**LETTER**

# Context-dependent reproductive habitat selection: the interactive roles of structural complexity and cannibalistic conspecifics

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## Abstract

Structural complexity generally reduces predation and cannibalism rates. Although the benefits from this effect vary among environmental contexts and through time, it has been the common explanation for high species abundance in complex habitats. We hypothesized that oviposition habitat selection for structural complexity depends on the expected trophic function of the progeny. In *Salamandra infraimmaculata* larvae, expected trophic function is dictated by their sequence of deposition. First cohorts cannibalize later-arriving cohorts, while all compete for shared prey resources. In a mesocosm experiment, we show that gravid salamanders facing conspecific-free pools preferred structurally simple habitats (no rocks), while females facing only pools with older conspecific larvae preferred complex habitats (with rocks). Context-dependent preference of habitat complexity for managing food/safety trade-offs may be extended from classic foraging patch decisions to breeding habitat selection. These trade-offs vary with dynamic larval processes such as priority effects and ontogenetic diet shifts, potentially leading to complex maternal parturition behaviours.

## INTRODUCTION

Habitat structure can be defined as the arrangement of physical objects in the space in which species interact (McCoy & Bell 1991). An important feature of habitat structure is its degree of complexity, a feature that has been much studied in the context of predation. High structural complexity generally reduces the encounter rate between active predators and their prey because of limited visibility and manoeuvrability, and it provides prey with protected, enemy-free spaces to escape predation (Huffaker 1958; Smith 1972; Crowder & Cooper 1982; Warfe & Barmuta 2004). Thus, ecologists have historically recognized that structural complexity tends to reduce predation rates, prevent prey extinction and stabilize predator–prey co-existence (MacArthur 1972; Smith 1972; Janssen *et al.* 2007).

Experimental evidence indicates that structurally complex habitats tend to promote higher abundance for many species. While it is acknowledged that primary consumers and herbivores accumulate in complex habitats largely due to refuge from predation (Heck & Crowder 1991), the mechanisms underlying this pattern for predatory species remain understudied (Denno *et al.* 2005). Several hypotheses have been proposed, but most studies support the idea that habitat complexity provides predators with: (1) refuge from intraguild predation and cannibalism, (2) refuge from physical disturbances and (3) access to alternative resources (reviewed in Denno *et al.* 2005).

Both the availability of alternative food resources and refuge from physical disturbances are qualities of complex habitats that are similarly relevant for both predatory species and herbivores. On the other hand, reduced predation rates have different implications for organisms with different trophic functions. Primary consumers benefit from reduced predation rates due to structural complexity because they are strictly victims of predation. In contrast, top predators lacking natural

enemies suffer from the reduction in predation rates because it reduces their energy intake. However, the trophic function of organisms is a continuum along which many species take intermediate positions. For such species, reduced predation may have both a positive effect on survival (as for primary consumers) and a negative effect on foraging and energy intake (as for top predators). Preferable habitat structure, then, is a species- and context-specific trade-off of foraging rate vs. safety. Complex habitats may be preferred when the cost of predation risk is considerably higher than that of food limitation. On the other hand, simple habitats may be preferred when the opposite cost relations occur. Furthermore, most organisms' trophic functions change throughout their ontogeny or are context-dependent (due to external factors) because of ontogenetic diet changes (e.g. Huss *et al.* 2008), growth to size refuge from predation (Persson & Eklov 1995; Rudolf & Armstrong 2008) and priority effects (Eitam *et al.* 2005). For these animals, the consequences of habitat structural complexity are not straightforward.

Three factors – migration (including habitat selection), survival and reproductive success – contribute to observed distributions and abundance of a particular species. Organisms with complex life cycles with discrete larval habitats (e.g. amphibians, parasitoids, insects with terrestrial adults, aquatic larval stages, etc.) are excellent systems for teasing apart the contributions of these factors due to their strict stage-specific habitat separation. Furthermore, oviposition habitat selection in such systems is a single behavioural action that determines the conditions under which the offspring will grow throughout their entire larval stage, as they cannot emigrate. This single action provides more decisive information on the relative importance of ecological factors than short-term patch selection studies, as its fitness consequences are equivalent to those of the sum of numerous habitat or patch choices that freely moving organisms in continuous habitats make over extended periods of time. In addition, the trade-off between foraging rate and risk of predation is more critical in systems with ephemeral larval habitats as insufficient larval development rates may result in their failure to emerge in time to the next life stage (Audo *et al.* 1995). In these systems, competitive superiority may be defined as the ability of an individual to exploit the limited food resources at a higher rate than, and at the expense of, other individuals, thus out-competing them in the development race to timely emergence. This form of competition may be just as lethal as the effects of predation, making the food vs. safety trade-off more balanced than is generally considered (e.g. the 'life-dinner principle', Stephens & Krebs 1986).

Previous studies of organisms with complex life cycles have shown that in species whose larvae function as prey, mothers tend to prefer structurally complex habitats for them, in order to provide refugia from their predators and increase the rate of successful emergences (Price *et al.* 1980; Orr & Resh 1992; Meiners & Obermaier 2004; Bond *et al.* 2005). In contrast, we found no literature on oviposition habitat selection into discrete habitats for species whose larvae function as top or intermediate predators in the context of habitat complexity. One would expect that in the absence of predators and strong negative intraspecific interactions such as interference, predatory species would prefer simpler habitats, in order to allow their larvae more effective foraging.

We hypothesized that oviposition habitat selection for structural complexity depends on the expected trophic function of the progeny. To test this hypothesis, we studied the ovoviviparous fire salamander (*Salamandra infraimmaculata*; Steinfartz *et al.* 2000) whose larvae are deposited into temporary pools in northern Israel, where they function as top predators (Blaustein *et al.* 1996; Eitam *et al.* 2005), and often rely also on cannibalism because of strictly limited food resources (Degani *et al.* 1980; Eitam *et al.* 2005). The intensity of cannibalism is dictated by size differences between individuals, as bigger larvae deposited earlier into the pool consume their younger, smaller conspecifics (Reques & Tejedo 1996; Eitam *et al.* 2005). Thus, larval size structure and cannibalism constitute a special case of intraguild predation, where the trophic function of an individual depends on its position in the order of arrival. Similarly, strong priority effects are also likely caused by both interference and exploitative competition (Eitam *et al.* 2005). *Salamandra* females are capable of spreading larval clutches among pools and through time, as well as choosing pools to deposit into according to their perceived quality (O. Segev, unpublished data). A preliminary study indicates that gravid females avoid pools containing large conspecific larvae (O. Segev, personal communication). Pool structural complexity, in the form of rocks or aquatic vegetation, is predicted to reduce the degree of cannibalism and conspecific interference by providing shelter for smaller larvae, and by reducing the encounter rate between individuals.

We report the results of an outdoor larviposition choice experiment designed to test the hypothesis that gravid salamander females select their larviposition site according to the expected trophic function of their progeny, depending on their order of arrival. Thus, we predicted a switch in larviposition preference from low structural complexity when pools are free of conspecific larvae to high complexity when pools already contain older conspecific larvae. A larval survivorship experiment verified the hypothesized negative effect of structural complexity on intercohort cannibalism rates.

## METHODS

When rains begin in the autumn following a long dry summer, *Salamandra* females migrate to breeding sites to

larviposit and mate. Natural breeding sites include a few to tens of pools of volumes ranging from a few litres (most frequent) to thousands of litres. These pools vary greatly not only in size, but also in their structural complexity. Some are completely covered by rocks, a layer of sediment and/or terrestrial vegetation. Others have smooth rocky surfaces and little or no plants. During the first autumn rains of 2007 (9–11 and 19–21 November), we collected 26 gravid females on their way to breeding sites on Mt Carmel and the Galilee mountains. The number of individuals collected was the maximum allowed by the Nature and Parks Authority, as *S. infraimmaculata* is listed as locally endangered. Collection during the very first rains, when temporary pools only start to fill, assured that these females did not have a chance to deposit many, if any, larvae prior to their collection.

In order to compare the larviposition decisions of first-arriving females facing conspecific-free pools with those of later-arriving females facing already colonized pools, we conducted two bouts of larviposition trials in an outdoor site with ten 7.5 m$^2$ enclosures, each containing four evenly distributed 45 L plastic tubs (surface area 0.22 m$^2$) dug into the ground. The tubs were filled with tap and rainwater prior to the trial. For each enclosure, we placed four rocks per tub into two randomly selected tubs. The rocks were fully immersed and displaced ∼6 L of water per tub, covering ∼50% of its floor area. The other two tubs contained the same volume of rocks prior to the trial, in order to control for possible chemical effects of the rocks on the water. Control rocks were taken out just before the gravid females were introduced to the enclosures.

## Larviposition bout 1: conspecifics absent

During three nights in early December, 2–4 h after sunset, we introduced 13 gravid females, one in each enclosure. We used sprinklers to simulate rain as larviposition occurs almost exclusively during rainy nights. Once per hour, until all the females had each larviposited once (for a total of 8 h), we observed the females without illumination and from a distance of ∼2 m. We removed each female from its enclosure after it made its first choice of pool for larviposition, allowing it to finish depositing that first clutch into the pool and climb out without interruption. Similar mesocosm experiments indicate that the first chosen pool is the most preferred pool (O. Segev, unpublished data). Our hourly observations revealed that conservatively, at least 80% of the females also visited at least one pool other than the pool that was eventually chosen for larviposition.

## Larviposition bout 2: conspecifics present

After the first bout of larviposition, we removed all the larvae, pumped ∼75% of the water out of all pools,

homogenized the remaining waters between pools within each enclosure, and refilled the tubs with tap and rainwater. This was done to dilute and homogenize any potential signals emitted by the larvae or their mothers into the water. On 12 and 15 December, we collected 200 large larvae from pools in the Galilee site and the Carmel site (mean snout-vent length = 2.12 cm, SD = 0.15 cm). Within each enclosure, we placed five larvae in each of the four tubs, keeping larval biomass uniform across tubs. This density of first-cohort larvae is well within the range occurring naturally following the first larviposition into a pool (L. Blaustein, unpublished data). We left the larvae in the tubs for 24 h with rocks before taking the rocks out of half of the pools and placing one gravid female per enclosure. The 13 females used for the second bout were not the same individuals used in the previous bout. Gravid females from the Carmel site were placed in enclosures with larvae from the Galilee site, and vice versa. This was done to increase genetic distance and potential cannibalism of the older cohort on the newly deposited larvae (aggression between individual larvae increases with increasing genetic distance: Markman *et al.* 2009). The second bout of larviposition in the presence of an older cohort was conducted as in the first bout.

The 2-week time interval between the two larviposition bouts is ecologically relevant, as rain events in Israel are often that long apart, not allowing larviposition in between (mean inter-rain interval times in December during 1976 to 2008 on Mt Carmel = 5.73 days; SD = 5.44 days; range = 1–28 days; Laboratory of Climatology, Department of Geography and Environmental Studies, University of Haifa, Israel). This interval served to homogenize the time each individual was retained in the laboratory prior to experimentation. We did not expect a time-related reduction in pool selectivity by females due to the approaching end of the breeding season (Clark & Mangel 2000) because we conducted the experiment rather early in the 5–6 month long breeding season (October/November to March).

A total of four females in both larviposition bouts were deleted from analyses because they began depositing larvae in their containers just before being placed into the experimental enclosures, they deposited in more than one pool between observations or they did not larviposit at all.

## Larval survivorship experiment

The predictions of the larviposition experiment described above were based on the assumption that structural complexity reduces intercohort cannibalism. The following season (2008–2009), we set up a mesocosm experiment, in part to test this assumption. Here we briefly describe the study and present pertinent results. The full study will be presented elsewhere. In 20 tubs, identical to those used in

the larviposition bouts and filled with 35 L aged tap water, we established two structural complexity treatments by introducing rocks to half of them. The rocks covered 60% (SD = 2%) of the tubs' bottom area and displaced 5.8 L (range: 5.25–6.5 L) of water. We introduced a first cohort of three newborn larvae into each tub (mean wet mass: 268 mg, SD = 25 mg; mean snout-vent length: 1.74 cm, SD = 0.06 cm). Twenty-three days later, during which we fed the first-cohort larvae *ad libitum*, we added a second cohort of five newborn larvae into each pool (mean wet mass: 251 mg, SD = 12 mg; mean snout-vent length: 1.76 cm, SD = 0.05 cm). We recorded larval survivorship to day 80 following the addition of the second cohort. During the experiment, we observed the tubs regularly to distinguish cannibalism from other causes of mortality and emerging metamorphs.

In accordance with local authorities regarding ethical treatment and minimizing mortality to this species, all the field-collected females were safely returned to their capture location as soon as the studies were over, and before the breeding season ended. Similarly, all the remaining larvae were returned to their natal pools or the pools nearest to the capture locations of their mothers.

## RESULTS

### Larviposition trials

During the first larviposition bout (Fig. 1a), in the absence of an earlier cohort, one female chose a rock pool, depositing a single larva, while nine females chose rock-free pools and deposited a total of 109 larvae into them. The difference in pool choice was statistically significant (sign test: $P = 0.011$). During the second larviposition bout (Fig. 1b), in the presence of an older, unrelated cohort, a preference switch occurred as only two females deposited a total of 13 larvae in rock-free pools, whereas 10 females deposited a total of 89 larvae in 11 rock pools. Here, the preference for rock pools was significant (sign test: $P = 0.019$). The preference switch was also significant (normal approximation test of equality of proportions: $P < 0.001$).

### Larval survivorship experiment

First-cohort individuals displayed similar survivorship (mean with rocks: 93.3%, SE = 6.7%; mean without rocks: 83.3%, SE = 7.5%; Mann–Whitney: $U = 36.50$, $P = 0.178$), but more of them metamorphosed by that time in tubs without rocks (mean per cent of cohort remaining: 60.0%, SE = 8.3%) than with rocks (mean = 90.0%, SE = 7.1%; Mann–Whitney: $U = 20.00$, $P = 0.014$). The mean second-cohort survivorship was 42.0% (SE = 13.2%) with rocks
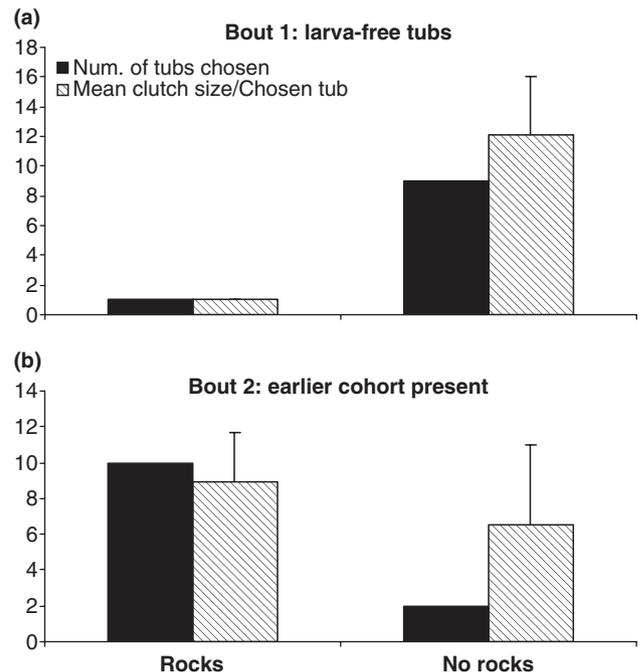


**Figure 1** First-tub structural complexity preferences of females facing (a) vacant tubs and (b) tubs containing older conspecifics. Solid bars present the number of first tubs chosen for larviposition of each type. Hatched bars present the mean deposited clutch size per tub where larviposition occurred. Error bars are 1 SE, where applicable.

and 4.0% (SE = 2.6%) without rocks (Mann–Whitney: $U = 25.00$, $P = 0.032$). This significant difference in mortality of the second cohort was entirely due to cannibalism by first-cohort individuals, even though tubs with rocks contained on average more first-cohort larvae over the observed time period. Thus, structural complexity reduces intercohort cannibalism, suppressing the predation rate of first cohorts upon later cohorts.

## DISCUSSION

We found a strong switch in larviposition pool preferences by gravid salamanders. These results are consistent with our hypothesis that oviposition/larviposition habitat preference in response to structural complexity depends on the expected future trophic function of the progeny, which is determined in this system by the order in which females arrive at a breeding pool. Recently, several hypotheses have been proposed to explain the superiority of complex habitats for predatory species (reviewed in Denno *et al.* 2005). Most of these habitat effects (i.e. more abundant prey, access to alternative resources and more favourable microclimate) usually have a fixed value for a given organism. In contrast, the importance of refuge from

predation or from cannibalism may be dependent on the order of colonization.

When a late-arriving female encounters a set of pools that is already populated by older conspecific larvae, her larvae are likely to be preyed upon by the larger conspecifics. Our larval survivorship experiment verified that habitat complexity reduces *Salamandra* intercohort cannibalism rates. Moreover, within both relative and absolute refuges that are available in complex habitats, individuals of younger cohorts may have more opportunities to forage compared to simple habitats, where reduced activity as a prey behavioural response to the risk of cannibalism may be stronger (Lima & Dill 1990). Hence, we conclude that late-arriving mothers prefer complex habitats for increased refuge from predation, in accordance with previous studies on other organisms (Price *et al.* 1980; Orr & Resh 1992; Meiners & Obermaier 2004; Bond *et al.* 2005; Denno *et al.* 2005).

In contrast, first-arriving females that confronted vacant pools preferred simple habitats. This behaviour may imply that the limited intracohort aggression and cannibalism are not as considerable for first-cohort larvae as exploitative competition that is exerted by individuals both of the same cohort and later cohorts. First-cohort larvae are generally deposited days after pools fill and have yet to accumulate invertebrate prey resources (generally microcrustaceans and dipteran larvae). As the season progresses temperatures drop, further slowing down the accumulation of basal and prey species. Thus, salamander larvae are confronted with an extended initial period of low food availability, during which insect colonization is negligible and in the vast majority of pools, the larviposition of additional conspecifics increases competition. The members of these later cohorts are the largest food items available for first-cohort individuals. In order to reduce the probability of failure to metamorphose and emerge before the pool dries, larvae are predicted to maximize their consumption and development rates. Structurally simple pools increase the encounter rates between first-cohort and later-cohort larvae, and deprive the smaller larvae of refugia, thus enabling the first-cohort larvae to prey on them more effectively as we have demonstrated in the larval survivorship experiment. This increase in food availability for larvae of the first cohort may alleviate competition among members of this cohort. Additionally, each later-cohort individual consumed represents not only a substantial meal for first-cohort individuals but also reduced competition for shared prey resources (Polis *et al.* 1989). Therefore, the preference for structurally simple pools by first arriving mothers can be explained also by the reduction in intercohort competition upon the first cohort.

We cannot infer from our experimental design the mode by which terrestrial females determine either structural complexity or predation risk. Oviposition site selection

behaviour can be responsive to indirect environmental cues or proxies that are correlated with risk of predation rather than the presence of predators *per se* (Blaustein 1999). The females may have responded to the time that has elapsed after the first rains as a reliable proxy for the presence of large conspecifics in the pools rather than detecting the larvae directly. However, in a preliminary study, gravid females avoided larvipositing in pools containing caged and hidden large conspecific larvae (O. Segev, personal communication), implying a capability for direct chemical detection of conspecifics.

The role of refuge from physical disturbances in preference for complex habitats (see Denno *et al.* 2005) was not tested here, but it is likely that this factor acts in combination with the behavioural effects of cannibalism rather than independently. Towards the end of the rainy season, the frequency of rains reduces and pools may dry for a few days or weeks between rains. Incompletely developed larvae in dried pools aggregate underneath rocks where retained moisture may extend their survival by a critical length of time (A. Sadeh, personal observations). Our experiment was conducted well before pools began to dry, as reflected in the results of the first larviposition bout. However, the presence of cannibalistic first cohorts induces reduced foraging in the later-cohort larvae, and their development rate is retarded until the first cohort metamorphoses (A. Sadeh, unpublished data). Therefore, much of their development is delayed towards the end of the larval season when the risk of desiccation is high. Thus, increased risk of desiccation as a possible cause for preferring complex pools early in the season may also be derived in this system from the order of larviposition and the ensuing risk of cannibalism.

This is the first study suggesting preference for habitat complexity as a maternal management strategy for larval foraging vs. predation risk trade-offs that produces complex switching behaviours in the selection of discrete larval habitats. The classic food vs. safety trade-off has been studied extensively in the context of animal foraging for food (Brown & Kotler 2004; Morris *et al.* 2008), and numerous species have been shown to prefer foraging effectively in structurally simple patches, but escape to safer complex patches when faced with a predator (e.g. Persson & Eklov 1995; Stoks 1999; Borcherding 2006), or predator cues (e.g. Rypstra *et al.* 2007). Physiological state was shown to influence foraging patch decisions, as hungry animals venture back to simple patches (Wellborn & Robinson 1987; Pettersson & Bronmark 1993). Oviposition site selection theory has addressed the problem of predation risk upon the forager as a trade-off between current and future reproduction and predicts shifts in site selectivity (reviewed in Godfray 1994; Clark & Mangel 2000). Our application of the food/safety trade-off to discrete breeding habitat selection is

not trivial as such decisions are irreversible when the offspring are confined and unable to emigrate until they have completed their larval stage. While foragers choosing patches have the luxury of responding in real time to their instantaneous body state and risk of predation, breeding mothers also make a long-term decision that will affect their offspring's trade-offs. Thus, breeding behaviours should not only respond to environmental conditions at the time of delivery but also reflect the expected future dynamics in food and safety. These dynamics may be driven by processes such as ontogenetic diet shifts (e.g. Huss *et al.* 2008), population size structures and growth race to size-refuge from predation (e.g. Rudolf & Armstrong 2008), and, as suggested here, order of habitat colonization and priority effects. Studying oviposition habitat selection with respect to such dynamic processes is expected to reveal more complex habitat-selection patterns than those described so far.

## ACKNOWLEDGEMENTS

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