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Kin-selective cannibalism and compensatory performance in larval salamander cohorts inhabiting temporary ponds

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ABSTRACT

Question: Related pairs of individuals tend to express reduced aggression. What are the consequences of this behaviour on groups of developing larvae under food and time limitations?

Hypothesis: The positive effects of reduced cannibalism among related larvae on their success at reaching metamorphosis may be neutralized or even outweighed by negative density-dependent effects.

Organism: Kin-discriminating, cannibalistic fire salamander (*Salamandra infraimmaculata*) larvae from two populations in northern Israel.

Methods: I compared sibling and genetically mixed larval cohorts throughout their larval period in short-lived, outdoor mesocosms.

Conclusions: The experiment supported the hypothesis. Rates of cannibalism were higher in mixed cohorts. Nevertheless, overall survival before habitat loss was similar between treatments. The probability that a larva would attain metamorphosis before early habitat loss was higher in the mixed cohorts than that in the sibling cohorts.

Keywords: competition, desiccation risk, ephemeral habitats, inclusive fitness, kin discrimination.

INTRODUCTION

Kin selection theory (Hamilton, 1964a, 1964b) has been used widely to explain individual behaviours and social interactions, including interference (Pakkasmaa and Aikio, 2003), cooperation (Nowak, 2006), cannibalism (Walls and Roudebush, 1991; Pfennig, 1997), coalition (Widdig *et al.*, 2006), and aggregation patterns (Kokko and Lindstrom, 1996). It predicts that aggressive behaviour will be directed preferentially towards unrelated individuals rather than siblings. Numerous behavioural studies have demonstrated larval kin discrimination, by directing interference, aggression, and cannibalism more towards unrelated conspecifics than towards siblings

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(reviewed in Pfennig, 1997). Kin discrimination tends to display context-dependent expression (Walls and Blaustein, 1995; Hokit *et al.*, 1996; Pakkasmaa and Aikio, 2003), varying with size differences between individuals, their densities and food availability. However, it is generally assumed that groups of pre-reproductive, potentially cannibalistic individuals perform (i.e. grow and survive to maturity) better if their members are genetically related, due to reduced aggression (reviewed in Wells, 2007). Focusing on the group-level consequences of this behaviour over the entire larval period might be informative for recruitment patterns to populations (Johansson and Crowley, 2008; Wissinger *et al.*, 2010), as well as for analysing female oviposition habitat selection strategies. In clutch-depositing organisms, such as clutch-spreading amphibians (e.g. Segev *et al.*, 2011) and superparasitism in gregarious parasitoids (e.g. Segoli *et al.*, 2010), maternal behaviour is expected to optimize the female's fitness payoff from her entire clutch.

Intra-specific larval interactions in temporary habitats are typically strongly competitive, and often aggressive, since the exploitation of the limited food resources determines the likelihood of emerging early enough to avoid death when the habitat disappears (Crump, 1983; Dennehy *et al.*, 2001; Wissinger *et al.*, 2004). Generally, a selfish act is predicted when its benefit to the actor (b) is greater than its cost to the victim (c), weighted by the relatedness (r) of the victim to the actor [i.e. when $b > rc$ (Hamilton, 1964a, 1964b)]. Specifically, the cost of full cannibalism to the victim is its expected fitness if it were not cannibalized, determined largely by its probability of surviving to emergence from the larval habitat, whereas the benefit to the cannibal is primarily the increase in its probability of survival to emergence (Eickwort, 1973). Several studies have shown reduced aggressive or cannibalistic behaviour towards kin in the larval stages of organisms inhabiting ephemeral habitats (Walls and Roudebush, 1991; Pfennig, 1997; Markman *et al.*, 2009; Segoli *et al.*, 2009). Consistently low rates of cannibalism can be hypothesized to result in lower mortality rates and therefore better performance of groups of relatives, compared with groups of unrelated individuals.

An alternative ecological outcome can be hypothesized when considering kin-selective behaviour and its effects in a group of larvae under food and time limitations. Consistently low rates of cannibalism in groups of related individuals may maintain high larval densities and therefore high levels of hunger (Polis, 1981). Under sufficient food limitation, this may result in increased non-cannibalistic, density-dependent mortality due to deterioration in physiological conditions, compared with populations that are thinned by cannibalism. Reduced food availability due to competition may also depress development rates, therefore increasing the risk of death when temporary habitats disappear (Wells, 2007). In addition, Hamilton's rule ($b > rc$) may lead to behaviours that vary temporally. As time runs out before the habitat disappears, cannibalism might be necessary to provide the cannibal with the amount of energy required to emerge in time (i.e. b is very large), whereas the victim might die due to habitat loss even if not cannibalized (i.e. c is very small). Thus, in food-deprived temporary habitats, the tendency of highly related individuals to avoid cannibalizing each other may be lost with time or neutralized by other, density-dependent sources of mortality. This may potentially lead to similar or even reduced performance of sibling cohorts compared with cohorts of more distantly related individuals.

In this study, I consider the performance of salamander larval cohorts in temporary pools. In a recent study, Markman *et al.* (2009) showed that pairs of same-sized larvae exhibited significant relatedness-biased aggression. However, their laboratory experiment isolated this behaviour from its potential interactions with other density-dependent and temporal factors, and kept the participating individuals at uniform feeding levels. Thus, the influence of relatedness-biased aggression on the larval cohorts' performance and expected

fitness remains unclear. To test this, I set up mesocosms with cohorts of either siblings or genetically mixed individuals under relatively low food availability and a short hydroperiod, and monitored their performance through most of their larval period.

METHODS

Study organism

Adult female fire salamanders (*Salamandra infraimmaculata*) in northern Israel are ovoviviparous and larviposit mostly into temporary pools. Most natural rock pools hold a few tens of litres of water (e.g. Spencer *et al.*, 2002), while a few ancient man-made pools are also utilized and support large populations (Segev *et al.*, 2010). Hydroperiods vary greatly both among pools and among years, ranging from several weeks to a few months and forcing the larvae to complete their development before the pools dry. This developmental race against time is often carried out with high larval densities and poor food resources that are crucial for fuelling development. *Salamandra* larvae are top predators in temporary pools and cannibalism and intra-specific interference are frequent (Reques and Tejedo, 1996; Sadeh *et al.*, 2009). The outcomes of these agonistic interactions are largely determined by the relative size of their participants, where large individuals of older cohorts dominate the pool, exerting detrimental priority effects on younger cohorts (Eitam *et al.*, 2005; Sadeh *et al.*, 2009). In highly ephemeral pools, excess energy acquired through cannibalism is allocated to development to accelerate metamorphosis and escape death by desiccation (Sadeh *et al.*, 2009). I used larvae from the Carmel and Galilee regions, two regions inhabited by genetically distinct populations of fire salamanders (Peleg, 2008; L. Blank *et al.*, unpublished). Individuals from these regions exhibit relatedness-biased aggression (Markman *et al.*, 2009).

Experimental design

I placed 20 mesocosms in the field during the winter and let them fill up with rainwater. The mesocosms were 35-litre opaque plastic tubs, within the water volume range of natural temporary pools used by salamanders. To each mesocosm I added three large limestone rocks for refuge, covering ~25% of the pool bottom area. I inoculated each pool with an equal volume of water from a well-mixed stock containing zooplankton from an outdoor, semi-natural pool. This inoculate was visibly dominated by *Arctodiaptomus similis* (Copepoda) and also included various daphnids. The concentration of invertebrates in the mesocosm following inoculation was similar to that of the pool from which they were collected. The mesocosms were organized spatially in pairs that I matched for similar daily periods of exposure to direct solar radiation. Within pairs, I assigned mesocosms randomly to two treatments – a cohort of siblings and a genetically mixed cohort.

On the first day of the experiment, I introduced six larvae into each of the pools. This density is within the range of larval densities in natural pools (L. Blaustein, personal observations). In each 'sibling' pool, all six larvae were the offspring of the same mother. These sibships were born in the laboratory by placing ten gravid females in tubs with aged tap water. Five of these females were collected from the Carmel region and five from the Galilee region. In each 'mixed' pool, three of the larvae were from the Carmel region and the other three from the Galilee region, such that none of the pool mates were siblings. In these mixed cohorts, most of the larvae were born in the laboratory to 13 females, while some of the larvae (21

individuals, distributed randomly among pools) were field-collected from natural pools, since I was limited by the Israel Nature and Parks Authority in the number of gravid females I could collect and in the duration of their retention in the laboratory. However, both their sizes and the visible amounts of remaining yolk in their bodies were similar to those of the laboratory-born larvae, indicating similarly young ages of individuals in both of these groups (estimated as up to 7 days old at the time of collection). The proportions of survival and successful metamorphoses among the field-collected larvae [identified individually by the spot patters on their tailfins (Eitam and Blaustein, 2002)] by the end of the experiment were similar to those of the laboratory-born larvae, and the statistical analyses for these response variables for the full data set (see Statistical analysis below) produced similar results to those conducted for cohort means that excluded the field-collected larvae (not presented).

The larvae grew in the pools under natural weather conditions, under the cover of screening (1 cm^2 holes) to exclude potential predation by birds. This screening also reduced oviposition by mosquitoes into the pools, therefore reducing the input of large prey species. I monitored the larvae's developmental progress and survival and weighed them to the nearest milligram every two weeks until Day 58. On the first three monitoring dates, I also sampled the number of cannibalistic events observed in each treatment, recording the cumulative number of detected events to Day 43. After this date, algal concentrations prevented direct observation of larvae in the pools. Instances of cannibalism were determined during survival counts either by direct observation of the act or by observing the typical appearance of the remains of partly cannibalized bodies; necrophagy is not known to occur in this species. This sampling protocol did not allow detection of the full extent of cannibalism that occurred up to Day 43, since in each survey I could only observe cannibalistic events that had occurred up to a few days earlier. However, it allowed me to compare the rates of cannibalism between the treatments as confirmation of the behaviour documented by Markman *et al*. (2009).

Due to a mild winter, temperatures rose abruptly approaching Day 58, and pools lost water quickly. Most experimental pools subsequently desiccated within 18 days, coinciding with the desiccation of many natural pools, and forcing larvae to either metamorphose or die. Such mild winters are a frequent occurrence due to the high among-year variability in temperature and precipitation. A number of individuals were observed on Day 58 to have initiated metamorphosis (abrupt darkening of skin colour, loss of tailfin coloration, shrinking of tailfin and external gills, developed walking ability). Since metamorphosis can, once initiated, be completed quickly even after pools dry (A. Sadeh, personal observations), these individuals were scored as successful metamorphs and their weight was assumed to approximate their size at metamorphosis – a correlate of an individual's expected lifetime reproductive success (Altwegg and Reyer, 2003). I terminated the experiment at Day 58 since afterwards it became impossible to distinguish between emerged metamorphs and perished larvae in accounting for missing individuals. However, metamorphosing individuals stop feeding and lose weight (A. Sadeh, unpublished data). Since the pool-mean weights of the remaining individuals showed no reduction, few additional larvae were likely to have reached metamorphosis during this experiment.

I returned all surviving larvae either to the pools where their mothers were collected, or to large pools in the same region for cases in which their natal pools had dried. Whenever possible, approaching the end of the experiment, I collected larvae that had not initiated metamorphosis from recently dried experimental pools and returned them to the field to reduce unnecessary loss of life.

Statistical analysis

To account for the spatial pairing of mesocosms while comparing larval performance between 'mixed' and 'sibling' cohorts, I used a paired *t*-test and Wilcoxon's signed ranks test (when parametric assumptions were not met) on survival proportions and the mean numbers of individuals initiating metamorphosis, respectively, by the time the experiment terminated. I used an independent-sample *t*-test to compare size at the initiation of metamorphosis between treatments, since the number of metamorphosing individuals was small and they had to be pooled in each treatment.

To test for differences in cannibalism rates between treatments, I used a *Z*-test for difference between treatments in the proportions of cumulative cannibalistic events detected. To detect negative density-dependent effects on larval performance, I used Pearson's correlation to test for the relationship between larval densities on Day 43 and average sizes of survivors per pool at the end of the experiment.

Low genetic relatedness among members of a cohort is often correlated with high variation in initial sizes, potentially contributing to increased levels of aggression (Ziemba and Collins, 1999) compared with sibling cohorts, in addition to the effect of kin-discriminating behaviour. Indeed, mean pool coefficients of variation in initial sizes were higher in mixed cohorts (14.4%) than in sibling cohorts (6.6%; paired *t*-test $P = 0.002$). While kin-discrimination and size variation may be confounded across treatments, they are not confounded within treatments. Specifically, within the mixed cohorts, both cannibalism rates and size variations were high, while the degree of relatedness among members was invariably small. Therefore, I used Pearson's correlations to determine whether the cohorts' coefficients of variation in initial body sizes predicted their performance variables, survival and metamorphic success.

RESULTS

By Day 43, six cases of cannibalism were detected in the mixed cohorts treatment (10% of the initial number of larvae) compared with only one case in the sibling cohorts treatment (1.7% of the larvae; $Z = 2.106$; $P = 0.035$), confirming previous findings in this species (Markman *et al.*, 2009). My ability to detect cannibalism in surveys that were spaced two weeks apart was partial. Therefore, these numbers of observed cannibalistic events are an underestimate of the magnitude of cannibalism that actually occurred during that period. However, detectability ought not differ between treatments, and undetected cases should be distributed among them by a similar ratio.

Despite the significantly higher rates of cannibalism in mixed cohorts, overall mortality by Day 43 was similar in mixed (15 deaths) and sibling (12 deaths) cohorts. This was also evident by the end of the experiment (Day 58); sibling and mixed cohorts did not differ significantly in survival (Fig. 1a; Table 1). During the 15-day interval between the two final surveys (Day 43 and Day 58), four individuals died in the mixed cohorts and two in the sibling cohorts, hinting that cannibalism was still stronger in mixed cohorts by the end of the experiment. Larval densities on Day 43 correlated negatively with the sizes of surviving larvae by Day 58 (Fig. 2; Pearson's $r = -0.54$; $P = 0.0136$).

By the end of the experiment, 5% of the initial number of larvae in the sibling cohorts had initiated metamorphosis, a significantly lower rate than that of the mixed cohorts (15%;

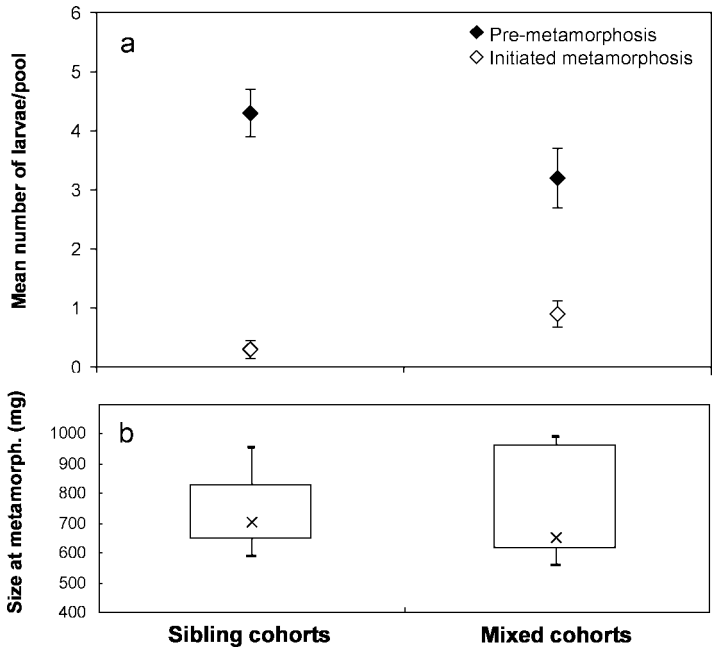

Fig. 1. (a) Mean number of larvae surviving to the end of the experiment in sibling and mixed cohorts (◆), and the number of which that initiated metamorphosis (◇). Error bars are ±1 standard error. (b) Distributions of sizes at the initiation of metamorphosis in sibling and mixed cohorts.

Table 1. Test statistics for treatment comparisons of larval performance variables

Variable measured	Cohort composition	Mean	Statistic	*P*-value
Survival	Siblings	76.7%*	$t_9 = 0.785$	0.453
	Mixed	68.3%*		
Initiation of metamorphosis	Siblings	5%*	Wilcoxon's	**0.034**
	Mixed	15%*	$Z = -2.121$	
Size at initiation of metamorphosis	Siblings	0.746 g	$t_{10} = 0.018$	0.986
	Mixed	0.744 g		

Note: Survival and initiation of metamorphosis were compared using paired tests, while size at initiation of metamorphosis was tested using an independent samples *t*-test.
* Percentages are of initial cohort numbers.

Fig. 1a; Table 1). The sizes of individuals at initiation of metamorphosis did not differ between treatments (Fig. 1b; Table 1).

Although the coefficients of variation in initial sizes of individuals were different between treatments, possibly reflecting differences in birth sizes of *S. infraimmaculata* larvae among populations (L. Blaustein *et al.*, unpublished data), the coefficients of variation in initial larval mass did not correlate significantly with survival rates or with successful initiation rates of metamorphosis in the mixed cohorts (Table 2).

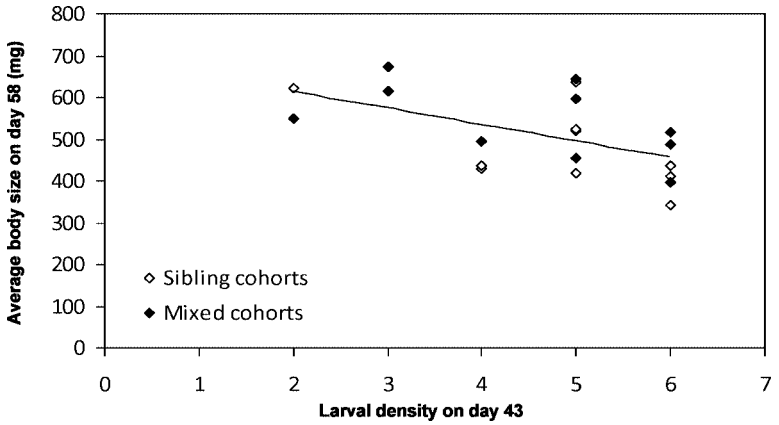

Fig. 2. Average larval size per pool by the end of the experiment as a function of larval densities observed on Day 43 (Pearson's $r = -0.54$; $P = 0.0136$).

Table 2. Pearson's correlations of mixed cohorts' coefficients of variation in initial sizes with their larval performance variables

Response variable	*N*	Pearson's *r*	*P*-value
Survival	10	−0.047	0.898
Initiation of metamorphosis	10	0.121	0.739

DISCUSSION

I found that reduced cannibalism among sibling cohorts due to kin-selective behaviour does not lead to lower total mortality rates than that of more cannibalistic, mixed cohorts. In addition, I found that reduced cannibalism can lead to over-compensatory mortality if pools dry early and therefore result in poorer performance of sibling larval cohorts. I suggest that these patterns may be driven by a density-dependent feedback to cannibalistic mortality as well as by the direct nutritional benefits of cannibalism.

Previous work on fire salamanders that isolated larval behaviour from the effects of density and risk of habitat drying showed that larval aggression towards conspecifics is inversely related to the degree of their genetic relatedness (Markman *et al.*, 2009). Such kin-selective behaviour was also evident in the present study, at least until Day 43 of the experiment by which time a greater proportion of mortality was the result of cannibalism in the mixed cohorts than in the sibling cohorts. These results provide support for other studies showing patterns of expression of aggressive behaviours that are consistent with kin selection theory (e.g. Walls and Roudebush, 1991; Pfennig, 1997; Segoli *et al.*, 2009). However, overall survival rates to Day 43 and to the end of the experiment were similar across treatments. Clearly, then, the reduced aggression among sibling cohorts was not sufficient to positively affect total mortality rates. Furthermore, if the ratio of detected cannibalistic events among treatments is similar to that of undetected events throughout the experiment, then the similar total mortalities are the result of some compensatory mortality process. Plausible mechanisms underlying such compensation may be density-dependent non-cannibalistic

mortality that resulted from the low per capita resource availability, or the loss of kin-discriminating behaviour between Day 43 and Day 58, shortly before the desiccation of the pools (e.g. Blaustein *et al.*, 1993). The negative relationship between larval densities and body sizes in the final part of the experiment lends some support to the former mechanism.

A greater number of early initiations of metamorphosis occurred in the mixed cohorts, lending further support to the idea that overall cannibalism was stronger in these cohorts throughout the larval period. In highly temporary habitats, animals often perceive cues for the approaching loss of their habitats and respond by accelerating their development rates (e.g. Laurila and Kujasalo, 1999; Johansson *et al.*, 2001; Marquez-Garcia *et al.*, 2009; shown in *S. infraimmaculata* by Sadeh *et al.*, 2011). In such cases, trophic energy is mostly allocated to differentiation and metamorphosis (Harris, 1999). Here, hydroperiods were undoubtedly short enough to induce accelerated development in all the larvae (see Sadeh *et al.*, 2011). Thus, the higher rates of initiation of metamorphosis in the mixed cohorts suggest that a greater proportion of individuals, compared with those of the sibling cohorts, were able to employ sufficient food resources and utilize them for reaching minimal size for metamorphosis and fuelling the required developmental changes. I suggest that this increase in food availability was due to greater overall rates of aggressive interference and cannibalism. A similar effect on metamorphic success was documented in this species when inter-cohort cannibalism was manipulated through habitat structural complexity (Sadeh *et al.*, 2009; A. Sadeh, unpublished data). In groups expressing high levels of cannibalism, the distribution of food resources (both conspecific victims and shared resources) among members is not uniform (Polis, 1981), and is biased in favour of the cannibals. This implies that if some loss of kin discrimination in the final days of the experiment had occurred, it was not sufficient to equalize overall cannibalism rates between the treatments.

Greater rates of cannibalism among distantly related individuals can therefore improve cohort performance in short-lived habitats by increasing development rates and metamorphic success. Both the direct nutritional benefit acquired by some larvae through cannibalism and the indirect benefit of relaxed competition fuel the acceleration of metamorphosis in genetically mixed cohorts. In contrast, siblings refraining from cannibalism may remain uniformly starved and susceptible to death by delayed development and habitat loss. West *et al*. (2002) argued that altruistic behaviour towards relatives may lead to increased competition between relatives, potentially reducing or even removing kin selection. How, then, might kin-discriminative aggressive behaviour be maintained in fire salamander populations? The effects of kinship demonstrated in this study may weaken or even act in the opposite direction in long-lived habitats with sufficient food availability, where large groups of siblings are neither impeded by densities nor are they at risk of metamorphic failure (Pakkasmaa and Laurila, 2004). If so, the spatio-temporal variation of pool hydroperiods may be the key to the retention of kin selection in this system.

The genetic composition of a cohort in nature may affect both kin-selective behaviours that determine the motivation to cannibalize, and differences in body sizes that determine the capacity to cannibalize (Polis, 1981; Dong and Polis, 1992). Sometimes, even small initial size differences that may result from genetically or maternally determined sizes at birth may diverge with larval growth, especially when size differences determine the beneficiaries of interference competition (Ziemba and Collins, 1999). Although these two mechanisms may have operated in concert in this experiment to increase cannibalism rates among mixed cohorts and influence metamorphic success and survival, Markman *et al.* (2009) provided evidence that similar-sized individuals of this species do express relatedness-biased aggression.

Moreover, coefficients of variation in initial larval sizes did not predict the patterns of mortality or metamorphosis by the end of the experiment within the mixed cohorts treatment, where initial size variation and kin-selective cannibalism were not confounded. Thus, it can be concluded that behavioural kin discrimination had a significant role in driving the observed interactions.

Predictions for maternal oviposition habitat selection strategies can be derived from these results. The mean performance of a cohort is an estimation of the expected performance of an oviposited clutch. Consider a case where a pregnant female encounters two habitats, in one of which she has recently oviposited, and in the other an unrelated female has recently oviposited. *Salamandra* females, as well as females of other organisms, are known to spread their larval clutches spatially and temporally, allowing such scenarios to occur (e.g. Spieler and Linsenmair, 1997; Segev *et al.*, 2011). Such organisms are often capable of demonstrating sensitivity to multiple ecological variables in their habitat preferences (e.g. Sadeh *et al.*, 2009). In solitary parasitoids where competition is also lethal but not relatedness-biased (Godfray, 1994), conspecific superparasitism generally has a higher pay-off than self-superparasitism (e.g. Visser, 1993). Where groups of larvae demonstrate kin-biased aggression, it might be intuitively expected that maternal behaviour would avoid the high levels of aggression in groups of distantly related larvae. However, depending on offspring food and time limitations, their expected performance may be worse if she chooses to deposit twice in the same habitat. Therefore, under such limitations females may prefer sites occupied by unrelated larvae.

Conservation strategies for highly cannibalistic species may require the consideration of the role of cannibalism in larval performance and recruitment patterns to the adult population (e.g. Wissinger *et al.*, 2010). While cannibalism might be perceived merely as detrimental to population growth, the results of this study imply that this behaviour may sometimes be important for larval recruitment, and measures to reduce it may not always be desirable. The spatial and temporal spreading of larvae demonstrated in *S. infraimmaculata* (Segev *et al.*, 2011), combined with their long-distance movements during the breeding season (Bar-David *et al.*, 2007), imply that the mixing of distantly related sibships may occur in natural populations. The conservation of landscape connectivity between breeding sites may be important to maintain this mixing, which, in turn, may influence the success of larval recruitment.

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