Cannibalism-mediated life history plasticity to combined time and food stress

Marjan De Block and Robby Stoks

De Block, M. and Stoks, R. 2004. Cannibalism-mediated life history plasticity to combined time and food stress. – Oikos 106: 587–597.

There is increasing awareness that combinations of biotic and time stress interact in shaping life history plasticity. Despite being widespread and abundant, the role of cannibalism in linking both types of constraints to life history plasticity has been largely neglected. Moreover, no studies disentangled direct (due to the extra meal) and indirect (due to the elimination of the competitor) life history effects of cannibalism, and little is known about their differential dependency on these constraints. We studied effects of cannibalism on the life history of the damselfly *Lestes viridis* under combinations of time stress (by manipulating the perceived time available in the growth season) and food stress. We reared larvae per two and disentangled direct and indirect effects of cannibalism by preventing cannibalism in half of the cups and by manipulating the per capita food increase after cannibalism. Cannibalism was more frequent under both time stress and food stress and our results show it may help cannibals to compensate for the negative effects of these constraints imposed on life history. Both direct and indirect benefits of cannibalism (increased development and growth rates, larger mass at emergence) were dependent on the timing of cannibalism, being more pronounced or only present when cannibalism occurred early. Moreover, we found that the ecological constraints (time stress and food stress) also differentially shaped some of the direct and indirect effects. Given the differential context-dependency of direct and indirect effects and the fact that direct and indirect life history effects may be both important in shaping life history, disentangling these effects is critical to mechanistically understand under which conditions cannibalism is expected to be adaptive or not.

M. De Block, Dept of Biology, Evolutionary Biology Group, Univ. of Antwerp, Groenenborgerlaan 171, BE-2020 Antwerp, Belgium. (marjan.deblock@ua.ac.be). – R. Stoks, Dept of Biology, Laboratory of Aquatic Ecology, Univ. of Leuven, Ch. De Bériotstraat 32, BE-3000 Leuven, Belgium.

Variation in age and size at life history transitions is tightly linked to fitness and therefore has been a central topic in life history studies (Roff 1992, 2002, Stearns 1992). Our insights into the occurrence and adaptive value of life history plasticity have been improved by including combinations of ecological constraints. Biotic constraints (e.g. food availability) may interact with time stress imposed by the seasonality of the environment (e.g. onset of winter) in shaping life history, as predicted by recent theoretical work (Abrams et al. 1996, Day and

Rowe 2002) and shown by the few empirical studies on this topic (Johansson et al. 2001, Altwegg 2002). Cannibalism may play an important role linking these constraints to life history plasticity (Polis 1981, Elgar and Crespi 1992). Therefore, a better understanding of life history plasticity may result from studies including both biotic and time stress as well as cannibalism.

A complex network of interactions links cannibalism with ecological constraints and life history plasticity. Several ecological constraints may determine the

occurrence of cannibalism. In general, cannibalism is favoured under high population densities and low food levels (Polis 1981, Elgar and Crespi 1992), while Johansson and Rowe (1999) recently showed that also time stress, by increasing activity levels, result in increased cannibalism. Furthermore, theoretical and empirical studies have shown that cannibalism can affect life history (Parker et al. 2001, Claessen et al. 2002). Typically cannibalism increases size, growth and development rates (Polis 1981, Elgar and Crespi 1992). Finally, there are several studies showing that cannibalism and ecological constraints may interact in shaping life history. For example, the beneficial effects of cannibalism on life history may only be present or be more pronounced at low food level (reviewed by Polis 1981, Church and Sherratt 1996, Chapman et al. 1999). There are, however, few studies that have looked at the effects of a biotic constraint on cannibalism coupled with their combined effects on life history (Wildy et al. 2001). Moreover, no studies so far looked at the joint effects of manipulated time stress and cannibalism on life history. Time stress imposed by the progress of the season is widespread (Nylin and Gotthard 1998) and cannibalism has been suggested as an important mechanism to reach the necessary development stage and size before a critical time horizon is reached (Crump 1983, 1992, Blaustein et al. 2001).

Cannibalism may induce life history changes either directly through the extra meal (Meffe and Crump 1987, Church and Sherratt 1996) or indirectly through the removal of a competitor (Fox 1975, Polis 1981) or the reduction of predation risk (Chapman et al. 1999, 2000). The direct effect may be positive or negative, depending on the balance between the nutritional gain and the risk of acquiring disease-causing parasites with the extra meal (Pfennig 2000). Most studies only considered direct effects (Church and Sherratt 1996, Chapman et al. 1999, Pfennig 2000), while few considered the combination of direct and indirect effects (Johansson 1996, Wildy et al. 2001). As far as we know, no studies discriminated between direct and indirect effects of cannibalism or studied whether they are affected to the same degree and in the same direction by ecological constraints. Knowledge of context-dependent fitness consequences of direct and indirect effects and their relative importance, will lead to a better mechanistic insight under which conditions cannibalism is expected to be adaptive.

In the present study we evaluated the effect of combined food stress and time stress on the occurrence of cannibalism as well as the joint effects of these ecological constraints and cannibalism on life history of the damselfly Lestes viridis. We also disentangled direct and indirect effects of cannibalism and evaluated their context-dependency. Our first three, ecological, predictions are directly linked to food availability (Polis 1981, Elgar and Crespi 1992). (1) If the negative direct effect of cannibalism is relatively unimportant, cannibalism will accelerate development and growth rate and increase mass at emergence. (2) These life history responses to cannibalism will be more pronounced when cannibalism occurs earlier or at low food level. (3) Under food stress, development and growth rates will be slower and mass at emergence will be reduced. Our last three, evolutionary, predictions are based on the adaptive role of cannibalism and life history plasticity (Abrams et al. 1996, Johansson and Rowe 1999). The optimal response of a damselfly is to emerge early at a size as large as possible because both are positively linked to future fitness (Crowley and Johansson 2002). Therefore, we predict that (4) Cannibalism will occur more frequently and/or earlier under food stress or time stress. (5) Under time stress, development will be accelerated and growth rate increased to keep mass at emergence constant. (6) The effects of cannibalism on life history will be more pronounced under time stress.

Material and methods

Study group

Cannibalism is sufficiently prevalent and intense in many odonate species to have a major impact on the dynamics of the populations involved (reviewed by Johnson 1991, Van Buskirk 1993, Corbet 1999), and especially in Lestes it is common (Jödicke 1997, Johansson and Rowe 1999). Lestes are sensitive to time stress in the larval stage as they are obligatory univoltine. After having overwintered in the egg stage, the aquatic larvae only have a short development period of about three months in spring (Jödicke 1997). Lestes, including the study species Lestes viridis (Vander Linden), have been shown to react to time stress (imposed by manipulation of day length) with decreasing age at emergence (Johansson and Rowe 1999, Johansson et al. 2001, De Block and Stoks 2003). Furthermore, field studies suggest that Lestes populations may be food limited (Pickup et al. 1984) and rearing experiments showed that they react to food stress with a reduced development and growth rate and a smaller size at emergence (Pickup and Thompson 1990, Stoks 2001).

Experimental setup

Lestes viridis lays eggs in branches of trees at the waterside. Branches with eggs can be easily detected because of gall-like extensions around the eggs. When the eggs hatch, larvae fall from the trees into the water. We collected larvae by attaching a funnel (diameter = 50 cm) with a removable plastic cup (diameter = 8 cm, height = 11.5 cm) filled to a height of 4 cm with pond water to branches with eggs. This technique allows us to

collect large numbers of larvae hatched on the same day. We collected freshly hatched larvae at the pond 'Staafwants' at 'Groot Schietveld' in Brasschaat (Belgium; 51°20′N, 4°33′E) on 29 April 2000.

Freshly hatched larvae were randomly attributed to one of two adjacent walk-in climate rooms (20°C ± 1°C). Time stress was imposed by manipulating day length (Nylin et al. 1996, Johansson and Rowe 1999, Johansson et al. 2001). Day lengths in the two rooms were set to simulate those that would be experienced by larvae hatching early (1 April; L:D 13:11; early photoperiod) and late (1 June; L:D 16:8; late photoperiod) in the growing season at the site of egg collection. Throughout the experiment, day lengths were adjusted weekly to simulate the natural progress of the light cycle. Note that the difference in day length between both time stress treatments was not constant and even switched: day lengths were longer in the late photoperiod treatment before 20 May and in the early photoperiod treatment afterwards. To minimize potentially confounding differences between the two climate rooms, larvae and their respective time stress treatment were rotated between climate rooms every week (Johansson and Rowe 1999, Johansson et al. 2001). Because larvae survive the critical first days better when held in group (M. De Block, pers. obs.) we initially kept the larvae per ten in plastic cups (10.5 × 10.5 × 6 cm) and fed them daily ad libitum with laboratory-reared brine shrimp (*Artemia* sp.) and protozoa. No cannibalism was observed during this period.

During the experiment, larvae were fed brine shrimp, which allowed manipulation of food level without causing exploitation competition. Because brine shrimp stay alive for only one hour in pond water and damselfly larvae only feed on living prey, larvae get a pulse of food (M. De Block, pers. obs.). Due to interference competition, the per capita shrimp portion (mean: 166, SE: 5, $N = 6$) is more than a single larva will eat during this limited time when in the presence of another larva (Johansson 1996). Therefore, exploitation competition between larvae is unlikely. Note, however, that larvae still can be food limited depending on the frequency of the pulses. The indirect benefit of cannibalism in our experiments is therefore restricted to the termination of interference competition. In other words, the larva will eat more brine shrimp during the food pulse in the absence of the other larvae. This is probably the most realistic indirect benefit of cannibalism for damselfly larvae, as exploitation competition seems to be weak or absent (Johnson et al. 1984, 1987, McPeek 1998), while interference competition can be very intense (McPeek 1998, Elkin and Baker 2000, McPeek et al. 2001, but see Anholt 1990), especially in *L. viridis* (Stoks 1998).

We combined two ecological variables known to affect cannibalism (time stress and food stress) with two other variables ('screen' and 'food correction') that were specifically manipulated to get information about the direct and indirect effects of cannibalism (below). This gave a design with two levels of time stress (early/late photoperiod), two levels of food stress (high/low food), two levels of screen (present/absent) and two levels of food correction (present/absent). In all cups we reared two larvae. This corresponds to a density of ca 182 larvae per m², which is intermediate for *Lestes* (Stoks and McPeek 2003, M. De Block, unpubl.). We set up 15 replicates per treatment combination on 2 May 2000. We transferred 480 larvae per two to 240 plastic cups (10.5 × 10.5 × 6 cm) filled to a height of 2 cm with filtered pond water. In the high food treatment larvae were given one food portion (ca 150 brine shrimp, or two chironomid larvae during the final larval stage) each day, in the low food treatment every other day (Johansson et al. 2001). Initially, each larva received one portion per feeding occasion; this is two portions per cup. Note that we a priori allocated cups to one of the two food correction treatments (present/absent). However, since cannibalism did not occur in all cups where it was possible (results), food correction was not always applied. This inevitably made the design unbalanced. We will now discuss the link between 'screen' and 'food correction' with the direct and indirect benefits of cannibalism, respectively (Table 1).

Ideally, the direct effects of cannibalism (life history responses to an extra meal) should be compared between larvae that only differ in this factor. Therefore, a control group of larvae should be kept under the same stressful conditions of interference competition, but not allowed to cannibalise and a cannibalism group should receive only the extra meal without any indirect benefits. Moreover, both groups of larvae should suffer from the presence of the competitor for the same amount of time. Given that a pilot experiment showed that cannibalism occurred in all cups with two larvae (M. De Block, unpubl.), we reared half of the larvae in groups of two in the same cup, but prevented cannibalism by separating the larvae with a screen. In this 'screen present' treatment, the cups were partitioned in two halves by very fine nylon netting (mesh size: 0.3 × 0.3 mm). A larva was placed at each side of the screen so that they could see and smell each other (interference competition), but they were unable to cannibalise. Experiments with coenagrionid and lestid damselfly larvae have shown that visual stimuli from another larva separated by glass walls are already enough to cause serious interference competition (McPeek et al. 2001, Stoks and McPeek 2003). In our setup, the larvae often were seen sitting head to head to each other, only separated by the screen. In the other half of the cups, the 'screen absent' treatment, larvae were able to interact and cannibalise. Special care was taken to equalize the duration larvae lived with a competitor in both groups. Therefore, each cup where cannibalism could occur was associated with a cup with a screen. At the moment

Table 1. Overview of the treatment combinations with regard to 'screen' and 'food correction' and their link to direct and indirect benefits of cannibalism. All these combinations are fully crossed with photoperiod (early/late) and food level (high/low).

Code[1]	Screen	Food correction	Before cannibalism or separation			Cannibalism	After cannibalism or separation			Benefit cannibalism or separation			
			Density	Per capita food	Competition[2]		Density	Per capita food	Competition	Extra meal	Loss wI[2]	Loss sI[2]	Per capita food increase
1	No	Yes	2	1	sI	Yes	1	1	Absent	X		X	
1*	Yes	Yes	2	1	wI	No	1	1	Absent		X		
2	No	No	2	1	sI	Yes	1	2	Absent	X		X	X
2*	Yes	No	2	1	wI	No	1	2	Absent		X		X
3	No	–	2	1	sI	No	–	–	–				
3*	Yes	–	2	1	wI	No	–	–	–				

[1] Cups with codes 1 and 2 are the focal ones were cannibalism actually occurred, cups with codes 1* and 2* are the associated ones where cannibalism was prevented by a screen. Cups with code 3 are the ones were cannibalism could, but did not occur and cups with code 3* are their associated ones.
[2] sI = strong interference competition, wI = weak interference competition.
– 'Not applicable since no cannibalism occurred.

cannibalism occurred, we also transferred the two larvae from the associated cup with screen to separate cups without screen. Despite these precautions, both groups probably not only differed in the presence of the direct effect, but also in the strength of the interference competition before cannibalism or separation. This is because interference competition may have been somewhat higher in the cups without screen where more direct physical contact was possible (codes 1–2) compared to the cups with screen (codes 1*–2*, Table 1). So, if we compare the life history of both groups of larvae that differed in the presence of cannibalism, the direct effects of cannibalism were probably underestimated because interference competition may have been initially stronger for cannibals.

To estimate the indirect effects of cannibalism, life history responses to the elimination of interference competition, we corrected the per capita food level in half of the cups after cannibalism and also in the associated cups after separation (Table 1). When interference competition ends, larvae will increase foraging in the time period brine shrimps are alive, and will eat more than their own per capita ration (M. De Block, pers. obs.). A 'food correction' meant that we kept the food ration fixed to one per capita, which implies reducing it from two to one portions per cup. So, although interference competition was eliminated, these larvae could not fully enjoy the indirect benefit by eating part of the other's food ration. In the other half of the cups, the number of portions per cup was not adjusted after cannibalism. For these larvae, the per capita food level increased from one to two portions when interference competition ended. Therefore, these cannibals and the larvae from the associated cups had the opportunity to increase food intake. Because also the larvae in the cups with food correction could increase food intake to some extent (eating more of their single portion), by comparing larvae with (codes 1–1*) and without (codes 2–2*) food correction, we probably underestimate the indirect effects of cannibalism.

Response variables

Larvae were checked daily for moults and cannibalism and we noted the date of emergence. We calculated age at emergence (development time) as the number of days from hatching until emergence. Freshly emerged individuals were sexed and mass at emergence was determined by drying individuals for 48 h at 60°C and then weighing them with an electronic balance (accuracy: 0.01 mg). Growth rate was calculated as ln(dry mass) divided by development time (Johansson et al. 2001).

Statistical analyses

We performed a loglinear analysis to test for effects of food level and photoperiod on the occurrence of cannibalism. Each cup where cannibalism could occur was a replicate here. Because the two larvae that survived in the cups where no cannibalism occurred could be of opposite sex, we could not include sex in this analysis. Instead, we tested for sex bias among the survivors in the cups where cannibalism did occur with a loglinear model including food level, photoperiod and sex. To assess the effects of food level, photoperiod and sex on the timing of cannibalism, we conducted a stepwise survival analysis (Fox 2001). As the larvae in the different categories were assumed to experience different predation risk, we applied a proportional hazard model using the procedure PHREG with the "exact ties" ties handling method in SAS version 8.02 (SAS Institute 2000). Initially, the survival analysis included a model with all main effects and their interactions. We proceeded with stepwise simplification of the model by always removing the highest-factor term that was not statistically significant (Crawley 1993). We only included those cups in the analysis where cannibalism occurred (codes 1–2, Table 1).

We tested for the effects of the presence of cannibalism (manipulated by the screen treatment) and its timing, food level, food correction and photoperiod on life history using an ANOVA approach. We included only those cups without screen where cannibalism effectively occurred with their associated ones with screen (focal cups with codes 1–2 and their associated cups with codes 1*–2*, Table 1). We excluded cups without screen where no cannibalism occurred and their associated ones (codes 3–3*, Table 1) for two reasons. First, in these cups the food correction treatment was not implemented; hence, the timing of food correction, a covariate in the analyses, was not defined. Note that for the cannibals this is also the timing of cannibalism. Second, because in these cups larvae had to endure the negative competitive effects of another larva for their entire larval life, they are not appropriate controls to make inferences about direct and indirect effects of cannibalism. For testing the direct effect (due to the extra meal); larvae reared without screen (code 3, Table 1) could be compared with cannibals with food correction (no per capita food increase after cannibalism) (code 1), but this comparison would overestimate the direct effect of cannibalism since only the cannibals (code 1) loose the strong interference competition (Table 1). For testing the indirect effect (the per capita food increase due to the elimination of a competitor), larvae reared with screen (code 3*) could be compared with larvae reared with screen and with per capita food increase (code 2*), but this comparison would overestimate the indirect effect of cannibalism since only the latter (code 2*) loose the weak interference competition (Table 1). In 87 cups

without screen cannibalism occurred, four of these cannibals died, and in three cases both associated larvae of a cup with cannibalism had died, leaving 80 cases where we had information on both the life history of the cannibal and of its associated larvae.

Initially, we tested for effects of our independent variables on life history with the timing of cannibalism (timing of food correction) as a continuous covariate. Because we consistently found interactions with this covariate, we converted this continuous covariate in a discrete variable 'period' with two levels (period 1 and period 2) as advocated by Underwood (1997). To obtain an equal number of observations in each period, all observations with cannibalism before or on day 50 were attributed to period 1, later ones to period 2. Specifically, we tested for the effects of food correction, food level, period, photoperiod, sex and cannibalism on life history (growth rate, and age and mass at emergence) with a repeated measures MANOVA (RM-MANOVA) with cannibalism as within-subjects (repeated measures) factor. As a first repeat we used the life history variables of the cannibal (cup without screen) and as a second repeat the mean for each of the life history variables of the two larvae in the associated cups with screen. In case one of these associated larvae died, we used the life history variable of the only survivor. Life history can be sex dependent in our study species (De Block and Stoks 2003). Therefore, if a larva in the associated cups had a different sex than the cannibal, we first adjusted its three life history variables by adding/subtracting the mean sex difference for each of its three life history variables separately. A general sex adjustment seemed justified and necessary as a MANOVA testing for effects of food correction, food level, period, photoperiod and sex on life history of the associated larvae showed a strong sex effect but no interactions with sex. Because we included period and sex in the analyses, we no longer had observations of each treatment combination (Fig. 1), and we only included all main effects and two-way interactions of the between-subjects factors and their interactions with the within-subjects factor in the analyses. Note that in these analyses a significant within-subjects factor, with more optimal values for life history variables of the cannibals, indicates a direct benefit of cannibalism, and a significant between-subjects factor food correction, with more optimal values in the absence of food correction (hence a per capita food increase), indicates an indirect benefit of cannibalism (above; Table 1).

Results

We never found a dead larva with signs of cannibalism (partly eaten) in a cup. All cases where a larva was missing, the other larva clearly showed the presence of a

cannibalised individual within its transparent gut. Therefore, all missing larvae could be unambiguously ascribed to cannibalism.

Cannibalism occurred in 87 (72.5%) out of 120 cups without screen. Photoperiod and food level independently determined the frequency of cannibalism (loglinear analysis, photoperiod × food level × cannibalism: $\chi^2 = 0.17$, df = 1, P = 0.68). Cannibalism occurred more frequently at the late photoperiod than at the early photoperiod (81.7% vs 63.3%; $\chi^2 = 5.27$, df = 1, P = 0.022) and more at low food than at high food (85.0% vs 60.0%; $\chi^2 = 9.57$, df = 1, P = 0.0020). We found neither sex bias among the cannibals (46 males vs 41 females, loglinear analysis, $\chi^2 = 0.27$, df = 1, P = 0.60), nor differences in the sex ratio of the cannibals in relation to food or photoperiod (both P > 0.65).

Cannibalism occurred on average after 52.5 days (SE: 1.7; range: 26–99). A survival analysis showed that the timing of cannibalism was not affected by food level, photoperiod, sex of the cannibal, or any of their interactions (all P > 0.11).

Besides cannibalism and its timing, also food correction, food level, photoperiod, sex, and several of their interactions affected the life history of the larvae (RM-MANOVA, Table 2). The significant within-subjects factor cannibalism and between-subjects factor food correction indicate the presence of a direct and indirect effect of cannibalism, respectively (methods). The effect of cannibalism interacted both with photoperiod and with the joint effect of period and food level in shaping life history. Note also that the cannibalism × food correction interaction was never significant, indicating that the benefit of the per capita food increase was similar for cannibals and associated larvae. We will discuss these effects in more detail using univariate RM-ANOVAs.

Overall, growth rate was higher at high food relative to low food (Table 2, Fig. 1A–B). This was especially true at the late photoperiod creating a significant food level × photoperiod interaction. Similarly, the absence of a food correction (hence a per capita food increase after cannibalism or separation) resulted in an increased growth rate compared to the situation with food correction (hence without such per capita food increase), especially when it occurred in period 1 (food correction × period, Table 2). On average, growth was higher when cannibalism/separation occurred in period 1, but only at the early photoperiod (period × photoperiod; effect of period, early photoperiod: $F_{1,26} = 9.34$, P = 0.0051; late photoperiod: $F_{1,32} = 1.29$, P = 0.26). Overall, cannibalism had a positive effect on growth rate. This effect was larger at the late than at the early photoperiod (cannibalism × photoperiod) and larger in period 1 than in period 2 (cannibalism × period).

Age at emergence was reduced at the late photoperiod compared to the early photoperiod and at high food

compared to low food (Table 2, Fig. 1C–D). Furthermore, the age reduction at the late photoperiod was more pronounced at high food (food level × photoperiod). The absence of a food correction (per capita food increase after cannibalism or separation) resulted in a decrease in age at emergence compared to the situation where there was a food correction (no such food increase), but only when it occurred in period 1 (food correction × period; effect of food correction, period 1: $F_{1,30} = 44.26$, P < 0.001; period 2: $F_{1,28} = 1.13$, P = 0.30). On average, males emerged before females. Compared to non-cannibals, cannibals had a lower age at emergence at the combination of low food level and period 1 (cannibalism × food level × period; effect of cannibalism, low food and period 1: $F_{1,12} = 69.42$, P < 0.001; all other combinations of food level and period: P > 0.21).

Overall, larvae had a higher mass at emergence at the early photoperiod than at the late photoperiod and at high food than at low food (Table 2, Fig. 1E–F). The absence of a food correction (per capita food increase after cannibalism or separation) resulted in a higher mass compared to the situation where there was a food correction (no such food increase). This was especially true at low food (food correction × food level) and in period 1 (food correction × period). On average, females were heavier than males. Compared to non-cannibals, cannibals had an increased mass at emergence, especially in period 1 (cannibalism × period).

Discussion

The imposed food stress, time stress and cannibalism jointly shaped the variation in age and mass at emergence. In general, larvae had a slower growth and development rate and a lower mass at emergence at low food, and a faster development and lower mass under time stress. Cannibalism occurred more frequently at the low food level and at the late photoperiod. Furthermore, cannibalism was able to accelerate life history and increase mass at emergence, but these positive effects were often context-dependent. Several effects on life history were only present or more pronounced when cannibalism occurred early. Moreover, our study shows that both direct and indirect positive effects of cannibalism were dependent on food stress and time stress.

Neither food stress nor time stress affected the timing of cannibalism, but in agreement with our prediction 4, assuming an adaptive role of cannibalism, they both increased its frequency. The higher frequency of cannibalism under food stress and time stress is in accordance with models that predict that foraging effort should increase with low food level (Sih 1984, McNamara and Houston 1994), and time stress (Werner and Anholt
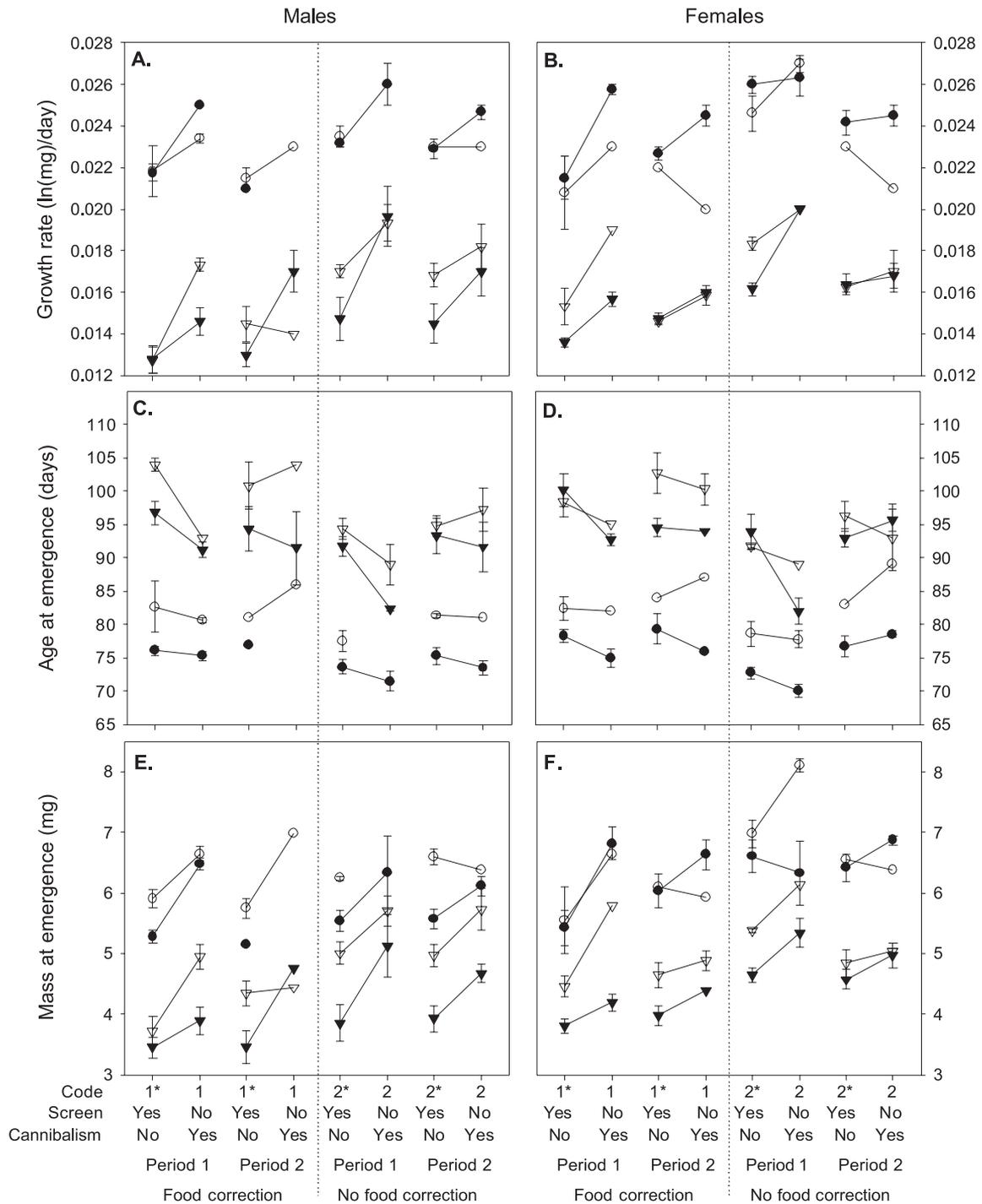
Fig. 1. The effect of cannibalism, food correction, food level, period of cannibalism, photoperiod, and sex on life history variables in *Lestes viridis*: (A–B) Growth rate, (C–D) Age at emergence, (E–F) Mass at emergence (Table 2). Circles denote high food level, triangles low food level; white symbols denote early photoperiod (low time stress), dark symbols late photoperiod (high time stress). Data are means ± 1 SE. Means of cups without screen and their associated cups with screen are connected with a solid line. For some of the treatment combinations we have only a single (no standard error) or no observations.

1993, Crowley and Hopper 1994, Abrams et al. 1996). A higher frequency of cannibalism at low food level is a general phenomenon in nature (Elgar and Crespi 1992). Several authors speculated about the higher frequency of

Table 2. RM-MANOVA and univariate RM-ANOVAs for the effects of the occurrence of cannibalism (within subject factor), food correction, food level, period of cannibalism, photoperiod and sex on growth rate and age and mass at emergence. We only included cups where cannibalism occurred and their associated cups. The first repeat was the life history of the cannibal and the second repeat was the mean life history of both larvae in the associated cups.

| Treatment | MANOVA | | | ANOVAs | | | | | | | |
| | | | | | Growth rate | | Age at emergence | | Mass at emergence | | |
	df	F	P	df	F	P	F	P	F	P
Food correction (FC)	3	17.5	<0.001	1	52.88	<0.001	24.94	<0.001	35.62	<0.001
Food level (FL)	3	282.7	<0.001	1	844.43	<0.001	571.55	<0.001	396.77	<0.001
Period (P)	3	7.5	<0.001	1	12.67	<0.001	20.48	<0.001	0.44	0.510
Photoperiod (F)	3	41.8	<0.001	1	0.02	0.889	58.90	<0.001	52.00	<0.001
Sex (S)	3	7.6	<0.001	1	0.59	0.444	8.08	0.0060	12.35	<0.001
FC × FL	3	5.4	0.0023	1	2.85	0.096	3.63	0.061	3.98	0.050
FC × P	3	4.2	0.0086	1	8.99	0.0039	7.18	0.0093	6.21	0.015
FC × F	3	3.9	0.013	1	0.56	0.458	0.35	0.556	2.88	0.094
FC × S	3	1.8	0.147	1	0.80	0.373	0.56	0.457	0.03	0.854
FL × P	3	3.7	0.016	1	1.97	0.166	0.00	0.961	0.75	0.390
FL × F	3	12.1	<0.001	1	14.08	<0.001	4.41	0.040	2.41	0.125
FL × S	3	0.9	0.456	1	0.12	0.728	0.03	0.865	1.21	0.275
P × F	3	1.8	0.155	1	4.29	0.042	2.11	0.151	3.87	0.053
P × S	3	1.4	0.242	1	3.75	0.057	3.20	0.078	0.91	0.343
F × S	3	0.4	0.720	1	0.21	0.645	0.49	0.484	0.16	0.690
Cannibalism[1] (C)	3	26.1	<0.001	1	71.53	<0.001	12.03	<0.001	70.37	<0.001
C × FC	3	0.7	0.567	1	0.98	0.326	0.17	0.682	1.49	0.227
C × FL	3	2.1	0.110	1	2.27	0.137	6.35	0.014	0.00	0.973
C × P	3	5.2	0.0029	1	12.97	<0.001	11.64	0.0011	4.84	0.031
C × F	3	5.5	0.0020	1	4.50	0.038	2.33	0.132	0.12	0.727
C × S	3	0.9	0.427	1	0.22	0.637	0.79	0.378	0.71	0.404
C × FC × FL	3	1.2	0.310	1	1.46	0.231	0.02	0.903	3.40	0.070
C × FC × P	3	0.7	0.548	1	1.18	0.281	0.29	0.589	0.35	0.559
C × FC × F	3	0.3	0.825	1	0.02	0.897	0.12	0.734	0.39	0.533
C × FC × S	3	0.3	0.847	1	0.50	0.481	0.58	0.449	0.21	0.647
C × FL × P	3	3.7	0.017	1	0.00	0.992	4.77	0.033	0.49	0.488
C × FL × F	3	1.2	0.328	1	1.80	0.184	0.54	0.465	0.43	0.517
C × FL × S	3	0.7	0.567	1	1.17	0.284	0.54	0.465	0.22	0.637
C × P × F	3	1.5	0.228	1	1.63	0.207	0.01	0.910	3.96	0.051
C × P × S	3	0.8	0.522	1	1.33	0.254	0.03	0.869	2.00	0.162
C × F × S	3	0.9	0.452	1	0.17	0.686	0.16	0.694	0.07	0.793
Error	62			64						

[1] Presence and absence of cannibalism.

cannibalism under time stress (e.g. associated with pond drying, Crump 1983, 1992, Fincke 1994, Jödicke 1997, Blaustein et al. 2001)), but only Johansson and Rowe (1999) explored the effects of manipulated time stress on cannibalism. They also found a higher frequency of cannibalism in time-stressed larvae of *L. congener*. While all studies that assume higher cannibalism in drying habitats suggested that either food shortage or high density were the proximate factors, our work and that of Johansson and Rowe (1999) suggest that under time stress cannibalism may become more frequent irrespective of other constraints.

In agreement with our ecological prediction 1, our results suggest that there are both direct and indirect benefits of cannibalism, namely an increased growth and development rate and reduced competition. Although we cannot exclude the possibility that there was a direct cost of cannibalism through increased disease transmission risk, if anything, this effect was overruled by the positive effect on life history due to the extra meal. As predicted (ecological prediction 2), both direct and indirect effects of cannibalism always depended on the timing of cannibalism, being more pronounced or only present when cannibalism occurred early. The larger indirect effect of early compared to late cannibalism can be easily explained by the fact that when cannibalism occurs early, the cannibal can enjoy the higher food intake (after the loss of interference competition) for a longer period of time (above). The larger direct effect of early cannibalism suggests that a large food item is more beneficial early in the larval life than late in the larval life. Several models and empirical studies show that life history may become resource independent at some point during development (Bradshaw and Johnson 1995, Hentschel 1999).

The two ecological constraints (food stress and time stress) affected life history in several ways. In general, independently from cannibalism, and in agreement with our ecological prediction 3, the low food level decreased growth rate and mass at emergence. As predicted by optimality models (Abrams et al. 1996, our evolutionary prediction 5) time-stressed larvae accelerated development, which, however, came at the cost of a decrease in mass at emergence. Both ecological constraints also interacted in shaping life history. Some adaptive changes in life history under time stress were easier (accelerated development) or only achievable (increased growth rate) at high food level (Johansson et al. 2001). Few studies looked at combined effects of time stress and another ecological variable on life history. Johansson et al. (2001) reported interactions between time stress and food level in shaping life history. They found in the damselfly *L. sponsa* similar life history responses to time stress at high food as in our present study. However, at low food, the time-constrained larvae unexpectedly decelerated development, and emerged at a higher mass than larvae with

no time stress. These time-stressed larvae may have favoured cohort splitting (postponed emergence until the next season, Johansson et al. 2001), which has been tentatively suggested in the field for *L. sponsa* but never for the present study species, *L. viridis* (Jödicke 1997).

The ecological constraints differentially shaped some of the direct and indirect effects of cannibalism. In agreement with our ecological prediction 2, some life history effects were only present (a reduced age at emergence (direct effect of early cannibalism)) or more pronounced (an increased mass at emergence (indirect effect of cannibalism)) at the low food level. This is in accordance with many empirical studies showing clearer benefits of cannibalism when food is more limiting (Polis 1981, Elgar and Crespi 1992, Church and Sherratt 1996). Furthermore, in accordance with our evolutionary prediction 6, the direct growth effect of cannibalism was larger when it occurred under time stress. This may reflect the phenomenon that larvae are better able to convert the extra meal into the predicted increase in growth rate under time stress when they get more food.

Future directions

We have shown that cannibalism occurs earlier or is more frequent under ecological constraints and that it may help cannibals to compensate for the negative effects of these constraints imposed on life history. Emerging early at a large size is indeed often linked with fitness advantages in animals with a complex life cycle like damselflies (Nylin and Gotthard 1998, Crowley and Johansson 2002). As such, we suggest that cannibalism may not only act as a lifeboat mechanism by enabling cannibalistic populations to survive detrimental ecological constraints (van den Bosch et al. 1988), but also as a compensatory mechanism (sensu Metcalfe and Monaghan 2001) to keep life history variables at life history transitions as optimal as possible. This view of cannibalism presents an alternative explanation for the evolution of cannibalism (Wissinger et al. 1996), besides seeing it as an extreme form of interference competition (Johnson et al. 1985, Polis 1988). More empirical work is needed to quantify the effects of cannibalism on fitness correlates at life history transitions (Wissinger et al. 1996), especially at different combinations of ecological constraints and for closely related species that differ in the ecological constraints they face. Damselflies of the genus *Lestes* are a good study group in this context because species diversified along the habitat gradient from vernal ponds to permanent fish lakes (Stoks and McPeek 2003). Preliminary results suggest that temporary ponds are the ancestral habitat (M. A. McPeek and R. Stoks, unpubl.). We are currently exploring the hypothesis that cannibalism will be higher in species that invaded habitats with more severe time stress (vernal

ponds), and lower in species that invaded habitats with less severe time stress (permanent lakes).

When evaluating the potential beneficial role of cannibalism, only looking at the direct effect of cannibalism may underestimate its net positive fitness effects. In situations where the direct effect of cannibalism is negative, for example due to parasite transfer (Pfennig et al. 1998, Pfennig 2000), cannibalism even seems maladaptive (Chapman et al. 1999). In such cases, including the indirect effect of cannibalism, which is always positive, may result in a net positive fitness balance of cannibalism. Crucial when evaluating the fitness balance for cannibalism will be the differential context-dependence of direct and indirect effects. Especially challenging will be the density-dependence of the magnitude of indirect benefits. On the one hand, the importance of the indirect benefit for the cannibal may decrease with the number of other larvae that may also benefit from the increased food supply. On the other hand, because cannibalism will be more frequent with increasing number of larvae, the indirect benefit may increase at higher density. Solving this issue will require experiments that separately quantify direct and indirect effects across a range of densities. Cannibalism is known to potentially regulate population structure and dynamics (Dong and Polis 1992, Van Buskirk 1993, Crowley and Hopper 1994, Hopper et al. 1996). Therefore, more studies should focus on the context-dependence of both effects of cannibalism to get a better picture under which conditions cannibalism is expected to be adaptive, and ultimately under which conditions cannibalism may act as a population regulating mechanism.

References

Abrams, P. A., Leimar, O., Nylin, S. et al. 1996. The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. – Am. Nat. 147: 381–395.

Altwegg, R. 2002. Predator-induced life-history plasticity under time constraints in pool frogs. – Ecology 83: 2542–2551.

Anholt, B. R. 1990. An experimental separation of interference and exploitative competition in a larval damselfly. – Ecology 71: 1483–1493.

Blaustein, A. R., Wildy, E. L., Belden, L. K. et al. 2001. Influence of abiotic and biotic factors on amphibians in ephemeral ponds with special reference to long-toed salamanders (*Ambystoma macrodactylum*). – Isr. J. Zool. 47: 333–345.

Bradshaw, W. E. and Johnson, K. 1995. Initiation of metamorphosis in the pitcher-plant mosquito-effects of larval growth history. – Ecology 76: 2055–2065.

Chapman, J. W., Williams, T., Escribano, A. et al. 1999. Fitness consequences of cannibalism in the fall armyworm, *Spodoptera frugiperda*. – Behav. Ecol. 10: 298–303.

Chapman, J. W., Williams, T., Martinez, A. M. et al. 2000. Does cannibalism in *Spodoptera frugiperda* (Lepidoptera: Noctuidae) reduce the risk of predation? – Behav. Ecol. Sociobiol. 48: 321–327.

Church, S. C and Sherratt, T. N. 1996. The selective advantages of cannibalism in a Neotropical mosquito. – Behav. Ecol. Sociobiol. 39: 117–123.

Claessen, D., Van Oss, C., de Roos, A. M. et al. 2002. The impact of size-dependent predation on population dynamics and individual life history. – Ecology 83: 1660–1675.

Corbet, P. S. 1999. Dragonflies: behaviour and ecology of Odonata. – Cornell Univ. Press.

Crawley, M. J. 1993. GLIM for ecologists. – Blackwell Scientific.

Crowley, P. H. and Hopper, K. R. 1994. How to behave around cannibals – a density-dependent dynamic game. – Am. Nat. 143: 117–154.

Crowley, P. H. and Johansson, F. 2002. Sexual dimorphism in Odonata: age, size, and sex ratio at emergence. – Oikos 96: 364–378.

Crump, M. L. 1983. Opportunistic cannibalism by amphibian larvae in temporary aquatic environments. – Am. Nat. 121: 281–289.

Crump, M. L. 1992. Cannibalism in amphibians. – In: Elgar, M. A. and Crespi, B. J. (eds), Cannibalism: ecology and evolution among diverse taxa. Oxford Univ. Press, pp. 256–276.

Day, T. and Rowe, L. 2002. Developmental thresholds and the evolution of reaction norms for age and size at life-history transitions. – Am. Nat. 159: 338–350.

De Block, M. and Stoks, R. 2003. Adaptive sex-specific life history plasticity to temperature and photoperiod in a damselfly. – J. Evol. Biol. 16: 986–995.

Dong, Q. and Polis, G. A. 1992. The dynamics of cannibalistic populations: a foraging perspective. – In: Elgar, M. A. and Crespi, B. J. (eds), Cannibalism: ecology and evolution among diverse taxa. Oxford Univ. Press, pp. 13–37.

Elgar, M. A. and Crespi, B. J. 1992. Cannibalism: ecology and evolution among diverse taxa. – Oxford Univ. Press.

Elkin, C. M. and Baker, R. L. 2000. Lack of preference for low-predation-risk habitats in larval damselflies explained by costs of intraspecific interactions. – Anim. Behav. 60: 511–521.

Fincke, O. M. 1994. Population regulation of a tropical damselfly in the larval stage by food limitation, cannibalism, intraguild predation and habitat drying. – Oecologia 100: 118–127.

Fox, L. R. 1975. Cannibalism in natural populations. – Annu. Rev. Ecol. Syst. 6: 87–106.

Fox, G. A. 2001. Failure-time analysis: studying times to events and rates at which it occurs. – In: Scheiner, S. M. and Gurevitch, J. (eds), Design and analysis of ecological experiments. Oxford Univ. Press, pp. 235–266.

Hentschel, B. T. 1999. Complex life cycles in a variable environment: predicting when the timing of metamorphosis shifts from resource dependent to developmentally fixed. – Am. Nat. 154: 549–558.

Hopper, K. R., Crowley, P. H. and Kielman, D. 1996. Density dependence, hatching synchrony, and within-cohort cannibalism in young dragonfly larvae. – Ecology 77: 191–200.

Jödicke, R. 1997. Die Binsenjungfern und Winterlibellen Europas. – Westarp.

Johansson, F. 1996. The influence of cannibalism and prey density on growth in the damselfly *Coenagrion hastulatum*. – Arch. Hydrobiol. 137: 523–535.

Johansson, F. and Rowe, L. 1999. Life history and behavioral responses to time constraints in a damselfly. – Ecology 80: 1242–1252.

Johansson, F., Stoks, R., Rowe, L. et al. 2001. Life history plasticity in a damselfly: effects of combined time and biotic constraints. – Ecology 82: 1857–1869.

Johnson, D. M. 1991. Behavioral ecology of larval dragonflies and damselflies. – Trends Ecol. Evol. 6: 8–13.

Johnson, D. M., Bohanan, R. E., Watson, C. N. et al. 1984. Coexistence of *Enallagma divagans* and *Enallagma traviatum* (Zygoptera: Coenagrionidae) in Bays Mountain Lake, Tenessee: an in situ enclosure exeriment. – Adv. Odonatol. 2: 57–70.

Johnson, D. M., Crowley, P. H., Bohanan, R. E. et al. 1985. Competition among larval dragonflies: a field enclosure experiment. – Ecology 66: 119–128.

Johnson, D. M., Pierce, C. L., Martin, T. H. et al. 1987. Prey depletion by odonate larvae: combining evidence from multiple field experiments. – Ecology 68: 1459–1465.

McNamara, J. M. and Houston, A. I. 1994. The effect of a change in foraging options on intake rate and predation rate. – Am. Nat. 144: 978–1000.

McPeek, M. A. 1998. The consequences of changing the top predator in a food web: a comparative experimental approach. – Ecol. Monogr. 68: 1–23.

McPeek, M. A., Grace, M. and Richardson, J. M. L. 2001. Physiological and behavioral responses to predators shape the growth/predation risk trade-off in damselflies. – Ecology 82: 1535–1545.

Meffe, G. K. and Crump, M. L. 1987. Possible growth and reproductive benefits of cannibalism in the mosquitofish. – Am. Nat. 129: 203–212.

Metcalfe, N. B. and Monaghan, P. 2001. Compensation for a bad start: grow now, pay later? – Trends Ecol. Evol. 16: 254–260.

Nylin, S. and Gotthard, K. 1998. Plasticity in life-history traits. – Annu. Rev. Entomol. 43: 63–83.

Nylin, S., Gotthard, K. and Wiklund, C. 1996. Reaction norms and size at maturity in *Lasiommata* butterflies: predictions and tests. – Evolution 50: 1351–1358.

Parker, H. H., Noonburg, E. G. and Nisbet, R. M. 2001. Models of alternative life-history strategies, population structure and potential speciation in salmonid fish stocks. – J. Anim. Ecol. 70: 260–272.

Pfennig, D. W. 2000. Effect of predator–prey phylogenetic similarity on the fitness consequences of predation: a trade-off between nutrition and disease? – Am. Nat. 155: 335–345.

Pfennig, D. W, Ho, S. G. and Hoffman, E. A. 1998. Pathogen transmission as a selective force against cannibalism. – Anim. Behav. 55: 1255–1261.

Pickup, J. and Thompson, D. J. 1990. The effects of temperature and prey density on the development rates and growth of damselfly larvae (Odonata: Zygoptera). – Ecol. Entomol. 15: 187–200.

Pickup, J., Thompson, D. J. and Lawton, J. H. 1984. The life history of *Lestes sponsa* (Hansemann): larval growth (Zygoptera: Lestidae). – Odonatologica 13: 451–459.

Polis, G. A. 1981. The evolution and dynamics of intraspecific predation. – Annu. Rev. Ecol. Syst. 12: 225–251.

Polis, G. A. 1988. Exploitation competition and the evolution of interference, cannibalism and intraguild predation in age/size structured populations. – In: Ebenmen, B. and Persson, L. (eds), Size-structured populations. Springer-Verlag, pp. 183–202.

Roff, D. A. 1992. The evolution of life histories: theory and analysis. – Chapman and Hall.

Roff, D. A. 2002. Life history evolution. – Sinauer Associates.

SAS Institute 2000. SAS/STAT User's Guide, Version 8. – SAS Institute Inc., Cary.

Sih, A. 1984. Optimal behavior and density-dependent predation. – Am. Nat. 123: 314–326.

Stearns, S. C. 1992. The evolution of life histories. – Oxford Univ. Press.

Stoks, R. 1998. Indirect monitoring of agonistic encounters in larvae of *Lestes viridis* (Odonata: Lestidae) using exuviae lamellae status. – Aquat. Insects 20: 173–180.

Stoks, R. 2001. Food stress and predator-induced stress shape developmental performance in a damselfly. – Oecologia 127: 222–229.

Stoks, R. and McPeek, M. A. 2003. Predators and life histories shape *Lestes* damselfly assemblages along a freshwater habitat gradient. – Ecology 84: 1576–1587.

Underwood, A. J. 1997. Experiments in ecology. – Cambridge Univ. Press.

van den Bosch, F., de Roos, A. M. and Gabriel, W. 1988. Cannibalism as a life boat mechanism. – J. Math. Biol. 26: 619–633.

Van Buskirk, J. 1993. Population consequences of larval crowding in the dragonfly *Aeshna juncea*. – Ecology 74: 1950–1958.

Werner, E. E. and Anholt, B. R. 1993. Ecological consequences of the trade-off between growth and mortality-rates mediated by foraging activity. – Am. Nat. 142: 242–272.

Wildy, E. L., Chivers, D. P., Kiesecker, J. M. et al. 2001. The effects of food level and conspecific density on biting and cannibalism in larval long-toed salamanders, *Ambystoma macrodactylum*. – Oecologia 128: 202–209.

Wissinger, S. A., Sparks, G. B., Rouse, G. L. et al. 1996. Intraguild predation and cannibalism among larvae of detritivorous caddisflies in subalpine wetlands. – Ecology 77: 2421–2430.