

# Predation risk suppresses the positive feedback between size structure and cannibalism

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## Summary

1. Cannibalism can play a prominent role in the structuring and dynamics of ecological communities. Previous studies have emphasized the importance of size structure and density of cannibalistic species in shaping short- and long-term cannibalism dynamics, but our understanding of how predators influence cannibalism dynamics is limited. This is despite widespread evidence that many prey species exhibit behavioural and morphological adaptations in response to predation risk.

2. This study examined how the presence and absence of predation risk from larval dragonflies *Aeshna nigroflava* affected cannibalism dynamics in its prey larval salamanders *Hynobius retardatus*.

3. We found that feedback dynamics between size structure and cannibalism depended on whether dragonfly predation risk was present. In the absence of dragonfly risk cues, a positive feedback between salamander size structure and cannibalism through time occurred because most of the replicates in this treatment contained at least one salamander larvae having an enlarged gape (i.e. cannibal). In contrast, this feedback and the emergence of cannibalism were rarely observed in the presence of the dragonfly risk cues. Once salamander size divergence occurred, experimental reversals of the presence or absence of dragonfly risk cues did not alter existing cannibalism dynamics as the experiment progressed. Thus, the effects of risk on the mechanisms driving cannibalism dynamics likely operated during the early developmental period of the salamander larvae.

4. The effects of dragonfly predation risk on behavioural aspects of cannibalistic interactions among hatchlings may prohibit the initiation of dynamics between size structure and cannibalism. Our predation trials clearly showed that encounter rates among hatchlings and biting and ingestion rates of prospective prey by prospective cannibals were significantly lower in the presence vs. absence of dragonfly predation risk even though the size asymmetry between cannibals and victims was similar in both risk treatments. These results suggest that dragonfly risk cues first suppress cannibalism among hatchlings and then prevent size variation from increasing through time.

5. We suggest that the positive feedback dynamics between size structure and cannibalism and their modification by predation risk may also operate in other systems to shape the population dynamics of cannibalistic prey species as well as overall community dynamics.

**Key-words:** cannibalism, dragonfly larvae, inducible offense, phenotypic plasticity, predation risk, salamander larvae, size structure, top-down effects, trait-mediated indirect effects, trophic polyphenism

## Introduction

Cannibalism is a prevalent form of trophic interaction (Fox 1975; Polis 1981) that is commonly observed in predator

populations. The outcome of cannibalistic interactions is expected to strongly influence the dynamics and structure of ecological communities (Rudolf 2007a,b), but our understanding of the ecological impacts of cannibalism and the underlying mechanisms remains limited. A better understanding of the ecological significance of cannibalism requires greater attention to the factors affecting the intensity of cannibalistic interactions. Several factors influence the

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intensity of cannibalism including population density, the availability of alternative prey and the size structure of interacting individuals (Elger & Crespi 1992; Rudolf 2008; Wisinger *et al.* 2010). In many cannibalistic interactions, size structure can be potentially important because the success of cannibals strongly depends on the size asymmetry between interacting conspecifics (e.g. the capturing organ of potential cannibals and the body size of potential victims (Kusano, Kusano & Miyashita 1985; Ohdachi 1994; Sogard & Olla 1994; Qin & Fast 1996)). Indeed, most theory on population and evolutionary ecology of cannibalism explicitly assumes that size structure plays a key role in cannibalistic interactions (Claessen, De Roos & Persson 2004; Rudolf, Kamo & Boots 2010).

Although the importance of size structure to cannibalism is well appreciated, it is important to note that cannibalism itself may operate to enhance size structure within populations (DeAngelis, Cox & Coutant 1979; Sogard & Olla 1994; Fangan & Odell 1996; Huss, Van Kooten & Persson 2010). For example, the energetic benefits of cannibalism can enhance size structure by increasing the growth rates of cannibals vs. noncannibals. This seems to be likely, when conspecific prey represent a richer nutrient source that is also easy to assimilate (Meffe & Crump 1987; Wildy *et al.* 1998) or when heterospecific prey are scarce in the environment. In addition, size-selective cannibalism can increase size structure within populations. For example, selective cannibalism on individuals in intermediate size classes can produce a bimodal size distribution within population. Hence, we suggest that while size structure promotes cannibalism, cannibalism may further drive asymmetries in size structure and such dynamics are fundamentally important to spatiotemporal variation in the size structure of cannibalistic populations. However, few empirical studies have explored the ecological importance of this positive feedback to short-term population dynamics (DeAngelis, Cox & Coutant 1979; Fangan & Odell 1996).

A growing body of work also demonstrates that the risk of being eaten can strongly influence trophic dynamics in natural communities via trait-mediated indirect interactions (reviewed by Schmitz *et al.* 2008). Such nonconsumptive predator effects are ubiquitous and can play an important role in cannibalistic systems by altering prey foraging behaviour (Rudolf 2008) and reducing the development of trophic polyphenisms (Kishida, Trussell & Nishimura 2009).

This study examined how cannibalism dynamics through time were influenced by the interaction between temporal changes in salamander size structure and predation risk imposed by dragonfly larvae. We found that cannibalistic interactions strongly depended on whether predation risk from larval dragonflies was present. In the absence of dragonflies, cannibalism was initially intense and the changes in salamander size structure caused by this interaction further intensified cannibalistic interactions through time. In contrast, this positive feedback was not observed in the presence of dragonfly predation risk. Hence, early behavioural responses to predation risk and subsequent developmental responses were keys to reducing the intensity of cannibalism.

## Materials and methods

### STUDY SYSTEM AND BACKGROUND

Salamander larvae are excellent organisms for studying the interactive effects of cannibalism and predation risk. The larvae of many salamander species exhibit size-dependent cannibalistic interactions, some of which induce trophic polyphenisms (e.g. an enlarged gape that allows swallowing of conspecifics) when local population density is high (Wakahara 1995; Hoffman & Pfennig 1999). Salamander larvae can be significant predators within pond communities by consuming small invertebrates and heterospecific amphibian larvae and will cannibalize conspecifics when alternative prey are locally unavailable (Collins & Holomuzki 1984; Urban 2007; Kishida *et al.* 2009). When density is high, these cannibalistic interactions can occur between different cohorts (Wisinger *et al.* 2010) and within the same hatchling cohort as they develop (Wakahara 1995). The intensity of cannibalism is also correlated with the degree of trophic polyphenism within the local population. For example, when hatchling density is high, a few individuals (5–20%) enlarge their gapes to produce a 'predaceous cannibal morph' that facilitates the swallowing of conspecifics (Wakahara 1995; Michimae & Wakahara 2002). Because the growth of this morph is so rapid, salamander populations are often comprised of a few large and many small individuals in habitats having high salamander density.

Salamander larvae are also vulnerable to other predators, such as other salamander species, dragonfly larvae and water bugs (Rudolf 2006; Urban 2007). In our system, dragonfly larvae (*Aeshna nigrolava* [Martin]) are top predators that consume invertebrates and amphibian larvae, including salamanders (*Hynobius retardatus* [Dunn]). As with many amphibians (see Relyea 2001; Van Buskirk 2002, 2009), *H. retardatus* alter their behaviour (reduced foraging activity) and morphology (high tails) in response to larval dragonfly risk cues (Iwami, Kishida & Nishimura 2007; Kishida *et al.* 2010) to reduce their risk of being consumed. These antipredator responses can also strongly influence salamander development and interactions with other members of the community (Rudolf 2006; Iwami, Kishida & Nishimura 2007; Kishida, Trussell & Nishimura 2009).

### GENERAL EXPERIMENTAL APPROACH

From late May to early June 2008, we collected salamander egg clusters ( $N = 30$ ) and dragonfly larvae ( $N = 50$ ) from several ponds in Hokkaido, Japan. Each salamander egg cluster was placed in a separate 2-L tank having aged tap water that was maintained at 5 °C and each dragonfly larvae was placed in a 0.25-L container filled with 0.2 L of aged tap water that was maintained at 16 °C. Salamander larvae used in the experiments were randomly selected from 10 egg clusters once hatchlings were 3–7 days old (mean body length  $\pm$  1 SD = 11.35  $\pm$  0.77 (mm),  $N = 20$ ).

The experimental units were 13-L, rectangular aquaria filled with 5 L of aged tap water. Each aquarium contained a covered colander (9 L  $\times$  6.5 W  $\times$  5 D; cm) that housed either one dragonfly ('risk' treatment) or no dragonfly ('no-risk' treatment). The colander was allowed to float in the middle of each aquarium and was perforated with small holes (1.5 mm  $\times$  20 mm) to allow salamanders to detect dragonfly presence via water-borne chemicals and visual cues while preventing dragonflies from consuming salamanders. Dragonfly larvae assigned in risk treatment were late instar and had body lengths of 30–45 mm. We assigned 20 salamanders to each experimental unit, and this initial density (147 individuals m<sup>-2</sup>) is representative of salamander hatchling density in the field (Michimae 2006). Throughout

the experiment, water was changed in each aquarium every fourth day and assigned dragonflies were replaced every two days with a new individual that had been fed one salamander the previous day. Salamanders in each tank were fed 400 brine shrimp (*Artemia salina*) every day. This amount of brine shrimp represents a resource-limited situation, which is appropriate because *H. retardatus* larvae frequently inhabit oligotrophic environments (Kishida, O. personal observation).

#### EXPERIMENT 1: APPROACH

Our first experiment examined whether predation risk influenced positive feedbacks between salamander size structure and cannibalism. Each treatment (risk and no risk) was replicated 13 times, and the experiment lasted 22 days. The total experimental duration was divided into four time periods: 1st (day 1–7), 2nd (day 8–12), 3rd (day 13–17) and 4th (day 18–22). At the end of the 3rd period, we reversed the risk treatments in six of the 13 replicates for each initial treatment to determine whether dragonfly risk effects operated during the final, 4th period. Hence, dragonflies were removed from six of the 13 risk tanks and dragonflies were added to six of the 13 no-risk tanks; the remaining seven tanks for each treatment remain unchanged so that either risk or no risk persisted for the entire experiment (see Fig. 1). Hereafter, we refer to our experimental approach as the initial and second manipulations.

We counted the number of surviving salamanders at the end of each period to estimate the number of individuals that had been cannibalized. Salamanders that had died from other causes besides cannibalism (0–2 individuals per tank, regardless of treatment) were excluded from these estimates. The number of cannibalized salamander ( $C_t$ ) in a given period ( $t$ ) was calculated as

$$C_t = N_{t-1} - N_t - D_t,$$

where  $N_{t-1}$  is the number of surviving salamanders at the end of the previous period,  $N_t$  is the number of salamanders surviving at the end of period  $t$  and  $D_t$  is the number of salamanders that had died because of other causes during period  $t$ .

At the end of 2nd, 3rd and 4th period, we ventrally photographed all surviving salamanders, and the resulting photographs were loaded onto a computer to allow measurement of maximum gape width, maximum head width and body length (snout-vent length). Salamanders with a maximum gape width to head width ratio  $> 0.9$  were considered to have the predaceous, cannibalistic salamander phenotype (Wakahara 1995; Kishida, Trussell & Nishimura 2009). To characterize salamander size structure in each replicate tank, we calculated the ratio of the gape width of the largest salamander to the average head width of all other individuals. This approach is appropriate because only one cannibalistic salamander, which was by far the largest among surviving salamanders, was present in most tanks where cannibalism was frequent. Moreover, cannibalism success depends highly on the ratio of cannibal gape width and victim head width (Kishida *et al.* 2009).

Three times each day (with a minimum of 30 min between each observation) we also recorded salamander activity levels. For days 4–12, we randomly selected 10 salamanders in each tank and counted those exhibiting movement at least once within 10 s. For days 13–22, we differentiated between the largest and other salamanders while scoring behavioural activity in each tank. Hence, the activity of the largest salamander and nine other randomly selected individuals was scored. If tanks had less than nine salamanders, all individuals were measured. We utilized this approach because (i) by day 13, one salamander was by far the largest individual in most no-risk tanks and (ii) we expected individual behaviour to partly depend on its size relative to other salamanders in the tank. Average salamander activity per day was calculated as

$$M_i/O_i,$$

where  $M_i$  represents the number of individuals exhibiting movement in each tank per day and  $O_i$  represents the number of individuals used to assess activity levels in each tank per day. We calculated the average activity of salamanders in 1st and 2nd period, the largest salamander in 3rd and 4th period, and the individuals other than the largest one in 3rd and 4th period in each tank. These variables were used in statistical analyses after arcsine square root transformation.

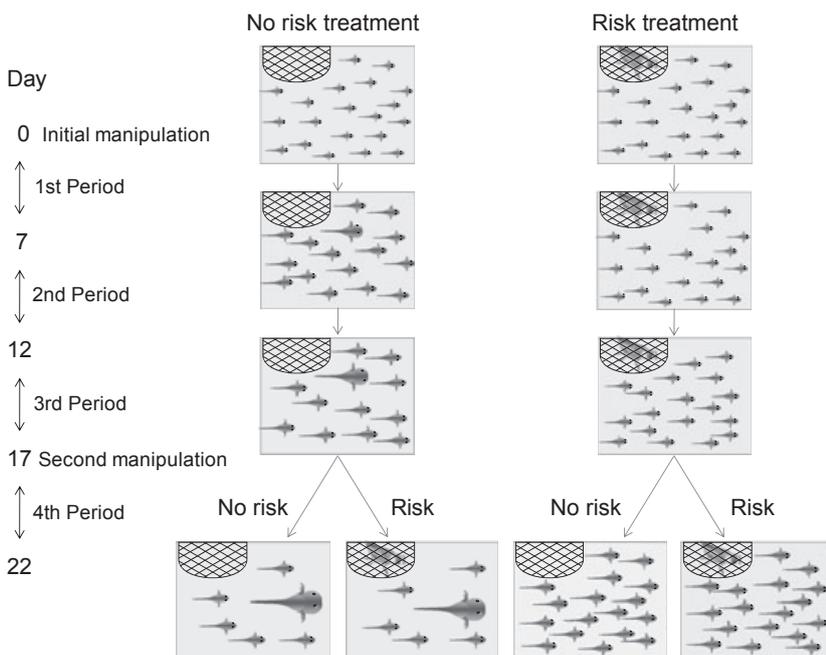


Fig. 1. Diagram describing the design of Experiment 1.

## EXPERIMENT 1: STATISTICAL ANALYSES

Our preliminary analyses found that the second manipulation and its interaction with the initial manipulation had no significant effects on our response variables (see Appendix S1). Hence, the data from both manipulations were pooled before conducting statistical analyses that focused exclusively on the effects of the initial manipulation.

To examine the influence of dragonfly predation risk on cannibalistic interactions between salamanders, we conducted a repeated-measures ANOVA on the number of salamanders cannibalized across all time periods.

During the 1st and 2nd periods, we measured the activity levels of ten randomly selected salamanders in each tank, but for the 3rd and 4th periods, we separately measured the activity of the largest and the smaller salamanders. Hence, we performed separate analyses for each pair of time periods. We used a repeated-measures ANOVA to examine how dragonfly presence affected salamander activity during the 1st and 2nd periods, and this analysis was followed by ANOVA on salamander activity for each time period with dragonfly treatment (risk, no risk) as a fixed effect. The same approach was used on activity data for the largest and other small salamanders for the 3rd and 4th periods.

To determine whether dragonfly presence influenced the emergence of the predaceous phenotype in salamanders, we conducted chi-square tests [i.e. tests of independence (Sokal & Rohlf 1995)] to test the null hypothesis that the number of tanks having zero, one or two predaceous salamanders did not differ among our risk treatments at the end of the 2nd, 3rd and 4th periods. To determine whether dragonfly predation risk affected the increase in salamander size structure, we conducted a repeated-measures ANOVA on size structure data obtained at the end of the 2nd, 3rd and 4th periods (i.e. ratio of the gape width of the largest salamander to the average head width of all other individuals). To further examine the details of size-structure dynamics, we conducted repeated-measures ANOVAs on the gape width of the largest individuals and the average head width of all other individuals at the end of the 2nd, 3rd and 4th periods.

In the aforementioned repeated measure ANOVAs, we conducted Mauchley's test to determine whether our data satisfied the sphericity assumption. If this assumption was not satisfied, we evaluated significance using Greenhouse–Geisser *F*-statistics (Quinn & Keough 2002).

Because our second manipulation had no effect on the number of salamanders cannibalized and salamander size structure, we only considered the effects of the initial manipulation on the positive feedback between cannibalism and size structure. To explore this feedback, we focused on two predictions to explore the sequential feedback dynamics between cannibalism and size structure: (i) Increases in size structure in the 3rd period depended on the number of salamanders cannibalized in the 2nd period and (ii) the number of salamanders cannibalized in the 4th period depended on increases in size structure in the 3rd period. We used linear regression and Spearman's correlation analyses to examine the association between increases in size structure during the 3rd period (i.e. the difference in size structure at the end of the 2nd and 3rd periods) and the number of salamanders cannibalized in the 2nd and 4th periods. All data for the no-risk treatment were normally distributed (Shapiro–Wilk's test,  $P > 0.1634$ ), but those for the risk treatment were not because of the low number of salamanders cannibalized (Shapiro–Wilk's test,  $P < 0.01$ ), so linear regressions and Spearman's rank-order, nonparametric correlation analysis were used, respectively.

## EXPERIMENT 2: APPROACH

In Experiment 1, we found that the initial absence of dragonfly predation risk produced a strong positive feedback between size structure and the number of salamanders cannibalized, whereas the second manipulation (reversal of dragonfly presence) had no effect on cannibalistic interactions in the 4th period (see Appendix S1). These results suggest that the influence of dragonfly predation risk on salamander cannibalism dynamics is most important at early stages of development. To obtain a more mechanistic understanding of this interaction, Experiment 2 (i.e. predation trials) examined how dragonfly predation risk influences the initiation of cannibalism between hatchling salamanders (11–12 days old). We focused on three important and sequential aspects of cannibalistic interactions: (i) initial encounters between prospective cannibals and victims, (ii) aggressive biting behaviour by prospective cannibals per encounter and (iii) swallowing success of prospective cannibals per biting behaviour.

We established nine and 12 replicates of the risk (dragonfly present) and no-risk (dragonfly absent) treatments, respectively, following the general approach outlined for Experiment 1. After 7 days, cannibalism had occurred in three of the no-risk tanks and we therefore assumed that cannibalism would soon commence in the remaining no-risk tanks. Hence, our final design had nine replicates per treatment. We immediately (on day 7) assessed salamander activity levels (i.e. encounters) by determining how many of 10 randomly selected individuals in each tank moved over a 10-s period. After measuring salamander activity, we terminated the experiment and ventrally photographed all individuals to allow measurement of body length, maximum gape width and head width as described in Experiment 1. After taking photographs, salamanders were individually placed into cups; more than half of these individuals were used in predation trials.

We based our selection of individuals for predation trials on morphological data. For each tank, we selected six individuals having the largest gape width (prospective cannibal) and six individuals having the smallest head width (prospective victim). One prospective cannibal and one prospective victim were randomly selected to be paired (i.e. each tank had six different pairs of prospective cannibal and victim.). The trial arena was a container (1.3 L) filled with 300 mL of water from the treatment tank in which the prospective cannibal and prospective victim had been reared either with or without dragonfly predation risk. Hence, the water used in predation trials for the risk treatment contained dragonfly risk chemical cues, whereas the water used in trials for the no-risk treatment did not contain these cues.

We conducted a total of 108 trials (i.e. six pairs  $\times$  nine tanks  $\times$  two treatments) in the following manner. First, we placed the prospective cannibal into the arena. After a 30-min acclimation period, we attempted to feed the prospective cannibal its smaller counterpart (prospective victim) that had been euthanized in 10% alcohol just prior to beginning a given trial. Each small salamander (held in tweezers) was offered by placing it in front of the prospective cannibal. We recorded whether the prospective cannibal bit at the prospective victim and whether it successfully consumed it. If the prospective cannibal did not bite within 3 s, the prospective victim was removed from the arena and then presented again after 5 s. This approach was repeated for no more than five times for each pair. If the prospective cannibal did not cannibalize the prospective victim after the 5th offering, the trial was terminated. To determine whether dragonfly predation risk affected the biting behaviour of prospective cannibals, we calculated the proportion of bites in each replicate pair and used the mean number of bites exhibited in each tank in subsequent statistical analyses. To determine how dragonfly predation risk influenced

the likelihood of cannibalism, we calculated the rate of cannibalism success ( $C_s$ ) per biting behaviour as

$$C_s = 1/B \text{ or } 0/B$$

where  $B$  is the number of bites delivered within five trials and 1 and 0 represent success and failure of cannibalizing, respectively in each trial pair. The mean rate of cannibalism success for each tank was used in statistical analyses.

## EXPERIMENT 2: STATISTICAL ANALYSES

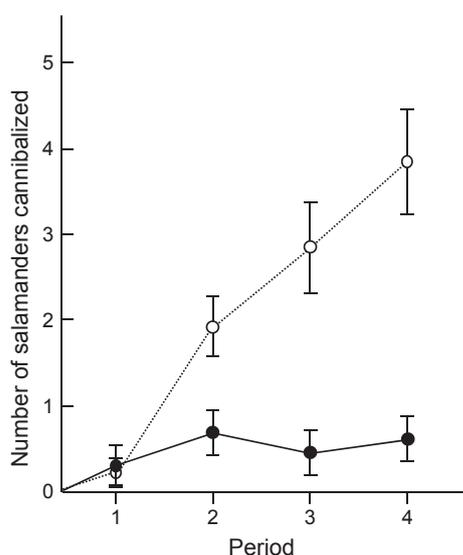
We used MANOVA, followed by one-way ANOVAs, to examine the influence of dragonfly predation risk on salamander activity levels (i.e. encounter rates), biting rates and cannibalism success. These analyses revealed that each aspect of cannibalism was suppressed in the risk treatment. We hypothesized that this risk effect was caused by differential size asymmetries between the prospective cannibal and the prospective victim among our treatments. To determine whether size asymmetry in no-risk treatment was greater than that in the risk treatment, we performed a nested ANOVA on the ratio of cannibal gape width to victim head width that considered risk treatment as a fixed effect and replicate tanks as a random, nested effect.

## Results

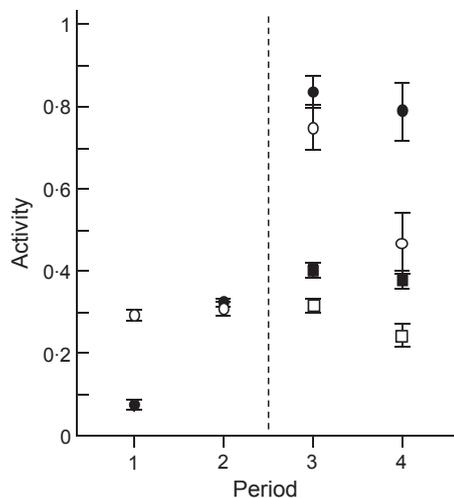
### EXPERIMENT 1

Cannibalism among salamanders was more intense in the absence of dragonflies (repeated-measures ANOVA,  $F_{1,24} = 17.75$ ,  $P = 0.0003$ ), and a significant interaction between risk treatment and time ( $F_{3,72} = 14.67$ ,  $P < 0.0001$ ) indicated that the number of salamanders cannibalized increased more strongly with time in the absence of dragonfly predation risk (Fig. 2).

For salamander activity levels during the 1st and 2nd periods, the interaction between the effects of dragonfly



**Fig. 2.** Mean ( $\pm$ SE) number of salamanders cannibalized in each period for the risk (black circles) and no-risk (white circles) treatments. Results of second manipulations were not represented because of their nonsignificant effects.



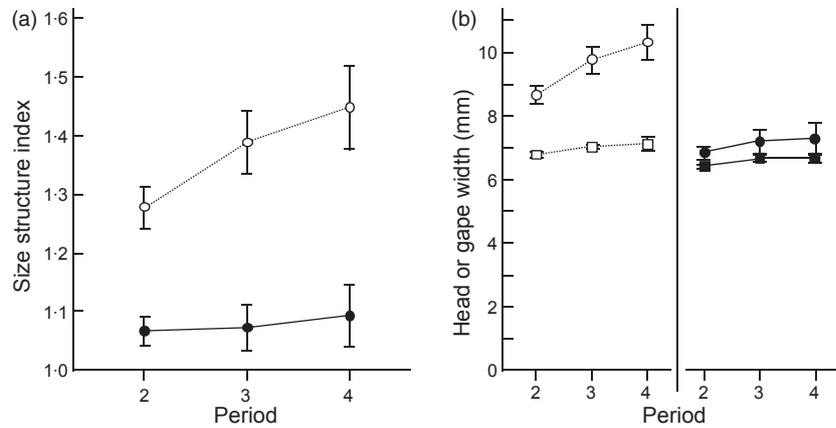
**Fig. 3.** Mean ( $\pm$ SE) behavioural activity of salamander larvae in the risk treatment (black circles) and no-risk treatment (white circles). In the 1st and 2nd period, average activities of randomly selected individuals are shown. In the 3rd and 4th period, average activities of the largest individuals (circles) and the remaining individuals (squares) are shown.

predation risk (repeated-measures ANOVA,  $F_{1,24} = 53.85$ ,  $P < 0.0001$ ) and time ( $F_{1,24} = 126.88$ ,  $P < 0.0001$ ) was significant ( $F_{1,24} = 103.96$ ,  $P < 0.0001$ ). Hence, while salamanders were more active in the absence vs. presence of predation risk during the 1st period (ANOVA,  $F_{1,24} = 110.17$ ,  $P < 0.0001$ ), these differences disappeared by the 2nd period (ANOVA,  $F_{1,24} = 0.85$ ,  $P = 0.3648$ ; Fig. 3).

We also detected a strong interaction (repeated measure ANOVA,  $F_{1,24} = 5.69$ ,  $P = 0.0253$ ) between the effects of risk treatment ( $F_{1,24} = 8.80$ ,  $P = 0.0067$ ) and time ( $F_{1,24} = 8.11$ ,  $P = 0.0089$ ) on the activity levels of the largest salamanders during the 3rd and 4th periods (Fig. 3). While there were no risk effects on the activity levels of large salamanders in the 3rd period (ANOVA,  $F_{1,24} = 1.37$ ,  $P = 0.2538$ ), large salamanders in the presence of dragonfly predation risk were more active than those in the absence of predation risk during the 4th period (ANOVA,  $F_{1,24} = 11.32$ ,  $P = 0.0026$ ). In contrast, the activity levels for the remaining salamanders in each tank were higher for those in the presence of predation risk (repeated-measures ANOVA,  $F_{1,24} = 19.86$ ,  $P = 0.0002$ ), and this effect persisted over the 3rd and 4th periods for both risk treatments (interaction;  $F_{1,24} = 2.79$ ,  $P = 0.1076$ ).

At the end of the 2nd period, predaceous salamanders were more prevalent in the no-risk treatment ( $\chi^2_1 = 28.84$ ,  $P < 0.0001$ ). In 11 of 13 no-risk tanks, there was one predaceous salamander, whereas in the risk tanks, only two of 13 had either one or two predaceous salamanders. This pattern was also evident at the end of the 3rd ( $\chi^2_1 = 18.34$ ,  $P < 0.0001$ ) and 4th periods ( $\chi^2_1 = 20.85$ ,  $P < 0.0001$ ). Thus, most of the no-risk tanks had predaceous salamanders while most of the risk tanks did not.

Repeated-measures ANOVA on the size structure of salamanders (i.e. the ratio of the gape width of the largest salamander to the average head width of all other individuals) revealed



**Fig. 4.** Mean ( $\pm$  SE) (a) salamander size structure in the risk treatment (black circles) and no-risk treatment (white circles) and (b) gape width of the largest salamanders (circles) and head width of the remaining salamanders (squares) in the risk treatment (black) and no-risk treatment (white).

that size structure increased through time (G-G,  $F_{1,25,28.65} = 13.35$ ,  $P = 0.0005$ ), and they were much larger at the end of the 2nd, 3rd, and 4th periods in the absence of dragonfly predation risk ( $F_{1,23} = 19.49$ ,  $P = 0.0002$ ). A significant interaction (G-G,  $F_{1,25,28.65} = 7.42$ ,  $P = 0.0073$ ) indicated that size structure index increased considerably through time in the absence of dragonfly predation risk but did not change in the presence of risk (Fig. 4a).

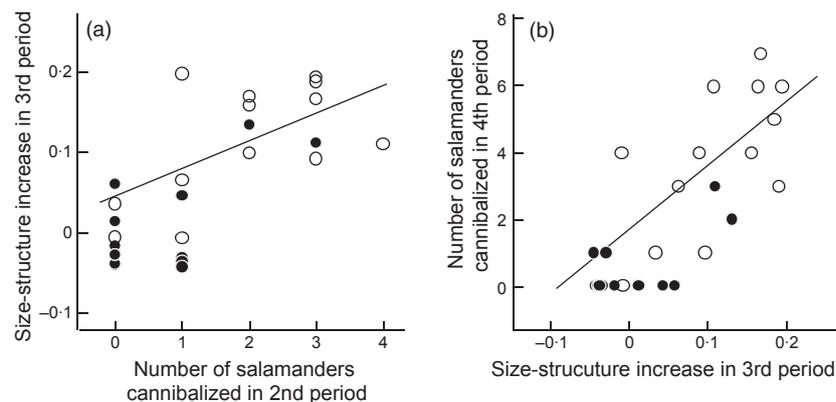
The largest salamanders had significantly larger gapes through time (repeated-measures ANOVA, G-G,  $F_{1,25,28.77} = 24.06$ ,  $P < 0.0001$ ) and in the presence rather than absence of dragonfly predation risk ( $F_{1,23} = 19.83$ ,  $P = 0.0002$ ). However, a significant interaction between risk treatment and time (G-G,  $F_{1,25,28.77} = 7.93$ ,  $P = 0.0056$ ) revealed that gape width increased throughout the experiment in the absence of dragonfly predation risk but remained unchanged in the presence of risk (Fig. 4b). Aside from the largest individual, the other salamanders in each tank had heads that were significantly wider in the absence of dragonfly predation risk (repeated-measures ANOVA,  $F_{1,23} = 9.91$ ,  $P = 0.0045$ ). Head width of the smaller salamanders also increased through time ( $F_{2,46} = 40.63$ ,  $P < 0.0001$ ) and did not depend on risk treatment ( $F_{2,46} = 1.9472$ ,  $P = 0.1543$ ).

Our analyses also revealed that positive feedbacks between the number of salamanders cannibalized and size structure only occurred in the absence of dragonfly predation risk (Fig. 5). In the absence of risk, the number of salamanders

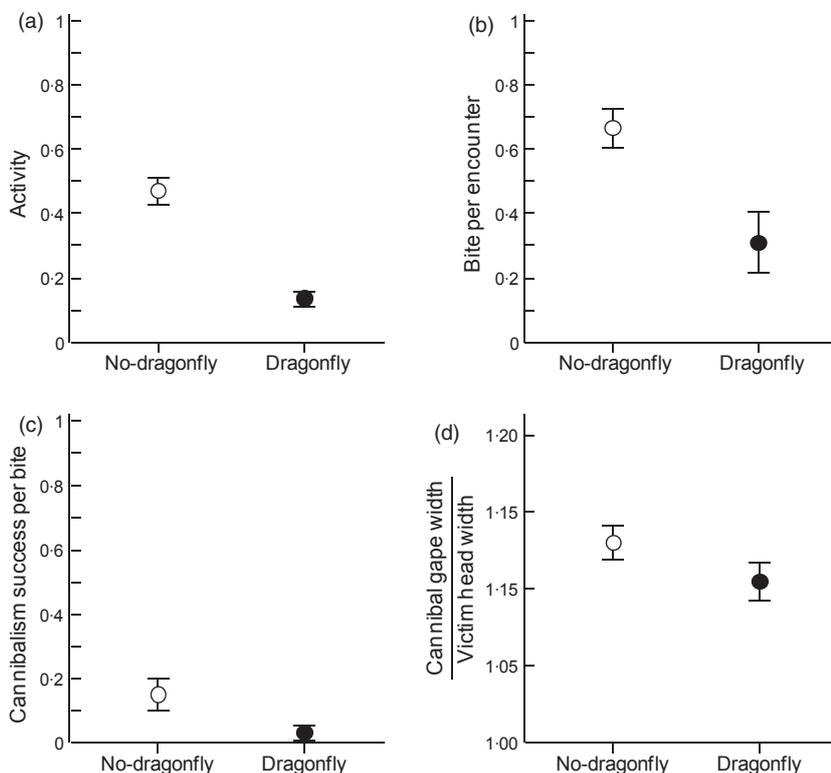
cannibalized in the 2nd period significantly explained the increase in salamander size structure in the 3rd period (linear regression,  $Y = 0.04 + 0.04X$ ,  $R^2 = 0.35$ ,  $F_{1,11} = 5.96$ ,  $P = 0.0327$ ), but there was no relationship in the presence of risk (Spearman's rank correlation coefficient,  $\rho = 0.296$ ,  $P = 0.3235$ ; Fig. 5a). Moreover, the increase in salamander size structure during the 3rd period explained the number of salamanders cannibalized in the 4th period in the absence ( $Y = 1.74 + 19.09X$ ,  $R^2 = 0.41$ ,  $F_{1,11} = 7.50$ ,  $P = 0.0193$ ) but not presence ( $\rho = 0.3092$ ,  $P = 0.3040$ ; Fig. 5b) of dragonfly predation risk.

EXPERIMENT 2

We found that dragonfly predation risk (MANOVA,  $F_{1,16} = 26.64$ ,  $P < 0.0001$ ) had the same effect (interaction:  $F_{2,15} = 1.40$ ,  $P = 0.2760$ ) on all three behavioural aspects of cannibalism. Dragonfly predation risk reduced encounter rates (ANOVA,  $F_{1,16} = 38.60$ ,  $P < 0.0001$ ; Fig. 6a), bites per encounter (ANOVA,  $F_{1,16} = 12.91$ ,  $P = 0.0024$ ; Fig. 6b) and cannibalism success per bite (ANOVA,  $F_{1,16} = 6.49$ ,  $P = 0.0215$ ; Fig. 6c). We found no effect of risk treatment on the cannibal gape width to victim head width ratio (Nested ANOVA,  $F_{1,16} = 2.16$ ,  $P = 0.1609$ ; Fig. 6d). Hence, the significant risk effects that we detected for cannibalism success were not governed by risk effects on the size asymmetry between cannibals and their prey.



**Fig. 5.** The (a) relationship between the number of salamanders cannibalized in the 2nd period and increase in size structure in the 3rd period and (b) relationship between increase in size structure in the 3rd period and the number of salamanders cannibalized in the 4th period in the risk (black) and no-risk treatments (white). Solid lines denote significant linear regressions in the no-risk treatment (see Results for details). There were no significant relationships in the risk treatment.



**Fig. 6.** Mean ( $\pm$ SE) (a) activity levels, (b) biting rates per encounter, (c) cannibalism success per bite and (d) the size balance between gape width of prospective cannibals and head width of prospective victims in the risk (black circles) and no-risk (white circles) treatments.

## Discussion

Availability of alternative prey and the density and size structure of cannibalistic species are important factors shaping the short- and long-term dynamics of cannibalistic interactions (DeAngelis, Cox & Coutant 1979; Van Buskirk 1989; Johansson 1992; Rudolf 2006; Kishida *et al.* 2009). Cannibalism is also known to play a prominent role in the structure and dynamics of natural food webs and communities (Polis 1981; Claessen, De Roos & Persson 2004; Persson, De Roos & Bertolo 2004; Persson *et al.* 2004; Woodward *et al.* 2005; Rudolf 2007a), but there has been considerably less attention to how predation risk, and its interaction with other factors, influences cannibalistic interactions among intermediate predator species (Rudolf 2007b, 2008; Rudolf & Armstrong 2008). Our study found that cannibalism among salamanders rarely occurred in the presence of dragonfly risk cues (Fig. 2). This pattern emerged because the positive feedback between salamander size structure and cannibalism was initiated in the absence, but not presence, of dragonfly predation risk.

When confronted with predation risk, many animals reduce their foraging activity to reduce their likelihood of being detected by predators (Lima & Dill 1990; Werner & Peacor 2003). In our first experiment, the effect of predation risk on salamander activity levels varied considerably through time (Fig. 3). Initially (1st period), salamanders were less active in the presence of dragonflies, but this risk effect was absent by the 2nd period and completely reversed by the 3rd and 4th periods with salamanders being most active in the presence of dragonflies. We suggest that both competition and the relative importance of risk from cannibals and

heterospecific predators can explain why salamander activity levels later in the experiment were higher in the presence of dragonfly predation risk. First, the high density of salamanders in the dragonfly treatment likely intensified competition for resources, and previous work has shown that individual foraging activity is higher under limited resources and higher conspecific density (Anholt & Werner 1995; Relyea 2002). Second, weaker cannibalistic interactions in the risk treatment allowed salamanders to be more active than those in the no-risk treatment. Small salamanders in the absence of dragonfly predation risk likely reduced their activity levels to minimize their encounters with the large cannibalistic salamanders that were typical of this treatment. Such reduced activity in noncannibals in response to cannibals is common in other systems where cannibalism is prevalent (Sih 1982; Leonardsson 1991; Ziemba & Collins 1999; Rudolf 2006; Wissinger *et al.* 2010). Alternatively, size effects may also explain the observed differences in activity levels of small individuals between treatments if there are differences in body size between treatments. However, there was no strong evidence suggesting that such size effects are important because the size of small salamanders in the risk treatment in the 3rd (ANOVA,  $F_{1,24} = 3.9382$ ,  $P = 0.0587$ ) and 4th periods ( $F_{1,23} = 3.8287$ ,  $P = 0.0626$ ) was similar to that of small salamanders in the no-risk treatment. Compared with the possible importance of conspecific interactions, which intensified through time (i.e. competitive interaction in risk treatment and cannibalistic interaction in no-risk treatment), the effects of dragonfly predation risk on salamanders were weak later in the experiment. Indeed, our treatment reversals did not affect salamander activity in the 4th period (Appendix S1). Therefore,

salamander larvae appear to have changed their activity levels to better match temporal changes in trophic interactions.

The high level of cannibalism was strongly associated with the broad size structure of salamanders in the absence of dragonfly predation risk; only one salamander in each replicate of the no-risk treatment was clearly larger and had the predaceous phenotype. This broad size structure expanded with time (Fig. 4a) because large salamanders were able to grow rapidly (Fig. 4b) as a result of their consumption of smaller individuals. It is worth noting that size-selective cannibalism (i.e. selection against individuals with intermediate size classes by large cannibals) can also broaden the size structure of the cannibalistic population. However, this scenario is unlikely in our system because cannibalism success in *H. retardatus* salamander larvae highly depends on the size asymmetry between cannibals and victims (Ohdachi 1994; Kishida *et al.* 2009). The positive feedback between cannibalism and size structure was clearly operating because the number of salamanders cannibalized in the 4th period was strongly associated with the expansion of salamander size structure in the 3rd period. Moreover, the early (1st and 2nd periods) effects of dragonfly predation risk on the number of salamanders cannibalized drove this positive feedback and thus the outcome of cannibalistic interactions (Fig. 5).

We found that reversals of dragonfly predation risk after the 3rd time period had no effect on salamander activity levels or the occurrence of cannibalism in the 4th period (Fig. 3; Appendix S1). Hence, in the treatment reversal (dragonfly to no-dragonfly) where salamander size structure was narrow, cannibalism was unlikely despite dragonflies no longer being present (Fig. 2; Appendix S1). Similarly, in the treatment reversal (no-dragonfly to dragonfly) where salamander size structure was broad, cannibalism was high regardless of dragonfly presence (Fig. 2; Appendix S1). These results highlight that risk effects from heterospecific predators on cannibalistic interactions among salamander larvae during their early developmental period are key to the dynamics of cannibalistic interactions.

Our second experiment examined how dragonfly predation risk influences the initiation of cannibalism among salamander hatchlings. Similar to the results of our first experiment, we found that average encounter rate in the risk treatment was 28.6% of that in the no-risk treatment (Fig. 6a). In our predation trials, where prospective cannibals were offered potential victims, average bites rate and swallowing success in the risk treatment were 46.3% (Fig. 6b) and 20.1% (Fig. 6c) of those in the no risk treatment, respectively. These combined effects of dragonfly predation risk reduced the overall probability of cannibalism in the risk treatment to 2.7% of that in the no-risk treatment. This reduction in cannibalism was not driven by salamander morphology because there were no treatment effects on the size asymmetry between cannibal gape width and victim head width (Fig. 6d). Hence, the effects of dragonfly predation risk on cannibal behaviour are also important to the initiation of cannibalistic interactions. Moreover, behavioural responses to predation risk may be the origin of the subsequent positive

feedback dynamics between cannibalism and size structure. We suggest that reductions in cannibalism under predation risk are adaptive because despite its obvious energetic benefits, this behaviour also increases the likelihood of cannibals being attacked by dragonflies. Cannibals require considerable time (up to an hour) to consume their victims (O. Kishida, personal observation). Moreover, cannibals swallow their prey head first and the tails of victims project out of the cannibal's mouth. This feeding mode likely limits the cannibal's mobility, thereby increasing its vulnerability to dragonfly predation.

Our study focused on the nonconsumptive effects of predators on cannibalism, but in natural settings, predators can have both nonconsumptive and consumptive effects. Because cannibalism and resulting effects on prey size structure often emerge under high conspecific prey density (Huss, Van Kooten & Persson 2010), we suggest that reductions in larval salamander density caused by dragonfly predation may further suppress cannibalistic interactions among salamanders. Indeed, this suppression may also be reinforced if dragonflies selectively consume cannibals. Because the predaceous salamander phenotype has slow swimming speeds, it is more susceptible to dragonfly predation than the nonpredaceous phenotype (G. Miyazaki, O. Kishida & K. Nishimura, unpublished data). Although more work in this area is clearly needed, our results highlight the importance of considering nonconsumptive predator effects to cannibalism dynamics in this and other systems.

Previous research suggests that positive feedbacks between size structure and the intensity of cannibalism are not unique to the *H. retardatus* system. Several salamander and frog larvae exhibit cannibalistic interactions that appear to be based on trophic polyphenisms where populations have a few large cannibals and many, smaller noncannibals (Pfennig 1990; Hoffman & Pfennig 1999; Ziemba & Collins 1999). Cannibalism can also be important in fish (DeAngelis, Cox & Coutant 1979; Sogard & Olla 1994; Baras & Jobling 2002) and carnivorous insects (Fangan & Odell 1996), and size structure could play important roles in their short-term population dynamics (DeAngelis, Cox & Coutant 1979; Sogard & Olla 1994; Fangan & Odell 1996). Although there is little evidence for feedback dynamics between size structure and cannibalism in natural systems, it is well recognized that a small number of larger individuals within fish hatchling cohorts of aquaculture systems become cannibals in subsequent life stages (Nakamura & Kasahara 1955; DeAngelis, Cox & Coutant 1979; Baras *et al.* 2000) and can cause significant declines in fish stocks (DeAngelis, Cox & Coutant 1979; Hecht & Pienaar 1993; Kubitza & Lovshin 1999). Given that behavioural changes induced by predation risk from heterospecific predators is very common in animals (Werner & Peacor 2003), the suppression of positive feedbacks between size structure and cannibalism may be prevalent in nature.

Theory has considered the potential implications of cannibalism to long-term population dynamics (Claessen, De Roos & Persson 2004; Rudolf 2008), and it is clear that factors such as size structure, energy gain by cannibals and

reduced competition can strongly influence the long-term stability of populations (reviewed in Claessen, De Roos & Persson 2004). However, to our knowledge, only one model explicitly considered positive feedbacks between size structure and cannibalism to long-term population dynamics, and the predicted effects of cannibalism on population stability were complex (Cushing 1992). Our study suggests that it is important to consider such feedback loops because their strong short-term effects on population dynamics may also operate in the longer term. For example, the extensive mortality caused by cannibalism may stabilize long-term population dynamics (see Rudolf 2007a,b) via dramatic population declines in successive generations. Conversely, such stabilizing effects in the long term could be disrupted by predation risk, especially if such risk strongly diminishes the intensity of cannibalism as observed in our study. We suggest that more effective synthesis of theory and empiricism that considers the feedback between size structure and cannibalism will improve our understanding of the long-term ecological significance of cannibalism and how it is shaped by different ecological contexts, such as the presence and absence of another predator in the system.

Recent work also reveals that individual energy gain and decreased population density associated with cannibalism can strongly influence community dynamics (Persson *et al.* 2003; Claessen, De Roos & Persson 2004; Rudolf 2007a,b, 2008). For example, Persson *et al.* (2003) found that cannibalistic interactions among perch can have cascading, top-down effects on phytoplankton populations that are transmitted through the effects of cannibalism on the zooplankton community. We suggest that similar, community-wide impacts may also emerge because of cannibalism dynamics among salamanders. In the absence of dragonfly predation risk, both reduced competition and high individual energy gain caused by increased cannibalism may lead to accelerated metamorphosis among surviving salamanders, which will diminish larval salamander impacts on the prey communities within ponds. In contrast, because dragonfly predation risk suppresses cannibalism, small salamanders may persist in the population for a longer time, especially if dragonfly predation on salamanders is not intense. As a result, high salamander population densities will persist and their impact on prey resources within the pond is expected to be high. This view suggests that the nonconsumptive effects of dragonfly predation risk on salamander cannibalism dynamics may result in a trophic cascade that diminishes (see Trussell, Ewanchuk & Matassa 2006) rather than enhances the abundance of basal resources. Hence, identifying the relative importance of nonconsumptive vs. consumptive dragonfly effects (in terms of both magnitude and sign) on salamander cannibalism dynamics will be essential to predicting the structure and dynamics of these communities.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Statistical analyses to consider effects of second manipulation.

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