ANTIPREDATOR BEHAVIOR AND PHYSIOLOGY DETERMINE *LESTES* SPECIES TURNOVER ALONG THE POND-PERMANENCE GRADIENT

ROBBY STOKS[1,2] AND MARK A. MCPEEK[1,3]

[1]*Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755 USA*
[2]*Laboratory of Aquatic Ecology, University of Leuven, Ch. De Bériotstraat 32, B-3000 Leuven, Belgium*

Abstract. Identifying key traits that shape trade-offs that restrict species to only a subset of environmental gradients is crucial to understanding and predicting species turnover. Previous field experiments have shown that larvae of *Lestes* damselfly species segregate along the entire gradient of pond permanence and predator presence and that differential predation risk and life history constraints together shape their distribution. Here, we report laboratory experiments that identify key differences in behavior and physiology among species that structure their distributions along this gradient. The absence of adaptive antipredator behavioral responses against large dragonfly larvae and fish of *Lestes dryas*, the only species to inhabit predator-free vernal ponds that dry each year, is consistent with its high vulnerability to predation and probably the key trait that excludes it from parts of the gradient with predators. The reciprocal dominance of two other *Lestes* species in permanent waters dominated by either dragonflies or fish can be explained by the lack of effective antipredator behaviors against dragonflies and fish, respectively. Maximal growth rates did not differ among *Lestes* along the gradient. However, in the natural predator environment of vernal ponds (only conspecific cannibals), the vernal-pond *Lestes* had higher growth rates than the other *Lestes* suggesting that this excludes other *Lestes* from vernal ponds. Similarly, *Lestes* species that inhabit temporary ponds (i.e., ponds that dry intermittently every few years but not every year) had a higher growth rate than the fishless permanent-pond *Lestes* in the presence of the syntopic dragonfly predator. These growth differences among *Lestes* in predator treatments were not due to differences in food intake, but due to differences in physiology. The vernal-pond *Lestes* converted more assimilated food into body mass compared to the other *Lestes* in the presence of conspecific larvae, and the temporary-pond *Lestes* had a higher conversion efficiency than the fishless permanent-pond *Lestes* in the presence of the syntopic dragonfly predators. In contrast, reductions in growth rate within species in the presence of syntopic predators were both physiologically and behaviorally mediated. The interplay between behavior and physiology may be a common feature of the growth/predation-risk trade-off, and their joint study is therefore critical to mechanistically link phenotype, performance, and community assembly along the freshwater habitat gradient.

Key words: antipredator behavior; community assembly; damselfly; environmental gradient; hydroperiod; life history; physiological stress; predation risk; trade-offs.

INTRODUCTION

Only a few fundamental fitness trade-offs seem to underlie species turnover along environmental gradients (Tilman 1988, Wellborn et al. 1996). If one can identify key traits that determine the outcome of these trade-offs one may generalize across taxa and predict species occurrence along gradients (Tilman 1987, Werner and McPeek 1994, Smith and Van Buskirk 1995). The freshwater habitat gradient from small ephemeral ponds to large permanent lakes is a gradient along which species within many taxa segregate (Wellborn et al. 1996). Species occurrence is mainly shaped by the ability to avoid the conflicting demands of pond drying and predation, hence by the trade-off balancing

growth rate and predation risk (Wilbur and Collins 1973, Werner and Anholt 1993, Wellborn et al. 1996).

Empirical studies identified behavior as a key trait linked to the growth/predation risk trade-off. Higher activity levels typically result in higher foraging returns, but also in more exposure to and a greater likelihood of detection by the predator (Werner and Anholt 1993). Baseline activity levels and behavioral responses to predators translate into ecological performance (growth rate and mortality by predation) in field experiments (e.g., Skelly 1995, Relyea and Werner 1999, Wissinger et al. 1999). Therefore, behavioral responses of individuals can explain community properties (Werner 1992, 1998, Werner and Anholt 1996).

However, other studies have shown that behavioral differences among species may not always translate into growth differences. For example, Anholt et al. (2000) report that activity levels were higher in green

[3] Corresponding author. E-mail: mark.mcpeek@dartmouth.edu

frog larvae (*Rana clamitans*) than in wood frog larvae (*R. sylvatica*) while mass gain was higher in the latter. McPeek et al. (2001) showed that, when reared in isolation, *Enallagma* species living in fish lakes ingested more food and had higher growth rates than *Ischnura* damselfly species. However, in the presence of predators foraging rates among both groups were similar while *Ischnura* had significantly higher growth rates. These differences were due to differential responses in physiology to the presence of predators (McPeek et al. 2001). The behaviorally mediated growth/predation risk trade-off can therefore be partly uncoupled by physiological differences among species.

The objective of the present paper is to test whether differences in behavior and physiology jointly contribute to the performance (i.e., growth rate and survival) and turnover of *Lestes* species (Hexapoda: Odonata) along the freshwater habitat gradient. Differential susceptibility to predators and life history constraints are the key ecological mechanisms restricting species to different parts of the gradient (Stoks and McPeek 2003). *L. dryas* is the only species able to occupy vernal ponds that dry each summer. Predation by large dragonflies and fish excludes *L. dryas* from the rest of the gradient. Four species (*L. congener*, *L. disjunctus*, *L. forcipatus*, and *L. rectangularis*) dominate temporary ponds that dry in late summer in some, but not every, year and where large dragonfly larvae are the top predators. Their longer larval period excludes these temporary-pond *Lestes* from vernal ponds, and intraguild predation by large permanent-pond *Lestes* prevent them from occupying permanent water bodies. Finally, two species are restricted to permanent water bodies because they have no overwintering egg stage and an aquatic larval stage of almost a year. *L. eurinus* dominates fishless water bodies where large dragonfly larvae are the top predators, but is excluded from fish-containing water bodies by fish predation. Likewise, *L. vigilax* dominates water bodies where fish are the top predators and is excluded from fishless waters by dragonfly predation. We expect higher growth rates in *Lestes* species occupying the more temporary end of the gradient (Arendt 1997), which can be achieved through higher activity rates and thus higher ingestion rates or higher conversion of ingested food into body mass (Slansky and Rodriguez 1987). Because predation is the other key agent restricting species along the gradient, we expect species to reduce activity only in the presence of syntopic predators (McPeek 1990*b*, Relyea 2001).

METHODS

Behavior under differential predation risk

A first behavioral experiment was conducted to test whether *Lestes* species at different positions on the freshwater habitat gradient differed in activity level and predator-induced behavioral plasticity, thereby closely following the procedure of McPeek (1990*b*). The larval behaviors of seven *Lestes* species were observed for 20 min in small tanks in the presence of (1) no predators, (2) three *Anax* dragonfly larvae, or (3) one *Lepomis gibbosus* sunfish. One *Lestes* larva was placed in a transparent inner compartment of the tank (10.0 cm × 10.5 cm) and could see and smell predators present in the surrounding outer compartment (34.5 cm × 24.0 cm with the inner compartment enclosed inside within this space against one wall: for a full description see McPeek 1990*b*). Each replicate started with 60 *D. pulex* in the inner compartment to serve as prey for the *Lestes* larva. A laptop computer was used to record 16 behaviors of the damselfly larvae. Walking was defined as a change in position on the substrate when a larva moved its legs. Swimming was defined as a larva leaving the bottom substrate and moving through the chamber by swinging its abdomen and caudal lamellae. *Lestes* used swimming to chase prey. Advancing toward prey was defined as a walk to chase a *Daphnia*. For each of these three behaviors, we determined not only their frequency but also total, mean, and maximum duration. Orienting toward prey was defined as a larva turning its head or body toward a *Daphnia* without changing its position on the substrate. We separately scored unsuccessful strikes at the *Daphnia* prey and successful strikes (i.e., captures). Further, we scored the duration of the longest motionless period. Each treatment was replicated eight times for *L. congener*, *L. dryas*, *L. eurinus*, *L. rectangularis*, and *L. vigilax*; six times for *L. forcipatus*; and three times for *L. disjunctus*.

Statistical analysis.—We first extracted principal component scores from the correlation matrix of the original ln(*x* + 1)-transformed behavioral variables (Sokal and Rohlf 1995). The resulting axes were then rotated using the normalized varimax method to aid their interpretation. First, we looked for differences in baseline activity (i.e., activity in the absence of predators) among the four species groups along the gradient: (1) vernal-pond *L. dryas*; (2) temporary dragonfly-pond *L. congener*, *L. disjunctus*, *L. forcipatus*, and *L. rectangularis*; (3) permanent dragonfly-pond *L. eurinus*; and (4) permanent fish-pond *L. vigilax*. We performed multivariate analyses of variance (MANOVAs) on the principal components scores. We expected the vernal-pond *L. dryas* to have the highest baseline activity, and for baseline activity to decline across groups from vernal ponds to permanent fish ponds (Wellborn et al. 1996). We tested this ordered a priori prediction about group differences using an a priori linear contrast (Sokal and Rohlf 1995). These analyses were imbalanced, because all habitat groups except the temporary dragonfly-pond group contained one species. Therefore, we performed the MANOVA with only one of these four temporary, dragonfly-pond *Lestes* included. This approach is warrantable because the four temporary-pond *Lestes* did not differ in the four be-
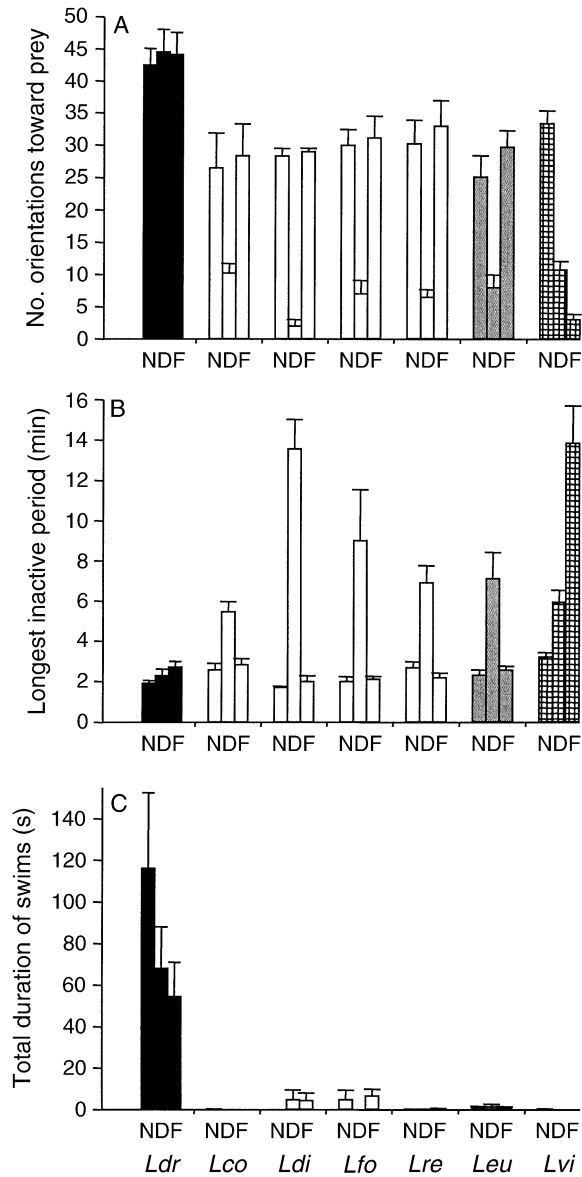
FIG. 1. Selected behavioral variables of the seven *Lestes* species in the behavior experiment under differential predation risk. The four ecological groups are identified as follows: the vernal pond *Lestes* by black bars, the temporary dragonfly-pond *Lestes* by open bars, the permanent dragonfly-pond *Lestes* by gray bars, and the permanent fish-water *Lestes* by hatched bars. Means + 1 SE are shown for each species in the no-predator (N), dragonfly (D), and fish (F) treatments. Species abbreviations: *Lco* = *L. congener*, *Ldi* = *L. disjunctus*, *Ldr* = *L. dryas*, Leu = *L. eurinus*, *Lfo* = *L. forcipatus*, *Lre* = *L. rectangularis*, *Lvi* = *L. vigilax*.

havioral principal component axes in the absence of a predator (MANOVA, species effect; $F_{12,48} = 1.64$, $P = 0.11$; Fig. 1), and the conclusions drawn did not depend on which temporary dragonfly-pond *Lestes* was included. If the overall MANOVA was significant, we examined the univariate ANOVAs to identify the behaviors that differed among the groups (results from these ANOVAs were completely consistent with interpretations based on the canonical coefficients derived from the MANOVA).

Since we expected species to react only or more strongly to their syntopic predators, we tested whether responses to predators differed among species with a different natural predator environment (no predators, *Anax*, or dragonfly larvae and *Lepomis*). Note that the four temporary-pond *Lestes* and the one permanent dragonfly-pond *Lestes* have the same predator environment (*Anax*), which would make the analysis very imbalanced. These five species did not differ in their response to the predators (MANOVA, species × predator effect; $F_{32,300} = 1.42$, $P = 0.072$; Fig. 1). Therefore, we performed the MANOVA testing for differences in the response to predators among species with a different natural predator environment with only one of these five species coexisting with *Anax* included. Again, the conclusions drawn did not depend on which dragonfly-pond *Lestes* was included.

Because we had different a priori hypotheses about the behavioral responses to predators depending upon the natural predator environment, we performed separate analyses for species from the three different predator environments. Because *L. dryas* does not coexist with large dragonfly larvae or fish we predicted that this species would not alter their behavior in either predator's presence. For this species, one contrast tested for behavioral differences between the no predator treatment and the combined responses in the dragonfly and fish treatments and a second contrast tested for differences between the dragonfly and fish treatments. The temporary dragonfly-pond *Lestes* and the permanent dragonfly-pond *Lestes* only coexist with large dragonfly larvae, and we predicted that they would only recognize and respond behaviorally only to dragonfly larvae. For these species, we tested the contrast of the dragonfly treatment vs. the combined responses in the no predator and fish treatments, and the contrast of the no predator vs. fish treatments. Finally, *L. vigilax* from permanent fish ponds coexists with both dragonfly larvae and fish, and therefore was expected to recognize and respond behaviorally to both predators. For this species, we therefore used the same contrasts as for *L. dryas*.

Behavior in response to attacking dragonfly

The previous experiment quantifies the behaviors of species when predators are imminently threatening but cannot actually attack. To quantify the response of *Lestes* larvae to an approaching and attacking dragonfly larva, we exposed *Lestes* larvae of the same species with a free ranging *Anax junius*. We closely followed the methodology of McPeek (1990*b*). We recorded the number of times a *Lestes* larva walked away or swam away from an approaching dragonfly and the number of times the dragonfly came within 2 cm (i.e., the typical strike distance for a final-instar *Anax*) of a *Lestes*

larva without the *Lestes* larva moving. Ten final instar *Lestes* were placed in a glass bowl (20 cm diameter), the bottom of which was covered with screening to provide footing for the odonates. After one hour of acclimation, we added one final-instar *Anax* that had been starved for two days. We monitored the behavior of the *Lestes* larvae for 30 min as the *Anax* foraged. We performed nine trials each for *L. congener*, *L. dryas*, *L. eurinus*, and *L. vigilax*.

Statistical analysis.—For each replicate, we calculated the relative frequency of the three behaviors (i.e., do nothing, walk away, swim away). We then tested for differences between the four *Lestes* species in the relative frequencies of these three behaviors using one-way MANOVAs with species as the independent variable. Because the relative frequencies of these three behaviors sum to one for each replicate, we only used the relative frequencies of not moving and swimming away. Relative frequencies were arcsine transformed prior to analysis (Sokal and Rohlf 1995).

Previous work on *Enallagma* damselfly larvae has shown that species co-occurring with *Anax* swim away from an approaching predator, while species co-occurring with fish do not move away from attacking predators (Pierce et al. 1985, McPeek 1990*b*). Therefore, we expected that *L. congener* and *L. eurinus*, who naturally co-occur with *Anax*, would swim away, while *L. vigilax*, the permanent fish-pond species, would most frequently not move when approached. *L. dryas* does not encounter predators in the vernal ponds it occupies; we therefore had no a priori expectation for how it would respond to an approaching dragonfly. Therefore, we could not set a priori contrasts in the MANOVA, and will report Duncan post hoc tests.

Growth in isolation

We conducted a growth experiment to quantify larval growth rates when reared under optimal conditions in terms of predation risk (complete isolation from all mortality threats) and food availability (ad libitum). Moreover, we examined differences among species in behavioral and physiological variables contributing to growth rate. We included four species to cover the entire freshwater habitat gradient: *L. dryas* (vernal ponds), *L. rectangularis* (temporary ponds), *L. eurinus* (fishless permanent water bodies), and *L. vigilax* (fish-containing water bodies). For each species we monitored the growth of 10 larvae for four days. To disentangle the contributions of foraging effort and physiology in shaping growth rates, we quantified both behavioral (food intake) and physiological variables (assimilation and conversion efficiency). The methodology closely followed that of McPeek et al. (2001).

Initial wet masses of larvae were measured using an Ohaus electrobalance (Ohaus, Florham Park, New Jersey, USA) to the nearest 0.01 mg after gently blotting them dry with tissue paper. Each larva was held in a 20-mL glass vial, and vials were held in trays separated from one another by cardboard dividers; larvae could therefore not see any other larva during the experiment. Each day, each larva was given a ration of 30 *D. pulex* of standardized size. After 4 d, the wet mass of each larva was again determined, and the larva was then dried for >24 h at 63°C in a drying oven to determine the larva's final dry mass. Species did not differ in the relationship between dry and wet masses ($P > 0.38$ for differences in slopes of the dry mass–wet mass regressions among species). Therefore, we used one overall conversion factor to translate initial wet masses into dry masses (i.e., dry mass = 0.1496 × [wet mass], $n = 40$). Growth rate was calculated as [$\log_e$(final dry mass) − $\log_e$(initial dry mass)]/4 d. This measure of growth is independent of initial larval wet mass (regressions of growth against initial wet mass had slopes not different from zero for each species [all $P > 0.18$]).

To quantify digestive variables, we determined dry masses of given food rations, uneaten food, and fecal pellets. The amount of food ingested was estimated as ([total dry mass of food rations given] − [total dry mass uneaten food]). The amount of food assimilated was estimated by subtracting the total dry mass of fecal pellets from the total amount of food ingested. Assimilation efficiency was calculated as ([amount of food assimilated]/[amount of food ingested]); conversion efficiency was calculated as ([gain in dry mass by the larva]/[amount of food assimilated]) (see Scriber and Slansky 1981, Slansky and Rodriguez 1987).

Statistical analysis.—We tested for differences among the four *Lestes* species in growth rate and the three digestive variables (amount of food ingested, assimilation efficiency, conversion efficiency) using a MANOVA with species as the independent variable. Because the three digestive variables completely account for growth rate, we include all but assimilation efficiency in the MANOVA. We were expecting *Lestes* species to have decreasing growth rates with increasing habitat permanence and given the expected lower baseline foraging rates in fish-containing water bodies compared to fishless water bodies an even lower growth rate in the fish-containing permanent-water *Lestes*. To test this we set the same a priori linear contrasts as described in *Behavior under differential predation risk*.

Growth under differential predation risk

In a second growth experiment, we studied growth rates and their behavioral and physiological underpinnings under three different predator treatments: (1) no predators, (2) six dragonfly larvae, or (3) one pumpkinseed sunfish. Again, the methodology closely followed that of McPeek et al. (2001). Larvae were reared in individual glass vials (20 mL) floating in nine 38-L aquaria (three per treatment) that contained the predators. Four vials were floated in each aquarium. Each larva was randomly reassigned daily to one of the three aquaria with its predator treatment. Damselfly larvae could see predators through the glass vials and could

TABLE 1. Contrast analyses testing for differences in the rotated behavioral principal components (A) between *Lestes* species groups in the absence of predators, and (B) between predator treatments in the behavior experiment under differential predation risk.

| | | Univariate analyses of variance | | | |
Contrast†	MANOVA	PC1	PC2	PC3	PC4
A) Between species groups in the absence of predators‡					
1. Linear contrast	19.57***	0.17	1.17	76.39***	1.15
B) Between predator treatments					
Lestes coexisting with no predators§					
2. *Ldr*: NoPred vs. Other	2.90¶	...	...	...	...
3. *Ldr*: *Anax* vs. *Lepomis*	1.30	...	...	...	...
Lestes coexisting with large dragonfly larvae‖					
4. *Lco/Ldi/Lfo/Lre/Leu*: *Anax* vs. Other	66.16***	227.29***	0.19	5.53*	1.11
5. *Lco/Ldi/Lfo/Lre/Leu*: NoPred vs *Lepomis*	1.85	...	...	...	...
Lestes coexisting with fish and small dragonfly larvae§					
6. *Lvi*: NoPred vs. Pred	23.72***	102.61***	0.27	4.67*	3.75¶
7. *Lvi*: *Anax* vs. *Lepomis*	15.03***	54.45***	1.43	0.00	0.01

  † Species abbreviations: *Lco* = *L. congener*, *Ldi* = *L. disjunctus*, *Ldr* = *L. dryas*, *Leu* = *L. eurinus*, *Lfo* = *L. forcipatus*, *Lre* = *L. rectangularis*, *Lvi* = *L. vigilax*.
  ‡ *F*-values from univariate analyses of variance with df = 1, 28; MANOVA with df = 4, 25.
  § ANOVA, df = 1, 21; MANOVA, df = 4, 18.
  ‖ ANOVA, df = 1, 84; MANOVA, df = 4, 81.
  ¶ $0.10 > P > 0.05$; * $0.05 > P \geq 0.01$; ** $0.01 > P \geq 0.001$; *** $P < 0.001$.

smell them via water exchange. Also, unlike the first experiment, each individual could also see the other damselflies in the aquarium. *Lestes* larvae are canni-balistic (e.g., Stoks 1998), and visual contact among larvae has been shown to reduce growth rates in *En-allagma* damselfly larvae and to generate patterns of relative growth rates as found in the field (McPeek et al. 2001). Larvae were handled as in the previous ex-periment, and we collected the same variables and cal-culated the same behavioral and physiological param-eters as in the first growth experiment. We performed ten replicates of each predator treatment for each of the four species used in the previous experiment, giving a total of 120 larvae.

Statistical analysis.—We examined hypotheses about species differences and predator treatment dif-ferences in a two step approach (for details see *Meth-ods: Behavior under differential predation risk*). First, a linear contrast was used to look for ordered differ-ences among the four *Lestes* that each live in a different habitat with contrasting hydroperiod and predator en-vironment. Second, we tested whether *Lestes* species with a different natural background predator environ-ment differed in their responses to predators.

RESULTS

Behavior under differential predation risk

Interpreting the principal components.—The first four principal components summarized 91% of the var-iation in the original behavioral data set (Appendix A). PC1 explained 24% of the variation and was highly positively correlated with variables describing foraging effort and negatively correlated with the duration of the longest inactive period spent motionless. PC2 and PC3 explained each 24% of the variation and were strongly positively associated with all walking and all swimming variables, respectively. PC4 explained 15% of the variation and was highly positively correlated with the mean and maximum duration of advances to-wards prey and to a lesser degree with the total time advancing toward prey.

Species group differences in the absence of preda-tors.—In the absence of predators, overall activity level decreased going from the vernal-pond *L. dryas* toward the fish-pond *L. vigilax* (MANOVA: linear contrast, Table 1). The univariate ANOVAs showed that this was entirely due to a higher swimming activity toward prey in the vernal-pond species (Table 1, Fig. 1C).

Responses of species groups to predators.—Species with a different natural predator environment also dif-fered in their behavioral responses to these predators (MANOVA, species × predator effect; $F_{16, 184} = 6.06$, $P < 0.001$; Fig. 1, Appendix B). The vernal-pond *L. dryas* did not significantly react to the presence of ei-ther predator. The temporary dragonfly-pond *Lestes* and the permanent dragonfly-pond *Lestes* all strongly re-acted to the presence of dragonflies but did not react to the presence of fish (MANOVAs, contrasts 2–3, Ta-ble 1). Their responses to dragonflies compared to their response in the no predator and fish treatments were most pronounced for decreasing foraging (PC1, AN-OVA, contrast 4, Table 1; Fig. 1A, Appendix B). The significance of the contrast for PC3 suggests that over-all these species also decreased swimming toward prey in the presence of dragonflies (Fig. 1C).

The permanent fish-pond *L. vigilax* responded sig-nificantly to the presence of both dragonfly and fish predators (MANOVA, contrast 6, Table 1). *L. vigilax*
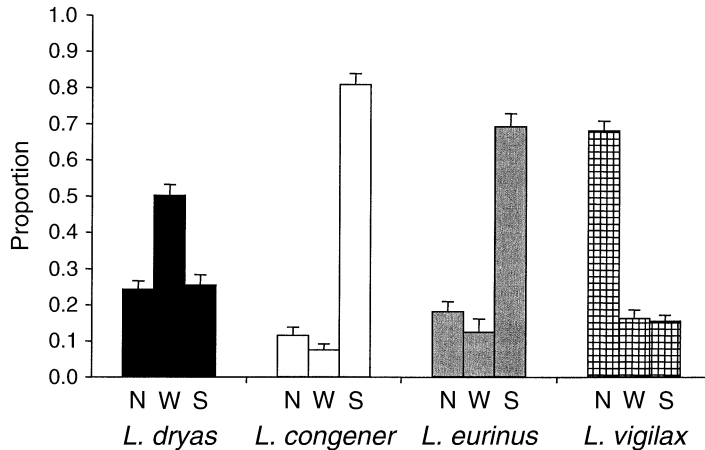
Fig. 2. Behavior of the four *Lestes* species when approached by an *Anax* predator in the "behavior in response to attacking dragonfly" experiment. Means + 1 SE are shown for each species for the behaviors no move (N), walk (W), and swim (S).

greatly reduced the number of orientations, the number and total duration of advances toward prey, the number of strikes and prey captures, while increasing the duration of the longest inactive period (PC1, ANOVAs, contrast 6, Table 1; Fig. 1A and B, Appendix B). *L. vigilax* responded more strongly to the presence of fish than to dragonflies, primarily because of reduced foraging and responsiveness to prey (MANOVA, contrast 7, Table 1, Fig. 1A and B, Appendix B).

Behavior in response to attacking dragonfly

When approached by the *Anax* dragonfly predator the four *Lestes* showed different behaviors (MANOVA, $F_{6,62} = 50.53$, $P < 0.0001$). *L. dryas* showed fundamentally different behaviors compared to all other *Lestes* (Duncan tests, all $P < 0.03$). *L. dryas* most often tried to walk away from an approaching dragonfly (Fig. 2). The two *Lestes* co-occurring with *Anax* (*L. congener* and *L. eurinus*) had similar behavioral responses, most frequently swimming away ($P = 0.21$). The fish-lake *L. vigilax* also differed from all three other *Lestes* (all $P < 0.001$); *L. vigilax* most frequently did not move away from an attacking dragonfly.

No *Lestes* larvae escaped a dragonfly attack when not moving or when walking away. Escape success by swimming away was 60% and did not differ among species (loglinear analysis, $\chi^2 = 4.80$, df = 3, $P > 0.19$). As a result, mean mortality by dragonfly predation was higher in *L. dryas* (7.8 ± 1.0 [mean ± 1 SE]) than in all other studied *Lestes* (Duncan test, all $P < 0.01$). The two *Lestes* co-occurring with *Anax* dragonflies (*L. congener* and *L. eurinus*) had very similar and low mortality rates, *L. congener* (3.3 ± 0.5 larvae/replicate) and *L. eurinus* (2.7 ± 0.6 larvae/replicate) ($P = 0.57$). The mortality rate of *L. vigilax* (4.8 ± 0.5 larvae/replicate) was somewhat intermediate, being higher than *L. eurinus* ($P < 0.04$) and not different from *L. congener* ($P = 0.09$).

Growth in isolation

The MANOVA indicated that growth rates and digestive variables did not differ significantly among the four studied *Lestes* species when grown in the complete isolation of all mortality threats (linear contrast, $F_{3,34} = 1.23$, $P = 0.31$; Appendix C).

Growth under differential predation risk

Species group differences in the absence of heterospecific predators.—In contrast to the first growth experiment where larvae were raised in isolation, the MANOVA showed decreasing growth rates and digestive variables going from the vernal-pond *Lestes* to the permanent-pond *Lestes* (contrast 1, Table 2). This pattern of reduced growth rates going to the more permanent part of the gradient could not be explained by differences in the amount of food ingested, or by differences in assimilation efficiency, but was due to lower conversion efficiencies (ANOVAs; contrast 1, Table 2, Fig. 3).

Responses of species to predators.—The response in growth rate and digestive variables to predators differed among the four *Lestes* species (MANOVA, predator × species effect; $F_{6, 108} = 3.27$, $P < 0.01$; Fig. 3). The vernal-pond *L. dryas* did not respond to the presence of dragonflies or fish with decreases in growth rate or changes in any of the digestion variables (MANOVA: contrasts 2 and 3, Table 2, Fig. 3). For the two *Lestes* co-occurring with dragonflies, *L. rectangularis* and *L. eurinus*, growth rates were on average 40% lower when these *Lestes* were reared in the presence of dragonflies than when reared in the absence of predators or in the presence of fish (MANOVA; contrast 4, Table 2, Fig. 3A). This growth reduction was due to both decreased ingestion of food (−24%) and decreased conversion of assimilated food into body mass (−30%) (Table 2, Fig. 3B and D). The MANOVA also indicated a difference between the no predator and fish treatments, which was due to a reduction of the amount of food ingested in the presence of the fish (−14%) (contrast 5, Table 2, Fig. 3B). However, this decreased ingestion rate did not result in a reduced growth rate. The permanent fish-lake *L. vigilax* had a reduced growth rate (−40%) in the presence of both dragonflies

TABLE 2. Contrast analyses testing for differences in growth rates and digestive variables (A) between *Lestes* species groups in the absence of predators, and (B) between predator treatments in the growth experiment under differential predation risk.

| | | | Univariate ANOVAs‡ | | |
| | | | | Digestive variables | |
Contrast†	MANOVA	Growth rate	Food ingested	Assimilation efficiency	Conversion efficiency
A) Between species groups in the absence of heterospecific predators§					
1. Linear contrast	8.66***	19.08***	0.31	0.00	5.49*
B) Between predator treatments					
Lestes coexisting with no predators‖					
2. *Ldr*: NoPred vs. Other	1.88	...	...	...	...
3. *Ldr*: *Anax* vs. *Lepomis*	0.99	...	...	...	...
Lestes coexisting with large dragonfly larvae¶					
4. *Lre/Leu*: *Anax* vs. Other	22.59***	27.70***	20.11***	0.36	7.25*
5. *Lre/Leu*: NoPred vs. *Lepomis*	3.46*	0.14	5.51*	0.01	2.69
Lestes coexisting with fish and small dragonfly larvae‖					
6. *Lvi*: NoPred vs. Pred	3.29*	10.63**	4.46*	0.97	1.46
7. *Lvi*: *Anax* vs. *Lepomis*	0.50	...	...	...	...

† Species abbreviations are given in Table 1.
‡ Univariate ANOVAs are only reported when the MANOVA was significant.
§ F values from univariate analyses of variance with df = 1, 36; from MANOVA with df = 3, 34.
‖ ANOVA, df = 1, 27; MANOVA, df = 3, 25.
¶ ANOVA, df = 1, 57; MANOVA, df = 3, 55.
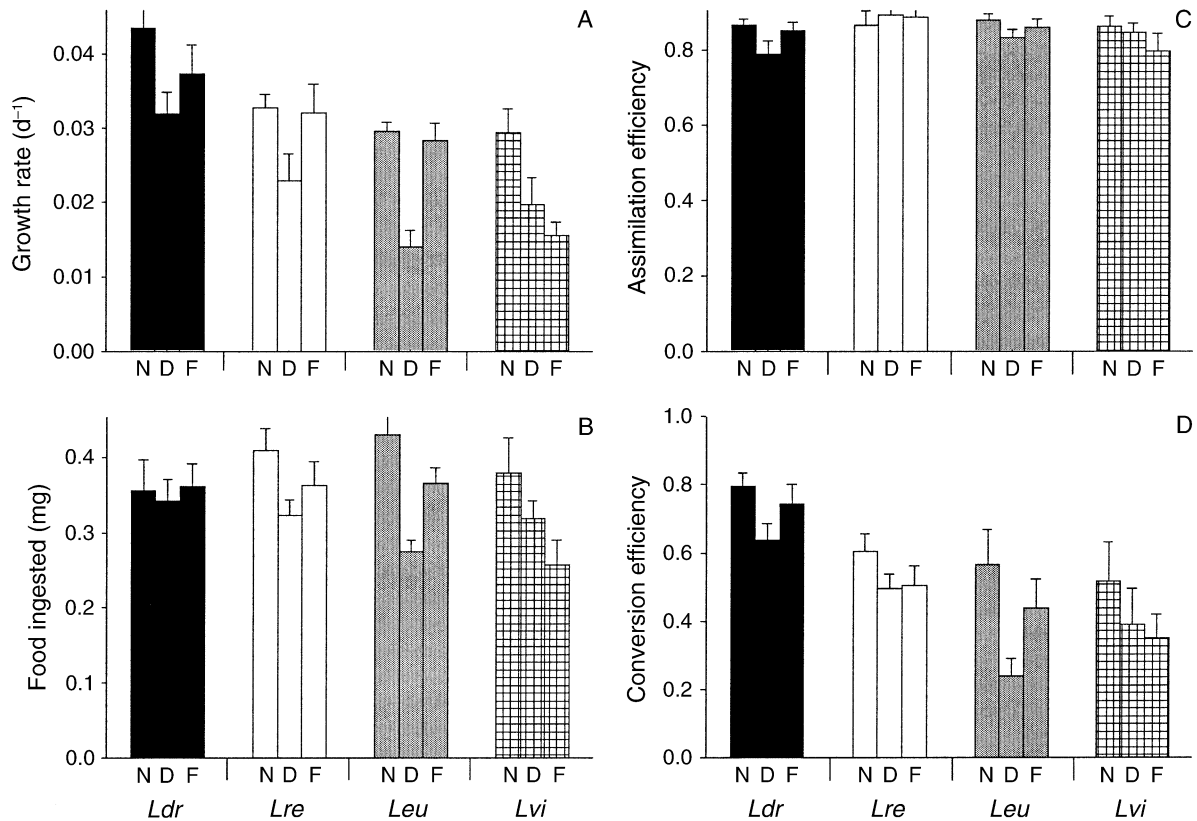* $0.05 > P \geq 0.01$; ** $0.01 > P \geq 0.001$; *** $P < 0.001$.

FIG. 3. (A) Growth rates and (B, C, D) digestive variables of the four *Lestes* studied in the growth experiment under differential predation risk. Means + 1 SE are shown for each species in the no-predator (N), dragonfly (D), and fish (F) treatments. The coding of the bars of the four species and the species abbreviations are given in Fig. 1.

and fish, which was caused primarily by a reduction in the amount of food ingested (-24%) (MANOVA; contrast 6, Table 2, Fig. 3). No differences in growth or digestive variables between the dragonfly and fish treatments were detected (MANOVA; contrast 7, Table 2, Fig. 3).

Discussion

Lestes species segregate along the extent of the freshwater habitat gradient from vernal ponds that lack predators, through temporary and permanent waters that have large dragonflies as top predators, and permanent waters with fish as top predators. Differences in predation risk and life history are the structuring mechanisms shaping these changes in *Lestes* species composition (Stoks and McPeek 2003). The results of this study identify key phenotypic traits that drive these mechanisms of species turnover along the gradient. The emerging pattern is that behavioral differences cause differences in vulnerability to predation, and that both behavioral and physiological responses to predators cause growth differences among *Lestes* groups along the gradient.

A general pattern across experiments was that *Lestes* species only responded to the presence of predators with which they coexist. All species decreased their movement and responsiveness to prey in the presence of coexisting predators; these behavioral responses should decrease their conspicuousness to predators and thus increase their survival when predators are threatening. *L. dryas*, which lives in vernal ponds without predators, showed no behavioral response toward large dragonflies or fish (Figs. 1 and 3B), did not commonly swim away from an approaching dragonfly (Fig. 2), and suffered the highest mortality by predation in the behavior in response to attacking dragonfly experiment. Consistent with these laboratory results, *L. dryas* suffered higher mortality by dragonfly predation than that suffered by temporary dragonfly-pond *Lestes* in field experiments in natural ponds (Stoks and McPeek 2003). Taken together, these results show that *L. dryas* is restricted to the most temporary part of the freshwater habitat gradient (i.e., vernal ponds) because it lacks adaptive behavioral responses to reduce predation by dragonflies and fish.

Lestes species in both temporary and permanent dragonfly-ponds coexist with large dragonfly larvae and not with fish, and accordingly reacted strongly only to the presence of dragonflies by decreasing their movement, feeding and responsiveness to prey (Figs. 1 and 3B, Appendix B). Similar decreases in activity and foraging in the presence of a perceived predator have been reported in other *Lestes* (Jeffries 1990, Stoks 1998, Stoks and Johansson 2000, Johansson et al. 2001), other damselflies (Baker 1981, Pierce et al. 1985, McPeek 1990a, Stoks et al. 2003) and are generally expressed by many other prey (review in Lima and Dill 1990, Lima 1998). These behavioral responses should in-

crease survival in the presence of predators (i.e., be adaptive), because movement attracts the attention of predators and thus increases the rate at which prey are detected by predators (e.g., Jakobsson et al. 1995, Skelly 1995). For example, predators are much more likely to detect and strike at damselfly larvae when they are moving than when they remain motionless (Baker et al. 1999, Elkin and Baker 2000). Also, damselfly larvae with higher foraging rates have higher mortality rates from predation (Stoks and Johansson 2000). Once detected and approached by the dragonfly, these *Lestes* most frequently used swimming to evade attacking dragonflies (Fig. 2). *Enallagma* damselflies that also inhabit permanent dragonfly-ponds are known to have recently adapted to dragonfly predation by adopting swimming as an evasive tactic and evolving morphological, behavioral, and biochemical traits that greatly increased their swimming speed (McPeek 1995, 1997, 1999, 2000, McPeek et al. 1996, McPeek and Brown 2000).

Finally, *L. vigilax*, which lives with both dragonflies and fish in permanent ponds and lakes, responded to the presence of both of these predator types by decreasing their movement and responsiveness towards prey (Figs. 1 and 3B, Appendix B). Fish are undoubtedly the top predators in fish lakes, and the dragonflies that inhabit fish lakes are smaller and less active than those that dominate fishless waters (McPeek 1990a, 1998, Werner and McPeek 1994). Accordingly, *L. vigilax* generally decreased activity more when confronted with fish than with dragonflies (Fig. 1A and B, Appendix B). *L. vigilax* also responded to attacking dragonflies most frequently by remaining motionless (Fig. 2). This is the appropriate response to an attacking dragonfly in a habitat where fish are present. Fish are much more effective at capturing *Lestes* than dragonfly larvae; in a series of laboratory trials, not a single *Lestes* escaped after detection by *Lepomis* sunfish (Stoks and De Block 2000). Second, dragonfly larvae from fish lakes are less active and smaller than those that are restricted to fishless water bodies by fish predation (McPeek 1990a, 1998, Stoks and McPeek 2003). Therefore, for *L. vigilax* it is most crucial to avoid being detected by fish, and swimming away from dragonfly larvae may seriously increase their chances of being detected by fish (Baker et al. 1999, Elkin and Baker 2000). McPeek (1990b) reports similar differences in the use of swimming as an evasive tactic among *Enallagma* damselflies living in dragonfly- and fish-containing lakes. This difference in evasive tactics toward an approaching dragonfly can explain the higher mortality of *L. vigilax* as compared to *L. eurinus* in the behavior to attacking dragonfly experiment and in our previous field enclosure experiments, and thus its distribution in only ponds and lakes where fish dominate (Stoks and McPeek 2003).

Phenotypic traits and growth rate

Given the shorter available time to complete development, we expected species living in temporary habitats to have faster growth rates than those inhabiting permanent water bodies (Arendt 1997). Interestingly, intrinsic growth rates measured in complete isolation and ad libitum food abundance did not differ among *Lestes* across the gradient. Only in the presence of mortality threats (i.e., other *Lestes*, dragonflies, or fish) did the growth rate differences among species become evident. Hence, behavioral and physiological species differences in responses to mortality threats ultimately shape species differences in growth rates in the field. In accordance with the assumed greater advantage for rapid growth in vernal ponds, *L. dryas* had higher growth rates than *Lestes* from other parts of the gradient in the presence of conspecific cannibals (Fig. 3A). Interestingly, their higher growth rate was not because they ate more; it was because they converted more ingested food into their own biomass.

The lower growth rates of the temporary dragonfly-pond *Lestes* are probably the main reason they cannot successfully exploit vernal ponds, and this too must be explained by a lower efficiency to convert ingested food into biomass and not by a lower feeding rate. Across the transition from temporary ponds to permanent water bodies we did not see a further decrease in growth rates in the presence of only *Lestes*. However, the temporary-pond *L. rectangularis* and the permanent-pond *L. eurinus* share the same predator assemblage dominated by large *Anax* dragonflies (Stoks and McPeek 2003), and we did find a higher growth rate of the temporary-pond species in the presence of dragonflies (ANOVA $F_{1,18} = 4.57$, $P < 0.05$; Fig. 3A). However, the main reason permanent-water *Lestes* are missing from temporary ponds is their lack of the typical *Lestes* overwintering egg diapause to survive periods of pond drying (Lutz 1968*a*, *b*, Lutz and Pittman 1968, Paulson and Jenner 1971, Ingram 1976, Jödicke 1997), which makes their long aquatic larval stage incompatible with the hydroperiod of temporary ponds in many years.

In contrast to our expectation (see also Wellborn et al. 1996), we found little evidence of baseline activity or feeding levels decreasing among *Lestes* species going from the vernal to the permanent part of the gradient, and thereby shaping growth differences among species. Only swimming activity decreased along this gradient. In the absence of predators, food intake did not differ in the behavior experiment under differential predation risk (Appendix B) or in the growth experiment under differential predation risk (Fig. 3B) among these *Lestes* species spanning the entire gradient. Although the experiment measured foraging success in a limited arena over the short term with unlimited food, we think our results hold in more natural circumstances because growth rates observed in the latter experiment

are similar to the ones observed in enclosure experiments (R. Stoks and M. A. McPeek, *unpublished data*). Taken together, this argues against the primary mediating trait of the growth/predation risk trade-off being activity in this study system (cf. Houston et al. 1993, Werner and Anholt 1993, McNamara and Houston 1994, Abrams and Rowe 1996).

Instead, physiology seems the key variable shaping species differences in growth rates among *Lestes* along the gradient. Apparently, species differ in the degree that nutrition absorbed by the digestive system finally results into growth (biomass increase). Different mechanisms may underlie this pattern. For example, the same amount of nutrition may be absorbed by the digestive system but then stored or utilized differently by the various species, or species may differ in how they allocate assimilates to different tissues with varying metabolic demands (see McPeek et al. 2001 for a full discussion). Species also differed in the changes in conversion efficiency in the presence of cannibalistic congeners and predators. Effects of predators on physiology related to growth of their prey have largely been neglected (e.g., see Scriber and Slansky 1981), but similar physiological responses to predators have been shown in larvae of *Enallagma* damselfly species (McPeek et al. 2001) as well as vertebrates (Boonstra et al. 1998), and indirect evidence suggests that such physiological responses may be quite typical of prey responses to predators (Duvall and Williams 1995, Werner and Anholt 1996, Hechtel and Juliano 1997, Stoks 2001). We hypothesize that this predator-induced growth rate reduction is a physiological stress response to predators (see McPeek et al. 2001 for a discussion on potential molecular mechanisms involved). We are currently exploring whether physiological stress molecules are indeed involved in this response.

Interestingly, *L. dryas*, which has been hypothesized to display the greatest levels of cannibalism, because it lives at the most temporary end of the gradient (Fischer 1961, Jödicke 1997), did not show such physiological responses in the presence of congeners (or in the presence of *Anax* and *Lepomis*). This might be advantageous for two reasons: (1) it avoids foraging costs usually associated with predation risk, and (2) converting more assimilated food into body mass would allow faster development. Similarly, the higher growth rate of the temporary-pond *Lestes* compared to the permanent dragonfly-pond *L. eurinus* in the presence of dragonflies is largely due to a higher conversion efficiency (Fig. 3D). Apparently, temporary-pond *Lestes* do not respond physiologically to the presence of dragonflies as strongly as the permanent dragonfly-pond *L. eurinus* as illustrated by a smaller decrease in conversion efficiency relative to the situation with only congeners present (ANOVA; $F_{1,18} = 14.02$, $P < 0.01$; Fig. 3D).

Phenotypic traits, trade-offs, and species turnover

It has often been demonstrated that the same traits that allow a species to be successful in some environments can exclude the species from other ones, leading to the development of discrete community types across environmental gradients (e.g., McPeek 1990*a*, Schluter 1995, Tessier et al. 2000, Wellborn 2002). Several studies comparing two or three species have shown that activity level is a key phenotypic trait mediating the growth/predation risk trade-off, and causes species turnover along the freshwater habitat gradient (Wellborn et al. 1996, Wissinger et al. 1999). However, when many frog species from across the entire hydroperiod gradient were compared, predicted interspecific patterns of activity were not apparent, which begs the question of the generality of activity as the key mediating trait of this trade-off (Richardson 2001*a*, *b*).

The conventional notion for the cause of a trade-off, namely the antagonistic influences of a single character (e.g., a phenotypic trait such as activity, or a pleiotropic gene) on multiple performance or fitness components (e.g., Rose 1982, Loeschcke 1987), does not seem to be at play in the studied *Lestes* system (nor in the *Enallagma* damselflies as well [McPeek et al. 2001]). Rather, different sets of characters appear to influence relative growth and predation risk attributes of different species. For example, the vernal-pond *Lestes* manages to complete its life cycle in vernal ponds due to its high growth rate, and its higher growth rate is not due to greater activity leading to greater foraging returns, but rather to a higher conversion efficiency of ingested food. However, higher conversion efficiency does not exclude it from temporary ponds; its absence from other parts of the gradient is mediated by its overall higher activity level and lack of antipredator responses. Thus, while the fitness component patterns associated with the growth/predation risk trade-off phenomenologically hold across species (i.e., species differ in mortality, overall activity and responsiveness to prey in ways that are consistent with the trade-off predictions, and they decrease activity and growth in the presence of perceived predators), activity and physiology appear to independently influence mortality and growth, respectively.

Because evidence is accumulating that predation risk not only affects a prey's behavior but also its physiology (Boonstra et al. 1998, McCormick 1998, McPeek et al. 2001, Scheuerlein et al. 2001, Stoks 2001) and that species may differ in foraging rate, physiology and the contribution of both to relative growth rates (e.g., Kause et al. 1999, McPeek et al. 2001) this pattern may be much more general than currently appreciated. We suggest that such interplay between behavior and physiology may be a common feature of the growth/predation risk trade-off in many taxa, and that the causes of this trade-off may not be simply the result of the antagonistic consequences of one character (i.e., time spent actively foraging) on growth and predation risk. Mechanistic studies testing the hypothesized relationships between phenotypes and fitness components are needed that explore the complex nexus of phenotypic traits influencing growth and predation risk. As the growth/predation risk trade-off is crucial in shaping species distributions in their environment, including both behavior and physiology will be critical for a mechanistic understanding that links how phenotypes of species have been shaped by past evolution with how these phenotypes now shape biological communities across the landscape.

LITERATURE CITED

Abrams, P. A., and L. Rowe. 1996. The effects of predation on the age and size of maturity of prey. Evolution **50**:1052–1061.

Anholt, B. R., E. E. Werner, and D. K. Skelly. 2000. Effect of food and predators on the activity of four larval ranid frogs. Ecology **81**:3509–3521.

Arendt, J. D. 1997. Adaptive intrinsic growth rates: an integration across taxa. Quarterly Review of Biology **72**:149–173.

Baker, R. L., C. M. Elkin, and H. A. Brennan. 1999. Aggressive interactions and risk of fish predation for larval damselflies. Journal of Insect Behavior **12**:213–223.

Boonstra, R., D. Hik, G. R. Singleton, and A. Tinnikov. 1998. The impact of predator-induced stress on the snowshoe hare cycle. Ecological Monographs **79**:371–394.

Duvall, C. J., and D. D. Williams. 1995. Individuality in the growth of stonefly nymphs in response to stress from a predator. Archiv für Hydrobiologie **133**:273–286.

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

Fischer, Z. 1961. Cannibalism among the larvae of the dragonfly *Lestes nympha* Selys. Ekologia Polska **7**:33–39.

Hechtel, L. J., and S. A. Juliano. 1997. Effects of a predator on prey metamorphosis: plastic responses by prey or selective mortality? Ecology **78**:838–851.

Houston, A. I., J. M. McNamara, and J. M. C. Hutchinson. 1993. General results concerning the trade-off between gaining energy and avoiding predation. Philosophical Transactions of the Royal Society of London B **341**:375–397.

Ingram, B. R. 1976. Life histories of three species of Lestidae in North Carolina, United States (Zygoptera). Odonatologica **5**:231–244.

Jakobsson, S., O. Brick, and C. Kullberg. 1995. Escalated fighting behavior incurs increased predation risk. Animal Behaviour **49**:235–239.

Jeffries, M. 1990. Interspecific differences in movement and hunting success in damselfly larvae (Zygoptera, Insecta): responses to prey availability and predation threat. Freshwater Biology **23**:191–196.

Jödicke, R. 1997. Die Binsenjungfern und Winterlibellen Europas. Westarp, Heidelberg, Germany.

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

Kause, A., E. Haukioia, and S. Hanhimaki. 1999. Phenotypic plasticity in foraging behavior of sawfly larvae. Ecology 80:1230–1241.

Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior 27:215–290.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Loeschcke, V. 1987. Genetic constraints on adaptive evolution. Springer-Verlag, Berlin, Germany.

Lutz, P. E. 1968a. Life-history studies on *Lestes eurinus* Say (Odonata). Ecology 49:576–579.

Lutz, P. E. 1968b. Effects of temperature and photoperiod on larval development in *Lestes eurinus* Say (Odonata: Lestidae). Ecology 49:637–644.

Lutz, P. E., and A. R. Pittman. 1968. Oviposition and early developmental stages of *Lestes eurinus* (Odonata: Lestidae). American Midland Naturalist 80:43–51.

McCormick, M. I. 1998. Behaviorally induced maternal stress in a fish influences progeny quality by a hormonal mechanism. Ecology 79:1873–1883.

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

McPeek, M. A. 1990a. Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. Ecology 71:83–98.

McPeek, M. A. 1990b. Behavioral differences between *Enallagma* species (Odonata) influencing differential vulnerability to predators. Ecology 71:1714–1726.

McPeek, M. A. 1995. Morphological evolution mediated by behavior in the damselflies of two communities. Evolution 49:749–769.

McPeek, M. A. 1997. Measuring phenotypic selection on an adaptation: lamellae of damselflies experiencing dragonfly predation. Evolution 51:459–466.

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

McPeek, M. A. 1999. Biochemical evolution associated with antipredator adaptation in damselflies. Evolution 53:1835–1845.

McPeek, M. A. 2000. Predisposed to adapt? Clade-level differences in characters affecting swimming performance in damselflies. Evolution 54:2072–2080.

McPeek, M. A., and J. M. Brown. 2000. Building a regional species pool: diversification of the *Enallagma* damselflies in eastern North American waters. Ecology 81:904–920.

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

McPeek, M. A., A. K. Schrot, and J. M. Brown. 1996. Adaptation to predators in a new community: swimming performance and predator avoidance in damselflies. Ecology 77:617–629.

Paulson, D. R., and C. E. Jenner. 1971. Population structure in overwintering larval Odonata in North Carolina in relation to adult flight season. Ecology 52:96–107.

Pierce, C. L., P. H. Crowley, and D. M. Johnson. 1985. Behavior and ecological interactions of larval Odonata. Ecology 66:1504–1512.

Relyea, R. A. 2001. The relationship between predation risk and antipredator responses in larval anurans. Ecology 82:541–554.

Relyea, R. A., and E. E. Werner. 1999. Quantifying the relation between predator-induced behavior and growth performance in larval anurans. Ecology 80:2117–2124.

Richardson, J. M. L. 2001a. A comparative study of activity levels in larval anurans and response to the presence of different predators. Behavioral Ecology 12:51–58.

Richardson, J. M. L. 2001b. The relative roles of adaptation and phylogeny in determination of larval traits in diversifying anuran lineages. American Naturalist 157:282–299.

Rose, M. R. 1982. Antagonistic pleiotropy, dominance, and genetic variation. Heredity 48:63–78.

Scheuerlein, A., T. J. Van't Hof, and E. Gwinner. 2001. Predators as stressors? Physiological and reproductive consequences of predation risk in tropical stonechats (*Saxicola torquata axillaris*). Proceedings of the Royal Society of London Series B-Biological Sciences. 268:1575–1582.

Schluter, D. 1995. Adaptive radiation in sticklebacks: trade-offs in feeding performance and growth. Ecology 76:82–90.

Scriber, J. M., and F. Slansky. 1981. The nutritional ecology of immature insects. Annual Review of Entomology 26:138–211.

Skelly, D. K. 1995. A behavioral trade-off and its consequences for the distribution of *Pseudacris* treefrog tadpoles. Ecology 76:150–164.

Slansky, F., and J. G. Rodriguez. 1987. Nutritional ecology of insects, mites, spiders and related invertebrates. John Wiley and Sons, New York, New York, USA.

Smith, D. C., and J. Van Buskirk. 1995. Phenotypic design, plasticity, and ecological performance in two tadpole species. American Naturalist 145:211–233.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. Third edition. W. H. Freeman and Co., New York, New York, USA.

Stoks, R. 1998. Effect of lamellae autotomy on survival and foraging success of the damselfly *Lestes sponsa* (Odonata: Lestidae). Oecologia 117:443–448.

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

Stoks, R., and M. De Block. 2000. The influence of predator species and prey age on the immediate survival value of antipredator behaviours in a damselfly. Archiv für Hydrobiologie 147:417–430.

Stoks, R., and F. Johansson. 2000. Trading off mortality risk against foraging effort in damselflies that differ in life cycle length. Oikos 91:559–567.

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

Stoks, R., M. A. McPeek, and J. L. Mitchell. 2003. The evolution of anti-predator behavior as lineages adapt to different habitats: damselflies in fish and dragonfly lakes. Evolution 57:574–585.

Tessier, A. J., M. A. Leibold, and J. Tsao. 2000. A fundamental trade-off in resource exploitation by *Daphnia* and consequences to plankton communities. Ecology 81:826–841.

Tilman, D. 1987. The importance of the mechanisms of interspecific competition. American Naturalist 129:769–774.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, New Jersey, USA.

Wellborn, G. A. 2002. Trade-off between competitive ability and antipredator adaptation in a freshwater amphipod species complex. Ecology 83:129–136.

Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27:337–363.

Werner, E. E. 1992. Individual behavior and higher-order species interactions. American Naturalist **140**:5–32.

Werner, E. E. 1998. Ecological experiments and a research program in community ecology. Pages 3–26 *in* W. J. Resetarits and J. Bernardo, editors. Experimental ecology: issues and perspectives. Oxford University Press, New York, New York, USA.

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

Werner, E. E., and B. R. Anholt. 1996. Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. Ecology **77**:157–169.

Werner, E. E., and M. A. McPeek. 1994. Direct and indirect effects of predators on two anuran species along an environmental gradient. Ecology **75**:1368–1382.

Wilbur, H. M., and J. P. Collins. 1973. Ecological aspects of amphibian metamorphosis. Science **182**:1305–1314.

Wissinger, S. A., H. H. Whiteman, G. B. Sparks, G. L. Rouse, and W. S. Brown. 1999. Foraging trade-offs along a predator–permanence gradient in subalpine wetlands. Ecology **80**:2102–2116.

APPENDIX A

The results of principle components analysis for the original ln-transformed behavioral variables of the behavior experiment under differential predation risk are available in ESA's Electronic Data Archive: *Ecological Archives* E084-091-A1.

APPENDIX B

A figure showing selected behavioral variables of the seven *Lestes* species in the behavior experiment under differential predation risk is available in ESA's Electronic Data Archive: *Ecological Archives* E084-091-A2.

APPENDIX C

A figure showing digestive variables of the four *Lestes* studied in the growth in isolation experiment is available in ESA's Electronic Data Archive: *Ecological Archives* E084-091-A3.