Behavioral syndrome over the boundaries of life—carryovers from larvae to adult damselfly

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Activity is an important behavioral trait that mediates a trade-off between obtaining food for growth and avoiding predation. Active individuals usually experience a higher encounter rate with food items and suffer higher predation pressure than less active individuals. I investigated how activity of the damselfly \textit{Lestes congener} is affected by larval state and predator presence and if larval behavioral type (BT) can be used to predict larval boldness, foraging success, and adult BT. Activity level of individual larvae was studied without predator at 2 different physiological states (hungry and fed) and in 2 predator treatments: familiar predator cues and unfamiliar predator cues. Larvae did not adjust their activity depending on state or when subjected to unfamiliar predator cues, but a general reduction in activity was seen in the familiar predator treatment. Hence, active individuals remained active compared with their conspecifics, independent of state or predator treatment. Active individuals were also bolder and more efficient foragers than their less active conspecifics. Furthermore, both adult activity and boldness were correlated with larval BT. The results illustrate that BT of a larva is carried over many different situations keeping active larvae active even in maladaptive situations, demonstrating how a behavioral syndrome may constrain behavioral plasticity. Furthermore, results showed that behavioral syndromes can carry over from larvae through metamorphosis and dictate the BT of the adult.

\textbf{Key words:} activity, behavioral syndrome, behavioral type, boldness, \textit{Lestes}, phenotypic plasticity. [Behav Ecol 20:30–37 (2009)]

\textbf{A}ctivity is an important behavioral trait that influences food intake and thereby energy gain. Higher activity usually results in more encounters with food and hence has the potential to result in higher energy gain that translates to higher growth rate and larger size and/or shorter development (Werner and Anholt 1993). However, a high activity also implies a higher encounter rate with predators. Hence, individuals are faced with a growth/predation risk trade-off (Lima 1998). Two types of situations can generate the growth/predation risk trade-off (Sih et al. 2003). The first situation is termed “within-situation conflicts” and is often associated with a time budget conflict. Here individuals that spend more time foraging actively gain more food and probably grow faster but suffer a higher predation risk. Active individuals may do well in the absence of predators but suffer in the presence of predators. In contrast, the less active individuals should do well in the presence of predators, but poorly in the absence of predators. Continuing in this line of reasoning, one would expect to be advantageous for animals to have unconstrained plastic behavior, that is, being able to optimize behavior according to the current environment to maximize foraging while minimizing predation risk. Yet, this is not the norm, instead constrained behavioral plasticity is the dominating pattern. One reason for such constraints is the other type of conflicts, termed “across-situation conflicts.” It involves suites of correlated behaviors called behavioral syndromes (or personalities) that make individuals differ consistently in their behavioral tendencies, and the behavior in one context is correlated with behavior in many other contexts (Sih, Bell, Johnson, and Ziemb 2004). Such suites of correlated behaviors are, in ecology, often called behavioral syndromes (Sih, Bell, Johnson, and Ziemb 2004) or animal personalities (Dall et al. 2004; Groothuis and Careere 2005). A behavioral syndrome exists if, even as individuals alter their behavior depending on the context, some are consistently more active than others across multiple contexts (e.g., in how they feed and cope with predators, but also in contests with conspecifics, in how they mate and disperse) (Sih et al. 2003; Sih, Bell, and Johnson 2004; Sih, Bell, Johnson, and Ziemb 2004). Over the last few years, several evolutionary and/or ecological studies on animal personalities have been produced on mammals (Reale et al. 2000), birds (Sol and Lefebvre 2000; Sol et al. 2002; Both et al. 2005; Carere et al. 2005; Mettke-Hofmann 2005; Quinn and Cresswell 2005; van Oers et al. 2005), lizards (Sinervo 2001; Stapley and Keogh 2005; Dame and Petren 2006), salamanders (Sih et al. 2003), fish (Fraser et al. 2001; Overli et al. 2004; Bell 2005; Brown et al. 2005; Magnhagen and Staffan 2005; Overli et al. 2006), spiders (Johnson and Sih 2005), and insects (Hedrick 2000; Brodin and Johansson 2004; Slos and Stoks 2006). It has become clear that consistent individual differences in behavior exist in a wide range of contexts and organisms from humans to insects (Sih, Bell, Johnson, and Ziemb 2004). Note that if all personalities do well in some situations, but not others (i.e., no one is optimal everywhere), this trade-off can help to explain the maintenance of variation in individual behavior. Correlations among behaviors can also have important ecological effects. For example, the possibility that dispersers tend to be bold and aggressive has potentially important effects on the dynamics of biological invasions and on metapopulation dynamics.

Despite the surge of interest in this field, no study has yet investigated if personality carries over from early life stages in one environment (e.g., larvae) through a metamorphosis into adulthood in a different environment. Intuitively, one could suggest at least 2 scenarios of how larval and adult behaviors are connected. First, because several behavioral traits are inherited, it could be expected that adults would adopt
a similar behavioral type (BT) as when they were larvae. This seems like a plausible prediction, and similar results of behavioral carryover from juvenile to adult have been seen in other organisms, such as spiders (Johnson and Sih 2005). Furthermore, because behavioral traits have been shown to be inherited (Magurran 1990; Maurer and Sih 1996; O’Stein et al. 2002; Drent et al. 2003; Sih et al. 2003), juvenile behavior should give an indication of what adult BTs that were prosperous last generation. Hence, due to the above water surface selection pressure on adults, larval behavior might be more adapted to the above water surface selection pressure than to the selection pressures in the larval environment. However, there are few behavioral transformations as dramatic as those observed during insect metamorphosis, when the neural and motor systems are remodelled (Con caulas et al. 2000). For example, in aquatic insects, typical larval behaviors are crawling, feeding, and swimming, whereas adult behaviors include flying and reproducing. The alternative scenario would be that the remodelling of the neural and motor systems could facilitate a decoupling of the larval and adult behavior, freeing the adult from any constraints that a behavioral carryover from larval could impose (Moran 1994). It has been suggested that selection should decouple a behavioral syndrome through ontogeny when environmental conditions experienced by juveniles differ substantially from those experienced by adults (Sih, Bell, Johnson, and Ziemb a 2004). This issue is, to my knowledge, addressed for the first time in this paper.

In this study, I focus on individual activity correlations between different states and predator environments and how this behavioral syndrome affects boldness and foraging success in damselfly larvae. Furthermore, I investigate how these larval BTs are pronounced in the adult damselfly. Damselflies have complex life cycles with an aquatic larval stage and a terrestrial adult stage wherein reproduction occurs. Because reproductive success in the adult stage depends on time of emergence (De Block and Stoks 2005), fat content (Plaistow and Sva Jothy 1996, 1999), and adult size (Anholt et al. 1991; Sokoloska et al. 2000; De Block and Stoks 2005), activity in the larval stage has the potential to affect fitness parameters in the adult stage. Based on current empirical knowledge and theory presented above, I predict that 1) larvae will be more active when starved than when well fed, 2) individuals should show behavioral adjustments according to the growth/predation risk trade-off (the within-situation conflict), 3) highly active individuals should stay relatively active (compared with less active ones) independent of state or predator environment, 4) active individuals should be bolder and forage more efficiently than less active ones, and 5) larval BT will be positively correlated with adult BT.

MATERIALS AND METHODS

All experiments were run at the Aquatic Biology and Environmental Science facility on the University of California, Davis (USA) campus. Experimental rooms were kept constant at 22 °C and a light/dark regime of 14:10 h. Our target species was the damselfly Lestes congener (Hagen) (Odonata: Zygoptera), hereafter called Lestes. It is a very widespread species with transcontinental range that is commonly found in ponds without fish (Stoks and McPeek 2003). This Lestes species oviposits endophytically in the late summer and fall and overwinters as eggs (Walker 1953; Sawchyn and Gillott 1974). Eggs hatch in spring, and larvae grow and mature to breed overwinters as eggs (Walker 1953; Sawchyn and Gillott 1974). Species oviposits endophytically in the late summer and fall and overwinters as eggs (Walker 1953; Sawchyn and Gillott 1974). Species oviposits endophytically in the late summer and fall and overwinters as eggs (Walker 1953; Sawchyn and Gillott 1974). Species oviposits endophytically in the late summer and fall and overwinters as eggs (Walker 1953; Sawchyn and Gillott 1974). Species oviposits endophytically in the late summer and fall and overwinters as eggs (Walker 1953; Sawchyn and Gillott 1974).

I used Aeshna larvae (Odonata: Anisoptera) and tiger salamander, Ambystoma tigrinum, as predators. The Aeshna was labeled as “familiar predator” because Aeshna larva is a common predator that coexists with Lestes in lakes and ponds in Pope Valley (McCauley S, Brodin T, unpublished data). Tiger salamander, however, was labeled as “unfamiliar predator” because the species do not coexist with Lestes in the area.

In late April, 30 larvae (instar F-3, where F-0 denotes last instar, F-1 second last instar, and so on) were collected from a small fishless pond, Green pond, in the Wanatup Wildlife Reserve, Pope Valley, CA, approximately 80 km northwest of Davis. The dominant predators in Green pond are large dragonfly larvae (Aeshna), large dytiscid larvae, and belostomatid (McCauley S, Hammond J, Brodin T, unpublished data). The Lestes larvae were kept in separate plastic containers (25 × 15 × 8 cm) during the entire study and fed approximately 30 daphnia from laboratory cultures every second day. This food provisioning corresponds with an ad libitum approach. Remaining daphnia were removed prior to every feeding bout to eliminate the risk of unequal prey densities between containers. Late-instar Aeshna larvae were collected at Bear Creek, approximately 115 km northwest of Davis, and salamanders were taken from a laboratory stock at UC Davis. The predators were all fed either larval Chironomids (Diptera: Chironomidae) or Pacific tree frog, Pseudacris regilla, tadpoles (1–3) daily.

Larval behavioral experiment

To determine individual BT of each larva, I ran several behavioral trials where I monitored activity level of the larvae, in the absence of food, at different physiological states and in several predator environments. The trials were all carried out between 1230 and 1450 h on 10, 12, 15, and 16 May 2007. Each container (25 × 15 × 8 cm) was filled with 1.2 L aged well water and had a coordinate grid drawn on the bottom with a grid size of 1 × 1 cm. The larvae had all grown to instars F-3 or F-2 when used in the behavioral trials. I observed the containers once every 10 min, for 140 min, and noted whether the larvae had moved or not. A move was noted when the larvae had moved their head from one square to another. This procedure generated an activity score for each larva ranging from 0 (inactive) to 14 (very active). The first 2 trials focused on larval activity at different states and differed in larval hunger level. In the first trial, larvae were hungry (starved for 5 days) when observed, whereas in the second experiment, they were well fed (fed the same morning). The nonpredator trials were run first to avoid any risk of long-lasting antipredator response affecting subsequent experiments. In the third and fourth trials, well-fed larvae were studied in the presence of nonlethal predator cues from an unfamiliar salamander predator (tiger salamander) and a familiar dragonfly predator (Aeshna), respectively. One hour prior to both predator experiments, chemical cues (100 mL of water from predator containers) were added to prey containers. After each predator trial, prey containers were emptied and cleaned and aged well water was added to minimize the risk of future behavioral antipredator responses or stress caused by predator cues. All larvae that survived to the 10th of May were used in the behavioral trial, adding up to a total of 20 individuals. During the behavioral trials, 4 of the larvae moulted and were removed from the following trials making the total number of studied larvae 22. After the initial activity study (starved larvae without predator cues), larvae were assigned to either of 2 BTs. The highly active BT had initial activity scores of 10–14 (n = 12), whereas the less active BT had activity scores ranging from 0 to 7 (n = 10); no larvae in this experiment got activity scores of 8 or 9. This categorization was supported by a stepwise classical linear discriminant analysis (Wilks’s lambda = 0.098, F = 185.12, P < 0.0001). Furthermore, the categorization of BT was also supported by a stepwise classical linear discriminant analysis of the principal components analysis (PCA) scores from all
4 behavioral trials (Wilk’s lambda = 0.071, F = 216.32, Ptail < 0.0001).
In addition to the activity studies, I also measured individual larval boldness and foraging success. The boldness experiment was carried out after the initial activity assay but before the other 3 activity trials were done. Larvae were disturbed (touching larval lamellae with a prod) until they reacted with an escape response and swam away. Time until larvae started moving again after the initial swimming burst was measured. After 2 min, the observation was terminated and any larvae that had not moved were assigned the maximum value of 120 s. As suggested by Reale et al. (2007), boldness trials were carried out in the, for each larva, familiar environment of their holding container. This was done to reduce potential effects that other behaviors (e.g., exploratory behavior) might have on boldness. Boldness has repeatedly been reported of being positively correlated with activity level, and observing behavior after disturbance is a commonly used method to quantify the trait (Johnson and Sih 2005). However unlikely, I cannot exclude the possibility that a similar pattern of larval boldness as shown here could be generated as a side effect of individual activity because active larvae move more frequently than less active larvae. In the foraging experiment, I added 30 daphnia in each larval container and observed individual larva for 120 s while noting how many daphnia the larva captured.
A Shapiro–Wilk normality test revealed that larval activity, boldness, and foraging data did not fit to a normal distribution. Such lack of normality is not unusual in behavioral data, especially when sample sizes are fairly low. Boldness was ln transformed to meet the assumptions of normal distribution, whereas activity and foraging data were analyzed with Kruskal–Wallis 1-way analysis of variance (ANOVA). In addition, to check for differences in activity between trials, a Friedman 2-way ANOVA was used; it is a nonparametric analogue of repeated measures analysis.

Adult behavioral experiment
Sixteen adults successfully emerged between 2 June and 16 June 2007. After emerging, they were moved to individual glass aquaria (75 x 30 x 30 cm) containing a wooden structure (diameter = 8 mm, length = 50 cm) for perching, water, and potential prey (20 Drosophila sp.). Adults stayed in their aquaria for 24 h before the behavioral trial began. Three different behavioral measurements were made: 1) activity scores (0–14), using the same technique as for larvae (see above); 2) behavioral profile, all adult damselflies were observed for 20 min and every flying, walking, and “fluttering” behavior was noted; and 3) boldness, perching adults were approached by a bird decoy until they flew, the decoy was removed, and time until the adult returned to the perch was noted. Adults respond to risky situations with active flight behavior to escape risk, whereas larvae use inactivity to escape risk (see references in Corbet 1999). Hence, to get adequate measures of boldness for larvae (latency to move) and adults (latency to return to a perch), different methods that are appropriate to the behaviors of the respective life stage had to be used. Boldness is distinct from activity because it reflects the time required after a disturbance to return to a potentially risky behavioral pattern following the behavior typically adopted when the risk of predation is encountered. The fluttering behavior was scored when a damselfly fluttered its wings while remaining stationary. Activity scores turned out to be too crude a measurement of adult activity because all but one adult got scores between 10 and 14, and hence, these data were not used in any analysis. In order to summarize adult behavioral profile, I used PCA on a correlation matrix. There are advantages to use component scores rather than single behaviors in analyses. Foremost, by performing statistical tests on component scores rather than many different variables, problems of multiple comparisons can often be avoided. PC1 scores were not normally distributed and were hence analyzed with Kruskal–Wallis test, whereas the PC2 scores could be analyzed with a 1-way ANOVA. To ensure statistical accuracy, I also rank transformed PC1 scores and used them in a 1-way ANOVA that supported the result from the nonparametric test. These monitored adult behaviors represent general activity and dispersal behaviors related to foraging and antipredator behavior (Corbet 1999). Admittedly, scoring adult behavioral data in an aquarium is somewhat artificial compared with field observations and may increase the proportion of uncommon behaviors (i.e., walking). However, numbers of walking bouts recorded here were still very few compared with other monitored behaviors. The difficulties of making behavioral measurements on adult damselflies, particularly repeated measurements on a single individual, argued for the use of a more controlled but artificial context for measuring behavior. Future work should certainly follow this up with observations in increasingly realistic habitat settings. Adult boldness was analyzed with 1-way ANOVA and linear regression. All statistical analyses were done using the statistical package SYSTAT 11 (2004).
Larval activity (BT), foraging success, and boldness could be confounded by 3 factors: damselfly larvae size, time to emergence, and damselfly gender. However, linear regressions between these behaviors and size and these behaviors and time to emergence showed no significant relationships (P > 0.45 in all regressions). Female and male damselflies did not differ in activity, foraging success, or boldness (Kruskal–Wallis; all P > 0.23). The potential for adult size confounding the behavior of the adults was also tested for and subsequently rejected (linear regression; P > 0.18).
This research adhered to the Association for the Study of Animal Behavior/Animal Behavior Society Guidelines for the Use of Animals in Research, the legal requirements of USA, and all institutional guidelines.

RESULTS
Larval activity
Larvae of both the highly active BT (mean ± standard error [SE] = 13.08 ± 0.23, starved) and the less active BT (mean ± SE = 4.5 ± 0.64, starved) all retained their respective BT independent of hunger level or presence of predator cues and their activity levels consistently differed accordingly (Figure 1; Kruskal–Wallis test, all P < 0.001). This activity difference between larvae was consistent even when larvae reduced activity in response to the presence of Aeshna cues. A repeated measures test confirmed that larval activity differed between the behavioral trials (Friedman 2-way ANOVA, P = 0.004). The differences found between trials were accounted for by the activity reduction in the presence of Aeshna cues (Figure 1; Kruskal–Wallis test, P = 0.038), indicating a behavioral antipredator reaction to the familiar predator. Contrastingly, no behavioral antipredator response was seen in the experiment when larvae were subjected to Ambystoma cues (Kruskal–Wallis test, P = 0.29).

Boldness and foraging success
Larvae of the highly active BT were bolder than the less active larvae (mean ± SE = 38.5 ± 11.1 and 81.2 ± 13.1, respectively; 1-way ANOVA, F1,20 = 6.31, P = 0.021). Active larvae also foraged more successfully than less active larvae (mean ± SE = 1.5 ± 0.5 and 0.3 ± 0.1, respectively; Kruskal–Wallis test, P = 0.035). All in accordance with my predictions based on
that, one benefit of being active is found to be an increase in prey encounter and hence more opportunities to forage.

**Adult behavior**

Adult behavior was monitored in 16 out of the 22 individuals because 6 larvae were unable to emerge successfully. I used a PCA to compress the adult behavioral data collected into 2 principal components that together explained 90.6% of the variance (Table 1). PC1 explained 56.6% of the variation and was highly positively correlated with walking and fluttering. PC2 explained 34% of the variation and was strongly positively associated with flying. Larvae of the active BT emerged as more active adults than the less active larvae, a result supported by both PC1 (Kruskal–Wallis, $P = 0.009$; 1-way ANOVA, $F_{1,14} = 13.22, P = 0.004$, on ranked data) and PC2 (1-way ANOVA, $F_{1,14} = 5.92, P = 0.029$). In addition, a linear regression between PCA scores of larval activity and adult behavioral profile showed a strong positive correlation between active larvae and active adults (Figure 2; linear regression, $F_{1,14} = 12.13, P = 0.004$). Furthermore, was adult boldness positively correlated to larval boldness (Figure 3; linear regression, $F_{1,14} = 6.46, P = 0.011$); hence, bold/shy larvae gave rise to bold/shy adults (mean ± SE = 2.68 ± 0.16 and 4.17 ± 0.39, respectively) and the BTs differed accordingly (1-way ANOVA, $F_{1,14} = 11.38, P = 0.005$). These results are intriguing and clearly illustrate that BT is carried over from larvae, through a metamorphosis, to the adult damselfly.

**DISCUSSION**

My study is a longitudinal behavioral study that follows individual behavior of damselfly larva over multiple physiological states and in several predator environments and ultimately examines how larval behavior is translated into adult behavior. I focus on how individual activity level responds to changes in the environment and how activity correlates to larval boldness and foraging success. In addition, I follow each larva into adulthood and survey their behavior as adults to see if behavioral syndromes may cross the barrier of metamorphosis and carry over from the aquatic larvae to the terrestrial adult.

The study shows that *Lestes* individuals differ consistently in their activity across several situations and life stages and that more active larva are bolder and better foragers than less active larvae. This clearly illustrates the existence of an

**Table 1**

Results of PCAs on adult behavior

<table>
<thead>
<tr>
<th>Behavior/Loading</th>
<th>PC1</th>
<th>PC2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult activity</td>
<td>0.928</td>
<td>0.027</td>
</tr>
<tr>
<td>Fluttering</td>
<td>0.850</td>
<td>-0.401</td>
</tr>
<tr>
<td>Flying</td>
<td>0.341</td>
<td>0.927</td>
</tr>
<tr>
<td>Cumulative variance explained</td>
<td>56.65%</td>
<td>34.00%</td>
</tr>
</tbody>
</table>

**Figure 1**

Mean activity of larval BTs in 4 different environments. Low state—starved larvae, high state—well-fed larvae, unfamiliar predator—salamander cues, and familiar predator—dragonfly cues. Open circles denoted highly active BTs and filled circles less active BTs. Error bar denotes ±1 SE.

**Figure 2**

Active larvae become active adults. PCA score of larval activity is positively correlated with the PCA score of the adult behavioral profile. Open circles denoted highly active BTs and filled circles less active BTs.

**Figure 3**

Bold larvae become bold adults. Individual boldness declines with increasing time on both axes because low time scores indicate high boldness. Open circles denoted highly active BTs and filled circles less active BTs.
activity–boldness behavioral syndrome in *Lestes* that not only carry over larval situations but also carry over into the behavior of the adults. The link between individual larval and adult behavior in an organism that metamorphosis from one distinct larval habitat type to a completely different adult habitat shown here is novel and may have important implications for dispersal, metapopulation, and fitness issues. I found a positive correlation between individual activity in different situations, illustrating a behavioral syndrome, and I also found a positive correlation between activity/boldness and activity/foraging rate, the latter illustrating a well-known benefit of being active. These benefits may have important consequences for damselfly fitness because they affect size and time of emergence, variables known to be important components of fitness in these organisms (Fincke 1982; Banks and Thompson 1987; De Block and Stoks 2005; however, see Fincke and Hadrys 2001).

Individual activity level seemed unaffected by physiological state of the larvae. This result was surprising and does not follow the empirical and theoretical predictions of low state–high activity and high state–low activity (Godin and Smith 1988; Godin and Crossman 1994; Godfrey and Bryant 2000). One explanation for this lack of state-dependent activity could be that larvae, in the absence of predators, take advantage of the predator-free environment and forage as active as they can independent of state. Another possible explanation for this result may be that larvae were foraging actively as a response to the risk of desiccation of Green pond. Response to pool desiccation is common among amphibians (Laurila and Kujasalo 1999; Johansson et al. 2005) and increase of activity has been shown in response to time constraints in *L. congener* (Johansson and Rowe 1999). Hence, the generally high activity caused by a time constraint is a very plausible explanation here because Green pond dried up about 1 month after the larvae were collected. However, if all larvae were foraging (relatively) actively, this implies that the less active BTs were behaviorally inhibited and that their activity-related plasticity was constrained by a behavioral syndrome.

Larvae reduced their activity in the presence of cues from a familiar predator. Previous studies have shown that when predation risk increases, prey usually decrease the time spent active, leading to a lower encounter rate with predators and hence a lower mortality rate than for more active individuals (Lima and Dill 1990; Anholt and Werner 1998; Brodin and Johansson 2004). As a result of low activity, encounter rates with potential prey are also lower and hence a decreased growth rate that ultimately translates into a smaller size and/or a longer time to maturation (Werner and Anholt 1993; Anholt and Werner 1998; Brodin and Johansson 2004). Any reduction in larval energy gain is predicted to invoke a negative influence on individual lifetime reproductive output. Despite this, I find a reduction in activity (i.e., energy gain) in the presence of familiar predator cues. This reaction to predator presence illustrates an important trade-off that most organisms face: “the growth/predation risk trade-off” (Werner and Anholt 1993; Lima 1998) or in terms of Sih et al. (2003) the within-situation conflict. Similar decreases in activity in the presence of a perceived predator have been reported in *Lestes* spp. (Jeffries 1990; Stoks 1998; Stoks and Johansson 2000; Johansson et al. 2001; Stoks and McPeek 2003) and other damselflies (Pierce et al. 1985; McPeek 1990a; Stoks et al. 2003; Brodin et al. 2006) and are generally expressed by many other organisms (review in Lima and Dill 1990; Lima 1998). When larvae were subjected to familiar *Aeshna* cues, they reacted by decreasing activity, whereas in the presence of cues from the unfamiliar *Ambystoma* larva did not change activity. These results are convergent with the lack of response to a non-coexisting predator that Stoks and McPeek (2003) found. This lack of response to *Ambystoma* cues might seem maladaptive; however, *Lestes* coexist with *Aeshna* larvae and not with *Ambystoma* and accordingly reacted strongly only to the presence of dragonflies by decreasing activity. These predator results are interesting and offer empirical support for a model presented by McElreath and Strimling (2006). Their model predicts that if information about the immediate environment is uncertain, prey should continue to behave the same way as before to avoid the risk of making a mistake. Because the larvae never encountered cues from the unfamiliar predator, they might perceive the environment containing the cues as uncertain and to avoid making the wrong behavioral adjustment they keep behaving as before.

My study shows consistently significant differences in activity between larval BTs in 2 different predator treatments. The differences in activity between larvae may cause the active larvae to grow faster than less active larvae, which in the absence of predators would give the active larvae a fitness advantage. However, I found no correlation between activity and size or activity and development time. One plausible explanation for the lack of apparent benefits of being active is that the larvae were fed ad libitum. This implies that high food availability might override potential effects on growth and development that differences in activity otherwise would lead to. In the presence of predators, larvae from the active BT will, due to higher encounter rates with the predator, be subjected to an increased predation pressure that might reverse the fitness advantage in favor of larvae from the less active BTs. Thus, larvae showed a behavioral correlation across situations that Sih et al. (2003) termed an across-situation conflict. The existence of interspecific variation in important traits like activity has long been known and thoroughly studied. 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 distinct community types across environmental gradients (e.g., McPeek 1990b; Schluter 1995; TESSIER et al. 2000; WELBORN 2002; STOKS and McPeek 2003).

The persistence of consistent behavioral variation between individuals in a population has long been an unexplained phenomenon. Some have even claimed it to be an artifact because natural selection will favor individuals that do best and remove less fit individuals from the population. Evolutionary theory predicts that variation in traits that are connected to survival or reproduction should, eventually, be lost from a population. However, several studies have shown that many behavioral traits are both heritable (e.g., Magurran 1990; Maurer and Sih 1996; O’STeen et al. 2002; DRENT et al. 2003; Sih et al. 2003) and connected to fitness (DINGEMANSE et al. 2004; Both et al. 2005). Recently Wolf et al. (2007) presented a model that uses the negative feedback of asset protection (Clark 1994) to illustrate one possible mechanism for why evolution favors animal personalities (behavioral syndromes). They show that animals that have more to lose should be less bold and less aggressive rather than risk losing their assets. In contrast, animals with little to lose should be bolder and more aggressive, and as long as assets do not change, animals should maintain a stable personality. This is an intriguing and counterintuitive thought, whose generality already has been questioned and debated, primarily because the negative feedback mechanism can produce animal personality only under restrictive circumstances (McElreath et al. 2007). A possibly more general way of explaining behavioral consistency and correlations is through positive feedback (McElreath et al. 2007). For example, if thorough explorers gain assets (energy, size, and knowledge) that improve their abilities to escape predators or win fights, then one might see positive correlations among exploration, boldness, and aggressiveness.
Additional behavior would have positive feedback on state, maintaining differences in assets and BPs. Behavioral correlations may differ in stability depending on what mechanism that underlies the correlation. Individual differences in single traits of animal personalities (e.g., activity) are usually moderately heritable and relatively stable over an individual’s life (Koolhaas et al. 1999; Bouchard and Loehlin 2001). Most stable over time (many generations) are phenotypic correlations caused by strong genetic correlations (van Oers et al. 2004; Bell 2005), such as pleiotropy, where the correlated behaviors (e.g., boldness and activity) are governed by a shared genetic mechanism. Evidence for strong genetic correlation between behavioral traits suggests that behavioral traits are often structured in personality traits because they are controlled by the same hormones (Ketterson and Nolan 1999; Koolhaas et al. 1999) or genes (Sih, Bell, and Johnson 2004; Sih, Bell, Johnson, and Ziembta 2004). Therefore, may components of personality be difficult to decouple (Ketterson and Nolan 1999). Another mechanism generating behavioral correlations is linkage disequilibrium caused by correlational selection. Correlational selection is selection for optimal trait combinations (Barton and Turelli 1991), and theory predicts that correlational selection will eventually produce an adaptive genetic correlation between traits because alleles influencing one trait will be coinherited together with alleles influencing the other trait (Jones et al. 2003). The correlation between boldness and activity shown in this study could potentially be explained by correlational selection favoring this particular combination of traits.

In this study, I show for the first time that larval behavior in one environment may carry over metamorphosis into adult behavior in a completely different environment. Active and bold larvae gave rise to active and bold adults, illustrating a behavioral syndrome from an aquatic life stage to a terrestrial life stage. This novel result is very intriguing because it has been suggested that selection should uncouple a behavioral syndrome through ontogeny when environmental conditions experienced by juveniles differ substantially from those experienced by adults (Sih, Bell, Johnson, and Ziembta 2004). For Lestes, it is highly likely that the selection pressures under and above the water surface differs. For example, a highly active larva will be favored in a low predation site, but a highly active adult might be more easily spotted by a predatory bird or will have a higher probability of ending its life in a spiderweb. Yet, the (potentially maladaptive) selection pressure that the aquatic larva experienced dictates the BT of the adult.

Another interesting implication of this study is the possibility that larval behavior might govern adult dispersal. My results suggest that less active larvae (commonly found in sites with high predator pressure) will emerge as less active and shy adults, whereas active larvae (commonly found in sites with low predation pressure) will emerge as active and bold adults. Following the reasoning of current knowledge of behavioral syndromes and dispersal, the less active and shy adults will have less tendencies to disperse compared with highly active and bold adults (Dingemans et al. 2003). Counterintuitively, this will lead to a high degree of dispersal from sites with low predation pressure and low degree of dispersal from high predation sites. It can be viewed as if predators, by eating active individuals, are locking the next generation of prey to their site by indirectly restricting prey dispersal.

My study contributes to a general growing appreciation of the existence and importance of behavioral syndromes (e.g., in aggressiveness, boldness, or general activity level) that carry over across multiple contexts (e.g., foraging, predator avoidance, mating, dispersal, etc.). In addition, I here present novel data of behavioral carryovers from one habitat, with certain selection pressures and constraints, to a totally different habitat with different selection pressures completely uncoupled from the larval environment. An interesting continuation of this work would be to compare survival and dispersal tendencies of adults emerging from highly active and less active larvae in different predator environments. I predict that highly active larvae will emerge, mainly from low predator pressure sites, as highly active adults with high tendencies to disperse from their suitable larval sites. Contrastingly, less active larvae will emerge, mainly from high predator pressure sites, as less active adults with low tendencies to disperse.

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**REFERENCES**


Plaistow S, Siva-Jothy MT. 1999. The ontogenetic switch between odonate life history stages: effects on fitness when time and food are limited. Anim Behav. 58:659–667.


