the question arises whether growth towards such a large adult size constitutes an evolutionary response to a size-dependent mortality in the field.

In natural conditions, predation is the most plausible source of size dependence in mortality: size often has been recognized as the relevant variable in prey choice (e.g. Elner & Hughes 1978; Mittelbach 1981; Pastorak 1981; Bence & Murdoch 1986; Osenberg & Mittelbach 1989; Persson & Greenberg 1990). Moreover, size-dependent predation has already been shown to be responsible for evolutionary shifts in

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prey life histories (Crowl 1990; Reznick, Bryga & Endler 1990).

Among freshwater gastropods, *Physa* appears surprisingly vulnerable to invertebrate predation (e.g. Brown & Strouse 1988). The only documented defence mechanism seems to be a rather inefficient shell shaking (Townsend & McCarthy 1980; Wilken & Appleton 1991; F. Tripet & N. Perrin, unpublished observation). Vulnerability differences among snail species probably stem from differences in resource allocation strategies. *Physa* allocates most of its resources to growth and reproduction, apparently at the expense of defence (Blandenier & Perrin 1989). Compared to the similarly sized *Lymnaea peregra*, *P. acuta* displays a very high growth rate, early maturity and high fecundity (Blandenier & Perrin 1989). All these traits increase fitness in the absence of predators (Perrin 1986) but, under predation, *Physa* pays the costs of its allocation strategy through increased vulnerability (e.g. Brown & Strouse 1988; unpublished observation).

The most common predator to *P. acuta* in western Switzerland appears to be the flatworm *Dugesia lugubris* (Schmidt) (unpublished observation), a relatively large-sized species widespread in European warm lakes, ponds and streams (Ball & Reynoldson 1981). Flatworms are predators or scavengers, and the genus *Dugesia* specializes on freshwater gastropods (Reynoldson & Davies 1970; Reynoldson & Piearce 1979), among which *Physa* is the most preferred prey (unpublished observation).

The present study aims at investigating the size dependence of predation by *D. lugubris* on *P. acuta* as a way of checking whether this predation may be responsible for the prey life-history patterns as documented in Perrin (1986).

Materials and methods

Approximately 200 *P. acuta* were sampled from five different populations in the vicinity of Lausanne (Switzerland) in early spring (March–April) 1992. No reproduction had yet occurred, so all individuals were adults or subadults (shell length 4 mm and above) from the previous year. In each case the first *c.* 40 individuals encountered were collected; 15–20 of them were measured with a Nikon Measurescope (Profile Projector, Nikon, Küsnacht, Switzerland) for the following four shell parameters: shell length (SL), shell width (SW), aperture length (AL) and aperture width (AW) (Fig. 1). These were reared in the laboratory (20 °C and 12:12 L:D photoperiod) and fed *ad libitum* with fish food (Tetramin): their eggs were collected and settled in separate tanks, where the F_1 generation developed. Only F_1 individuals were used for the predation experiments.

The *Dugesia* also originated from several localities around Lausanne. *Dugesia lugubris-polychroa* constitutes a species complex, which encompasses several chromosomal races whose relationships and geographical distributions are not yet fully clarified (Ball & Reynoldson 1981; Pattée & Gourbault 1981). According to body-shape and genitalia-morphology criteria (squash technique of Ball & Reynoldson 1981) our *Dugesia* belong to the *lugubris* taxon *sensu stricto*. They were maintained for 2–3 weeks in the laboratory (20 °C, 12:12 L:D photoperiod, fed *ad libitum* with *P. acuta*) before use in the experiments.

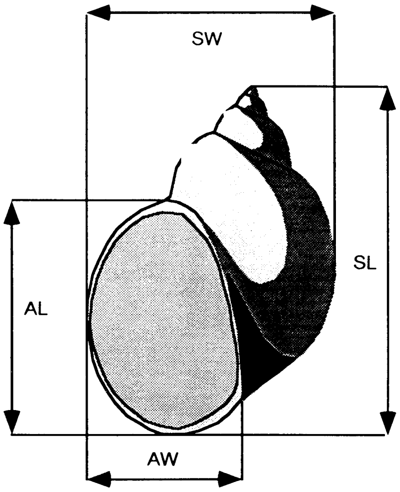

Fig. 1. Measurements on *Physa* shell: SL, shell length; SW, shell width; AL, aperture length; AW, aperture width.

The experiments were conducted on animals of specific size classes. Triclad lengths (in mobile state) were estimated in transparent plastic dishes on graph paper by eye to the nearest centimetre. These measurements were accurate enough for our purpose, as only three size categories were retained for subsequent analyses. These categories were established on a linear scale: <1 cm, 1–2 cm and >2 cm. No animals larger than 3 cm were found. As for *Physa*, SL and AW were measured with the Nikon Profile Projector. From the shell length measurements, 10 size categories were similarly defined on a linear scale: <1 mm, 1–2 mm, 2–3 mm, and so on until the last category (>9 mm).

The experiments involved placing a single *Dugesia* of one of the three size categories with *Physa* of six different size categories in a small cylindrical plastic (polystyrol) jar (9·5 cm height, 5·7 cm diameter) for 48 h. Preliminary investigations had revealed a dependence of triclad's feeding frequency on prey size: when fed with mean-sized *Physa* (4–6 mm SL), *Dugesia* consumed 1–2 prey per day, but 3–6 of them when fed with small snails (1–2 mm). Thus, in order to make predation pressure (i.e. proportion of prey eaten per experiment) comparable among experiments, the number of *Physa* was varied by triplicating the individuals from the two smallest size categories. As a result, the total number of prey available per experiment ranged from 6 to 10.

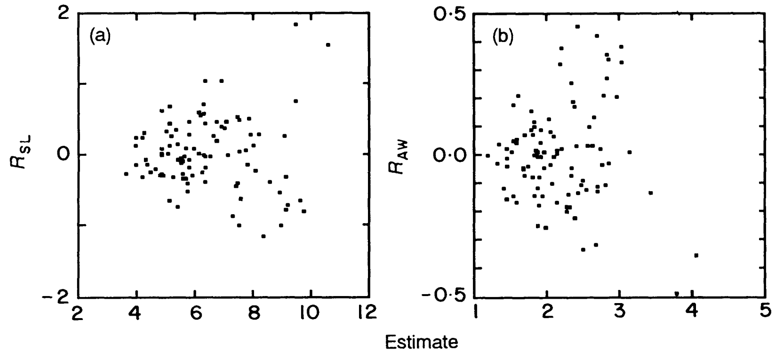

Fig. 2. (a) Residuals R_{SL} of the regression of SL on AW against estimate of SL (mm). (b) Residuals R_{AW} of the regression of AW on SL against estimate of AW (mm).

Whether simultaneous choice is the normal situation in nature depends on *Physa* densities. These snails usually have patchy distributions within ponds (unpublished observation), locally matching our experimental densities; this suggests that simultaneous choice for *Dugesia* might be quite a common situation.

After 48 h, empty shells and living snails were measured in order to quantify the size dependence of predation. The probability P_{ij} for a *Physa* of size category i to be eaten by a *Dugesia* of size category j was defined as the proportion of experiments where predation occurred; that is, the number of times an i category *Physa* was eaten by a j category *Dugesia*, divided by the number of experiments in which individuals of each of these two categories were involved. The observed probability distributions were fitted (least-squares non-linear fitting) using a Poisson model:

$$P_{ij} = ce^{-m}\, m^i / i! \qquad \text{eqn 1}$$

where $m = m(j)$ is the mean (and variance) of the distribution, c is the total probability of being eaten, e is the base of natural logarithms and $i!$ is the factorial of i, given by the product $\prod_1^i n$.

All statistical analyses, including non-linear fitting of the model, were performed using Systat (Wilkinson 1989).

Results

FIELD POPULATIONS

The four morphological traits measured were highly correlated ($r = 0{\cdot}95$–$0{\cdot}98$, $n = 95$, $P < 0{\cdot}001$ in every case) which, as a result of allometry, is not surprising. Only the two least correlated variables (SL and AW, $r = 0{\cdot}95$) were retained for subsequent analyses. From these, a SL-independent measure of aperture width (R_{AW}) was computed as the residuals of the linear regression of AW on SL (Fig. 2a); similarly, an AW-independent measure of shell length (R_{SL}) was also computed (Fig. 2b). All variables differed significantly among populations (SL, $F = 12{\cdot}1$; AW, $F = 14{\cdot}6$; R_{AW}, $F = 18{\cdot}2$; R_{SL}, $F = 15{\cdot}2$; df = 4,90, $P < 0{\cdot}001$ in every case), thus providing evidence of differences between natural populations in shell size and shape.

EXPERIMENTS

One hundred and twenty-eight experiments were performed, which led to a total number of 921 observations (average 7·2 snails per experiment). The overall mean ± SD shell length of the snails used was 3·92 ± 2·46 mm and the mean aperture width was 1·37 ± 0·84 mm. Predation occurred 354 times, which means an average of 2·77 prey eaten per experiment. Predation activity was quantitatively small in the triclads' time budget: handling and eating time together usually took less than 1 h per prey. *Dugesia* spent a large part of the day being quiet, digesting or laying reproductive capsules (total handling time is thus much larger if digestion time is included).

SIZE-SELECTIVE PREDATION

Predation was strongly size dependent: surviving snails had a larger shell than the dead ones (SL = 4·93 ± 2·35 mm *vs* 2·28 ± 1·60 mm; $P < 0{\cdot}001$, t-test, $n = 354$, 567), and a wider aperture (AW = 1·72 ± 0·81 mm *vs* 0·82 ± 0·54 mm; $P < 0{\cdot}001$, t-test, $n = 354$, 567). Thus, the selection differentials (i.e. departure of survivors from mean population) on both SL and AW were large and positive (1·02 mm and 0·35 mm, respectively). As these two variables were strongly correlated ($r > 0{\cdot}99$, $n = 921$, $P < 0{\cdot}001$; NB, this correlation exceeds that from field specimens, as a result of a greater range of size), the one under direct selection could not be identified. This was confirmed by the non-significance of t-tests on residuals (R_{AW}, $P = 0{\cdot}478$; R_{SL}, $P = 0{\cdot}066$; $n = 354$, 567). However, as the probability associated with R_{SL} was quite small and almost significant, the trait under direct selection was certainly more correlated with SL than with AW. Thus, SL only was considered in the further analyses, as the best surrogate for the selected trait.

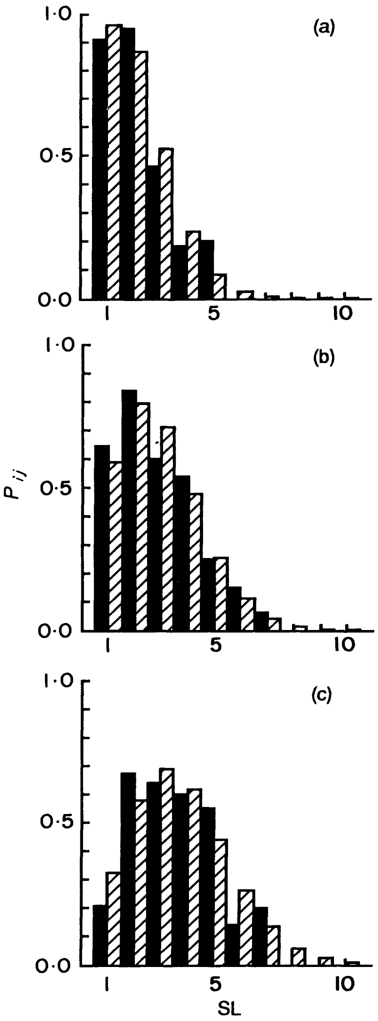

Fig. 3. Predation probability as a function of *Physa* shell length (SL; mm) for the three *Dugesia* size categories [(a) $j=1$; (b) $j=2$; (c) $j=3$]. Black bars are observed values and hatched bars are fitted values (Poisson distribution, equation 3).

PREDATION PROBABILITIES

The predation probabilities P_{ij} are plotted for the three *Dugesia* size categories j in Fig. 3. As can be seen, they show dependencies both on prey size i (SL) and on predator size (j). These three distributions were fitted using a Poisson model; parameter values, together with the proportions of variance explained, are given in Table 1.

From these analyses, the parameter c (total probability of being eaten) appears very constant (Table 1). Furthermore, the m value (mean prey size) bears a simple linear relationship to predator size j (Fig. 4):

$$m = 0{\cdot}91 + 0{\cdot}89j \quad (r > 0{\cdot}99, n = 3, P < 0{\cdot}05) \qquad \text{eqn 2}$$

These two characteristics together strongly suggest the use of a generalized, three-parameter, Poisson model for the whole set of data:

$$P_{ij} = ce^{-a-bj}(a + bj)^i / i! \qquad \text{eqn 3}$$

where a and b are the intercept and the slope of the regression of m on j. Fitting this model provided the following values for the three parameters: $c = 0{\cdot}324$, $a = 0{\cdot}920$, and $b = 0{\cdot}884$. Despite the low number of parameters involved, this model explained most of the variance in the observations ($r^2 = 0{\cdot}96$, $n = 30$). The quality of the fit may be checked on Fig. 3, where the values predicted by the general model (equation 3) are juxtaposed to the observed data.

Discussion

From our results, the predation by *D. lugubris* on *P. acuta* is strongly size dependent. Both SL and AW appeared to be under positive selective pressure. As a result of their high correlation, we could not identify the variable under direct selection (Lande & Arnold 1983), but SL had a larger and nearly significant independent effect. Thus, a parsimonious hypothesis would be that *Dugesia* selects its prey according to SL, and that the observed selection on AW is indirect, mediated through its correlation with SL. More detailed observations as to how *Dugesia* handles *Physa* would be useful with respect to this topic.

This selective pressure is certainly very important in the field, because *Dugesia* is such a common predator. Size-dependent predation by invertebrates (leeches, crayfish) on several physid species has already been evidenced (Brown & Strouse 1988; Crowl 1990; Crowl & Covich 1990; Crowl & Schnell 1990; Wilken & Appleton 1991), and indeed might be an important feature of these snails' ecological and evolutionary environments.

The present results help to interpret previous data on *Physa* growth strategies, in particular the large adult size (Perrin 1986; see Introduction). They also suggest that *Dugesia* may play an important role in maintaining among-population variance in *Physa* life history: as optimal adult size depends on whether a predator is present or not, a patchy predator distribution would result in a high interpopulation variance in adult sizes—as reported in the literature (Germain 1931) and confirmed here. It is worth noting that the within-population variance (most of which is usually due to age differences among individuals) was minimized by our early-spring sampling: all individuals measured were adults or subadults (≥4 mm) from the previous year.

Table 1. Estimated values for the parameters c and m of the Poisson distribution (equation 1) and proportion of variance explained (r^2) for the three *Dugesia* size categories (j)

j	c	m	r^2
1	0·323	1·83	0·978
2	0·326	2·63	0·976
3	0·324	3·61	0·916

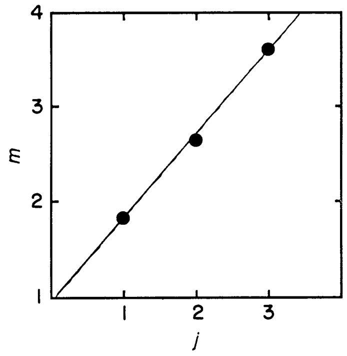

Fig. 4. Mean prey size *m* as function of *Dugesia* size class *j*. The fitted line corresponds to equation 2.

Whether predation is responsible for this variance could be tested by measuring the correlation between adult size and predator occurrence or density. Such a relationship has already been evidenced in a *Physa*–crayfish system (Crowl 1990): on the one hand, predation by crayfish was shown to decrease with *Physa* size and on the other hand, adult size was larger in *Physa* from crayfish localities. This point is also worth investigating experimentally in the *Dugesia–Physa* system: although the role of predators in moulding prey life-history patterns is certainly very important, very few cases of predator-mediated life-history evolution have yet been documented convincingly (e.g. Reznick *et al.* 1990; Crowl & Covich 1990).

Our experiments also demonstrate a significant predator-size effect on predation patterns [as shown by the increase in mean prey size with predator size (equation 2)] so that both predator and prey size had to be included in the descriptive model (equation 3). The goodness of fit of this Poisson-probability distribution is surprisingly good, given the low number of parameters. Why is this so? A first point to make is that the data fitted were probabilities, averaged over several experiments, which certainly reduces the sampling variance. This also suggests that the 'true' underlying distribution must be very close to the fitted model. This true distribution might be log-normal, of which Poisson is a good approximation for discrete categories.

It is worth noting that similar distributions commonly appear among published data of prey choice (e.g. Mittelbach 1981; Osenberg & Mittelbach 1989; Persson & Greenberg 1990). We chose our model for phenomenological reasons only, with no reference to the basic assumptions that underlie the Poisson distribution (Sokal & Rohlf 1981). Nevertheless, we think that the main features of this distribution may be interpreted in biological terms.

First, referring to optimality principles, unimodality may be understood in terms of the predator's strategy and constraints. Predators should select prey according to profitability, i.e. to the ratio of energy gain *e* on the handling time *h* (Stephens & Krebs 1986). It can be shown that, under realistic assumptions about how *e* and *h* vary with prey size, profitability is a unimodal function of prey size (e.g. Schoener 1979); too small a prey is not worth the energy investment and handling time becomes prohibitive as prey size increases. Thus, a correlation between prey and predator sizes is to be expected on time- and energy-budgets accounts. The fact that the mode of the distribution increased with predator size in our experiments (equation 2) corroborates our point.

The asymmetry in the distribution is also expected because of the logical argument that prey cannot have negative sizes. This truncation leads to an asymmetry that decreases as the mean prey size increases. For this same reason an increase in variance with the mean is expected, because the left part of the distribution is missing for small *m* values, not for large ones. The observation that both the mean and the variance in prey size increase with predator size is a classical result in experimental studies of predator–prey relationships (Wilson 1975).

The result that the parameter *c* is a constant means that the average probability of being eaten ($c = 0{\cdot}324$, i.e. about 1/3) was independent of predator size. This presumably reflects simultaneously physiological features of the predator (e.g. *Dugesia* might not be able to attack and digest more than a few prey per day) and constraints imposed on the experiments via the fixed number of prey available per predator. Furthermore it provides indirect confirmation that our adjustment of prey number (see Materials and methods) was effective in maintaining predation pressure comparable among experiments.

Coupled with data on *Dugesia* numerical response, this model should lead to testable predictions on the dynamics of size-structured interacting populations (Metz, de Roos & van den Bosch 1988). Our results suggest that large adult size may constitute a refuge against predation: we did not observe any predation on *Physa* larger than 7 mm, even from the largest *Dugesia* individuals found. In the field, adult *Physa* commonly exceed 7 mm in length; in the laboratory, this size corresponds broadly to the onset of maturity and can be reached in about 5–7 weeks, while longevity may exceed 20 weeks (Perrin 1986). Hence, large *Physa* may be protected from *Dugesia* predation for a significant part of their total life span, including the period when reproductive value is highest (early reproductive period). Predation of course still occurs during the juvenile developmental period; whether it is sufficient to lead to population extinction cannot be decided from the present experiments. Frequent co-occurrence in the field (unpublished observation) suggests that stable coexistence is possible, and thus the size–refuge effective, although the high level of natural predation on triclads (from fish and dragonfly larvae; Ball & Reynoldson 1981) certainly also affects the outcome.

Acknowledgements

We are grateful to the Institute of Zoology and Animal Ecology, University of Lausanne, for logistic support during the experiments, to T.C.M. Bakker and K. Wedekind for statistical advice, and to T.A. Crowl, M. Milinski and H. Richner for comments on the manuscript.

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Received 26 April 1993; revised 9 September 1993; accepted 22 December 1993