Original Article

Spatiotemporal reproductive strategies in the fire salamander: a model and empirical test

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Although density-dependent processes and the risk of pool desiccation dominate temporary pool ecology literature, the spreading of larvae across pools and time as a strategy for managing these central stress factors has not been rigorously addressed as an adaptive mechanism. We develop a state-dependent oviposition habitat selection model predicting that females of the endangered fire salamander, *Salamandra infraimmaculata*, will split their larval load temporally during the rainy season and across multiple pools and will adjust the number of larvae deposited according to pool quality. These strategies are predicted to reduce the negative effects of larval density-dependence and limited habitat duration. We tested the qualitative predictions of the model in an outdoor experiment. Consistent with our predictions, gravid females, when allowed to choose deposition sites among pools of different depths, spread their larvae both spatially and temporally and deposited more larvae into deeper pools. This study offers a novel theoretical and experimental framework for studying the evolution of reproductive strategies in ephemeral systems. *Key words:* density dependence, hydroperiod, larviposition, oviposition site selection, reproduction strategies, risk of desiccation, state-dependent model, temporary pools. *[Behav Ecol 22:670–678 (2011)]*

INTRODUCTION

Locally optimized life-history phenotypes, such as propagule size and number (Lack 1947; Wilbur 1977), cannot evolve without a consistent environmental context (Resetarits 1996). This consistency can be achieved by philopatry or site fidelity (McPeek 1989) when little spatiotemporal variation exists in the relative qualities of available habitats, as is the case in many anadromous fishes and some amphibians. Alternatively, when such variation is considerable, consistency may be achieved by active discrimination of breeding females among potential oviposition sites based on their perceived suitability (Resetarits 1996), as was empirically shown for numerous species (e.g., Mayhew 1997; Wilson 1998; Blaustein et al. 2004; Blouin-Demers et al. 2004; Rieger et al. 2004).

Oviposition site selection has direct implications for the reproductive success of amphibians, particularly when larvae are spatially confined in small temporary water bodies (Resetarits 1996; Blaustein 1999). In order to respond to pool variables that determine its quality as potential larval habitat, females must be capable of assessing them (Clark and Mangel 1984; Boulinier and Danchin 1997; Doligez et al. 2003). Although temporary pools are highly variable and unpredictable in many aspects, some physical and biological properties may provide breeding females with reliable information regarding the pool's current and future quality. Pool depth, for instance, may provide indication on the pool's hydroperiod (Skidds and Golet 2005).

Amphibian oviposition habitat selection has been empirically studied in the context of risks of predation and competition (Marsh and Borrel 2001; Rieger et al. 2004; Brown et al. 2008; Glos et al. 2008; Sadeh et al. 2009), risk of parasitism (Kiesecker and Skelly 2000), timing of deposition (Matsushima and Kawata 2005; Matsushima and Borrel 2001), pool volume (Crump 1991; Spieler and Linsenmair 1997; Rudolf and Rodel 2005; Brown et al. 2008; May et al. 2009), and pool hydroperiod (Egan and Paton 2004). Although density-dependent processes and the risk of pool desiccation dominate temporary pool ecology literature, the spreading of larvae across pools and time as an adaptive strategy for managing these central stress factors has not been rigorously addressed as an adaptive mechanism. Few studies on amphibians have explored the spatial and temporal distribution of offspring in an individual-based experimental setting (Spieler and Linsenmair 1997). Breeding habitat selection has implications for population dynamics (Pearman and Wilbur 1990; Spencer, Blaustein, et al. 2002) and species distributions, and its understanding is essential for conservation (Jonzen 2008).

Fire salamander biology and breeding environment

In Israel, female fire salamanders, *Salamandra infraimmaculata*, conceive during the winter and deposit their larvae into breeding pools during the following winter. They utilize permanent water bodies but mostly temporary ones. The latter are much more abundant but vary in volume and duration. Small temporary rock pools in regions containing *S. infraimmaculata* are often found in wadis or exposed bedrock areas where many pools are clustered in an area of less than 100 m^2 (e.g., Spencer, Schwartz, et al. 2002). Three major causes for larval mortality in temporary pools are cannibalism (Degani 1993; Reques and Tejedo 1996; Sadeh et al. 2009), competition (Eitam et al. 2005), and an unpredictable timing of pool desiccation followed by death of all larvae failing to

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metamorphose in time (Sadeh et al. 2011). It was previously reported that *Salamandra* demonstrate a high degree of philopatry or site fidelity (*S. salamandra*: Rebelo and Leclair 2003; *S. infraimmaculata*: Warburg 2007). Pool fidelity implies that an individual returns to the same pool each season and deposits all or most of its larvae in it and is likely to evolve if females are constrained to depositing their entire larval load, or most of it, in a single deposition.

Within a season, individuals of many amphibian species do not spread their progeny but deposit a single clutch (Wells 2007); once they begin to deposit, all progeny are deposited into the same pool at the same time. Very few studies have demonstrated temporal and spatial spread of progeny of the same brood (Spieler and Linsenmair 1997). Although gravid *S. infraimmaculata* carry complements of ~100–200 developed larvae at the start of the rainy season, field surveys revealed high variability in the number of newborns per pool, including numerous pools containing <20 newborn larvae (Segev O, unpublished data).

We are thus lead to ask:

1. Do salamanders spread their offspring spatially and/or temporally?
2. Do salamanders adjust their clutch sizes according to the depths of encountered pools?

To answer these questions, we developed a state-dependent behavioral model implemented by stochastic dynamic programming (Clark and Mangel 2000) incorporating larval density dependence as a partially predictable stress factor combined with stochastic pool depth and risk of desiccation. The model was used to generate predictions regarding temporal and spatial larval spread of pregnant salamanders. We then tested the qualitative predictions of the model empirically in an outdoor pool choice experiment.

THE MODEL

State-dependent life-history theory (Mangel and Clark 1988; Houston and McNamara 1999; Clark and Mangel 2000) allows modeling the influences of dynamic environments and organism states on decisions, which in turn feed back on the organism state and the environment. It requires characterizing the environment, the physiological state and survival of the larvipositing female, the increment in reproductive success obtained from deposition of a known number of larvae, and the overall accumulated reproductive success during the season. In computing the latter, we predict larviposition as a function of the female's larval load and the environment, and compare the fitness of plastic and fixed clutch size strategies. For a full list of parameters used and their values, see Tables 1–3.

The environment

We assume that there are 3 kinds of pools indexed by $i = 1, 2, 3$ that are similar in shape and productivity but differ in their maximal depths. The frequency of pool type i is denoted by p_i, and pool maximal depth is denoted by $D_{\max(i)}$ (see Table 1 for pool characteristics). All pools are assumed to be full at $t = 1$ and dry by $t = T$, where the time units are nights. During this breeding season, the pools fill by rains and lose water by evaporation. (Table 2). We assume that pool depth is linearly proportional to pool volume and floor area. The volume of the pool influences its duration (Altermatt et al. 2009), whereas its floor area influences density-dependent interactions among larvae (Eitam et al. 2005; Segev and Blaustein 2007). For computational simplicity, we assume that all pools that have not yet dried experience identical changes in depth due to rainfall and evaporation, and that each pool type has only one hydroperiod (i.e., once a pool dries out, it remains dry for the rest of the breeding season). These assumptions are added to simplify the model but are also conservative because they restrict the possibility of larval spreading. Thus, at time t, the states of pools in the environment are given by the vector $H(t) = \{D_1(t), D_2(t), D_3(t)\}$ where $D_i(t)$ is the current depth of pool type i. Because this model focuses on the basic larval distribution strategy, it also assumes an infinite number of pools in the landscape and a single searching female. An investigation of the effects of competition over pools between depositing females and of priority effects between larval cohorts would require to relax these assumptions but is beyond the scope of this paper.

The probability of rain on night t, $\Psi(t)$, as in a Mediterranean climate, varies across the season (see Table 2). On a rainy night, the female has U time units to search for pools, with the probability ρ of finding a pool in each time unit, allowing her to find up to U pools per rainy night. On dry nights, she does not search for pools.

Larval load and survival

We characterize the larvipositing female by a single state variable

$$L(t) = \text{Female larval load at the beginning of night } t \quad (1)$$

At the start of the breeding season, females have a full complement of larvae so that $L(1) = l_0$. The larval load is reduced by the female's deposition of larvae into pools. The female experiences a constant daily rate of mortality, μ, so that the probability of surviving from t to $t + 1$ is $e^{-\mu}$.

Increment in reproductive success

When a pool of type i is encountered and the female larviposits, her lifetime reproductive success is incremented. We characterize this increment in reproductive success by:

$$\Phi(c, i, d, t) = \text{Expected number of grand-offspring of the}$$
$$\text{focal female, produced by successfully}$$
$$\text{metamorphosed larvae from a clutch of}$$
$$c \text{ larvae deposited on night } t \text{ into a pool of}$$
$$\text{type } i \text{ with a current depth of } d$$
$$(2)$$

To compute this increment, we must consider the growth, survival, and subsequent fecundity of the larvae, which successfully metamorphose within the pool. Imagine larvae

Table 1

The physical characteristics and frequency of pools in the model

Pool type (i)	Productivity (P)	Slope	Frequency in landscape (p_i)	Maximal depth ($D_{\max(i)}$) (cm)
1	0.167 g m^{-2} day^{-1}	0.2 m^2 cm^{-1}	0.25	16
2	(Blaustein L, unpublished data)		0.25	8
3			0.5	4

Pool floor area at each night, $A_i(t)$, is calculated as the pool's slope multiplied by its current depth, $D_i(t)$.

Table 2

Weather patterns in the model

t	Daily rain probability (Ψ)	Daily evaporation rate (cm)
1–30	0.65	0.0
31–60	0.52	0.5
61–90	0.36	0.5
91–120	0.25	1.0
121–150	0.11	1.0

Rain probabilities were estimated from data in Warburg (1985). Time begins on 1 December. Each rain event adds 1 cm to the depths of all the pools.

deposited on night $t = \tau$. Let $S(t)$ denote the mean size of the larvae on the nights following deposition and $n(t)$ denote the number of larvae at any time in the focal pool. If A is the pool floor area, we assume that

$$S(t + 1) = S(t) + \min\left[S(t) \cdot k \ , \ \frac{P \cdot A(t)}{n(t) - 1}\right] \quad (3)$$

Thus, growth is proportional to pool productivity, P, inversely proportional to the density of competitors, $n(t)/A(t)$, and limited by the maximum specific growth rate, k. We assume $S(0) = 0.2$ g for the mass of a newly deposited larva, S_0 (Degani 1996). Maximum specific growth rate, k, can be estimated as follows: an individual larva grows from 0.2 to 2.0 g in 90 days (for 1 larva growing alone in a 0.24 m^2 pool; Blaustein L, unpublished data). Solving Equation 3 for k when $n(t) = 0$ produces a value of 0.026 g day^{-1}.

To estimate P from empirical data (Blaustein L, unpublished data), we note that at a density of 4 larvae in a pool with a floor area of 0.24 m^2, a larva grows from 0.2 to 1.2 g in 100 days. Solving Equation 3 for P produces a value of 0.167 g m^{-2} day^{-1}. Clearly, in natural temporary pools, there may be high heterogeneity in

food resources. As a simplifying assumption, we assume a constant productivity among pools because we are interested in pool hydroperiod in this study.

We assume that larvae experience both density-dependent and density-independent mortality, characterized by μ_d and μ_t, respectively, so that the probability of survival from night t to $t + 1$ is $\exp\left(-\frac{\mu_d(n(t)-1)}{A(t)} - \mu_t\right)$. Larvae that survive and exceed a critical size S_c (see Table 3, value determined experimentally; Segev O, unpublished data) will metamorphose and produce offspring themselves, and we assume that the lifetime reproduction of offspring is given by aS_m^b, where S_m is the size at metamorphosis (Peters 1986). If this size is less than the critical size, then the individual obtains no fitness.

To compute the fitness increment, we used a backwards iteration algorithm, starting at each possible date on which a pool might dry for each possible size of larvae and number of larvae in the pool. For each combination of previous time t' and values of $n(t')$, $S(t')$, and $D(t')$, the expected increment in fitness is calculated as the sum of all possible future fitness possibilities multiplied by their associated prior probabilities. The process repeats for $t' = t' - 2, t' - 3$, etc., until the initial larval mass S_0 is reached. Such a backward algorithm accounts for the mother not knowing during larviposition when the pool will dry. Figure 1 shows how the female's fitness increment from a single larviposition, $\Phi(c, i, d, t)$, changes according to clutch size, time, pool type, and current pool depth. Fitness increment is highest in the deepest ($i = 1$) pool even when its current depth is equal to that of the shallower pools. Within any pool type, fitness increment is positively related to both current pool depth (D_i) and time remaining for larviposition ($T - t$).

Accumulated reproductive success

Once $\Phi(c, i, d, t)$ is known, we are able to compute the accumulated seasonal reproductive success of the focal female and through that the optimal larviposition strategy throughout the season as a function of state. In particular, we set

Table 3

Parameter values and units in the model

Parameter	Meaning	Value and units	Reference
T	Number of nights in the breeding season	150 nights	Goldreich 1995
l_0	Full larval load in uterus at $t = 1$	150 larvae	Degani 1996
$i, A, p_i, D_{\max(i)}, P$	Pool types and their characteristics	(see Table 1)	
μ	Nightly rate of female mortality	0.05	
$\Psi(t)$	Time-dependent nightly rain probability	(see Table 2)	
U	Number of time units per night available for pool searching	5	
ρ	Probability of finding a pool per time unit	0.2	
S_0	Initial larval size at birth	0.2 g	Degani 1996
S_c	Minimal larval size allowing metamorphosis	0.45 g	Segev O, unpublished data
k	Maximum specific larval growth rate	0.026 g day^{-1}	Blaustein L, unpublished data
μ_d	Density-dependent larval mortality factor	1×10^{-4}	
μ_t	Time-dependent larval mortality factor	8.5×10^{-4}	
a	Allometric relationship constant for egg production	0.5	Peters 1986
b	Allometric relationship constant for egg production	0.26	Peters 1986
State-dependent variables			
$D_i(t)$	Current depth of pools of type i		
$H(t)$	A vector containing all the current depths, $D_i(t)$, at time t		
$L(t)$	Female's current larval load		
$\Phi(c, i, d, t)$	Increment in reproductive success of a female by larvipositing c larvae at time t into a pool of type i with a current depth of d		
$S(t)$	Mean size of the larvae on the nights following deposition into a pool		
$F(l, h, u, t)$	Expected accumulated fitness from a plastic clutch strategy from period u on night t to the end of the season given a current larval load l and pool depths h		
$W(l, h, u, t\|c_f)$	Expected accumulated fitness from a fixed clutch (of size c_f) strategy from period u on night t to the end of the season given a current larval load l and pool depths h		

$F(l, h, u, t) =$ Maximum expected number of grand-offspring resulting from Larviposition from period u on night t to night T, given that $L(t) = l$ and $H(t) = h$

$$(4)$$

Because there is no evidence for maternal reabsorption of remaining fetuses toward the end of the breeding season, we set the end condition for all l and h that

$$F(l, h, U, T) = 0 \qquad (5)$$

That is, at the time that all pools are dry, a female can no longer accumulate fitness. The female's state at the end of search on night t and at the start of night $t + 1$ must be the same, so that we have the sequential coupling condition $F(l, h, U, t) = F(l, h, 1, t+1)$ (sensu Mangel and Clark 1988; Clark and Mangel 2000).

If it does not rain on night t, to accumulate future fitness the female must survive to the next night, and her larval load does not change. Similarly, if it does rain but she does not encounter a pool, then she must survive with no change in larval load. If it does rain and the female encounters a pool, she must survive, and then we assume that she optimizes the number of larvae deposited, accumulating fitness increment due to this deposition, and reducing her larval load. Taking these 3 possibilities into account allows us to link fitness from one search period to another on each night:

$$
\begin{aligned}
F(l, h, u, t) = {}& (1 - \Psi(t)) e^{-\mu U} F(l, h', 1, t + 1) \\
& + \Psi(t)(1 - \rho) e^{-\mu} F(l, h, u + 1, t) \\
& + \Psi(t) \rho e^{-\mu} \sum_{i=1}^{3} p_i \max_c \{ \Phi(c, i, d, t) \\
& + F(l - c, h, u + 1, t) \}
\end{aligned}
\qquad (6)
$$

Where h' denotes the value of $H(t + 1)$, given that $H(t) = h$. In the course of solving Equation 6 backwards in time, we generate the optimal clutch sizes $c^*(l, i, d, t)$ as a function of larval load, pool type, and current depth and time.

Accumulated reproductive success of a fixed clutch strategy

The logic leading to Equation 6 can also be used to compute the accumulated reproductive success of a fixed clutch strategy. To do this, we let:

$W(l, h, u, t | c_f) =$ Expected number of grand-offspring resulting from larviposition from period u on night t to night T, given that $L(t) = l$ and $H(t) = h$, and that the female always deposits a fixed clutch of c_f larvae

$$(7)$$

Reasoning analogous to that leading to Equation 6 leads to:

$$
\begin{aligned}
W(l, h, u, t | c_f) = {}& (1 - \Psi(t)) e^{-\mu U} W(l, h', 1, t + 1 | c_f) \\
& + \Psi(t)(1 - \rho) e^{-\mu} W(l, h, u + 1, t | c_f) \\
& + \Psi(t) \rho e^{-\mu} \sum_{i=1}^{3} p_i \{ \Phi(c_f, i, d, t) \\
& + W(l - c_f, h, u + 1, t | c_f) \}
\end{aligned}
\qquad (8)
$$

with the understanding that if $l < c_f$ then only l larvae are deposited. The optimal fixed clutch strategy c_f^* is then the value of the fixed clutch that maximizes $W(l_0, h, 1, 1 | c_f)$.

Predictions from the model

We use the fixed clutch model in order to answer our first question, whether females are predicted to deposit all their larvae into a single pool or to spread their young across pools. An optimal fixed clutch of equal size to the maternal full complement at the beginning of the season ($c_f^* = l_0$) would indicate that females are predicted to deposit all of their larvae in the first encountered pool, in accordance with previous reports (Rebelo and Leclair 2003; Warburg 2007). However, our model predicts that $c_f^* < l_0$, that is, that a salamander female will spread larvae in time and across pools (Figure 2).

To answer our second question, whether a plastic clutch size strategy is predicted to evolve by which females adjust the number of deposited larvae according to pool quality, we compare the expected fitness of the optimal fixed clutch size strategy (Equation 8), with that of the optimal plastic clutch size strategy (Equation 6). The results of this comparison for different initial larval loads (Figure 3) predict that the plastic clutch size strategy will be favored by natural selection. A 3–5% difference in fitness over evolutionary time scale would accumulate to a considerable difference and lead to the prevalence of a plastic deposition strategy over other, less favorable, breeding strategies, assuming that these strategies breed true. Note that the difference between plastic and fixed strategies is larger for larger larval loads, implying that if there are long periods of individuals with small larval complements, then the fixed strategy could persist for longer times. In Figure 4, we show the relative allocation of clutch sizes to each pool type during every day of the season, assuming certain depths of these pools on encountering them and a constant full larval load. At any time and current depth, pools of higher quality receive larger clutches (Figure 4a–c). When pools are at maximum water capacity (Figure 4a), clutch size increases around day 30 in all pool types because time is approaching a horizon—the expected drying up of the smaller pools (considering the time the larvae have to grow in them). Because mothers will gain zero fitness for any of their larvae that are deposited after this time horizon, they increase clutch sizes on encounter with any pool type to the maximum allowed by that pool, before that time horizon is reached. After the time horizon has been reached, pools of lower quality, that is, type 2 and 3, have no fitness value at all and consequently zero clutch sizes, because of the future chances of finding a better, type 1 pool. Type 1 pools receive an ever increasing clutch size because mothers have to larviposit somewhere, and these pools present their best available option at any time (Figure 4a).

Our model includes an infinite number of pools and does not treat their spatial structure. Spatial structure would limit the information of salamanders on their environment as well as their ability to move freely and choose where to deposit larvae. However, this is often irrelevant to our system because pools may be clustered together in a small area (Spencer, Schwartz, et al. 2002). Therefore, apart from systems, where ponds are extremely distant from each other or highly fragmented; that is, our general predictions hold; that is, individuals will spread their offspring spatially and temporally, and clutch sizes would be responsive to pool quality. We explored the values of our model's parameters over their reasonable ranges, and the qualitative predictions remain the same.

LARVIPOSITION EXPERIMENT

To test these predictions, we conducted a larviposition experiment to determine whether, given a choice of several pools, a gravid salamander 1) Spreads its larval complement across
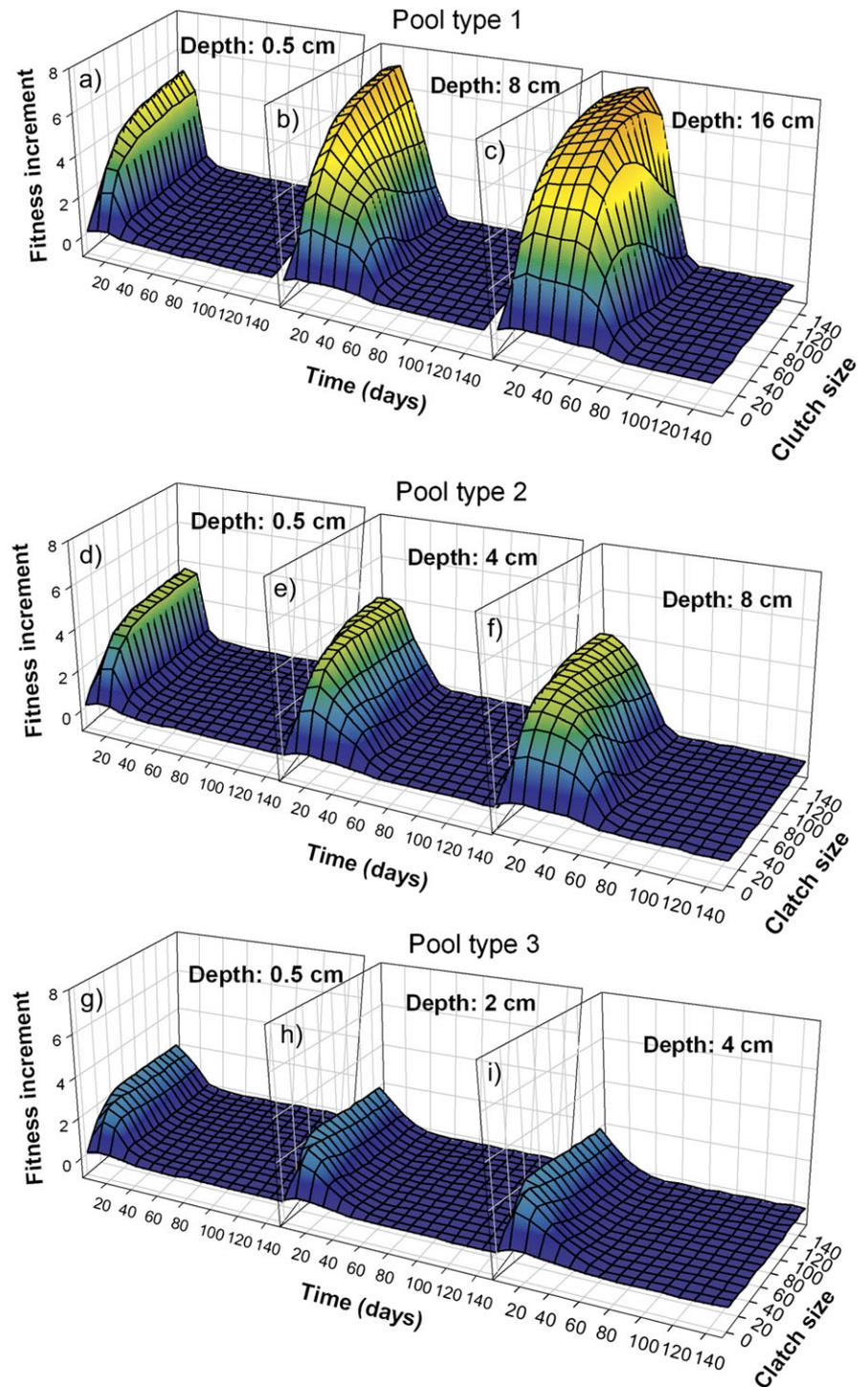
Figure 1
Fitness increment from a single larviposition, $\Phi(t, c, d, i)$, as a function of time (t), clutch size (c), current water depth (d), and pool type (i). Each row of panels corresponds to a different pool type, with different current depths at the time of larviposition.

time and/or into multiple pools and 2) Adjusts clutch sizes according to pool depths/volumes. We collected gravid females from 2 breeding sites located on Mt. Carmel, Israel: Secher Pool (lat 32°44′04″N, long 35°01′52″E) and Ein-al-Balad (lat 32°43′13″N, long 35°04′17″E). Details of these pools can be found in Segev et al. (2010). We used 6 enclosures (each 4 × 4 m in area), each containing 4 identical plastic tubs (surface area: 60 × 40 cm). In each enclosure, 2 tubs were 13.5 cm in depth, and the other 2 were 4.5 cm in depth. The tubs were dug into ground level and were equally spaced while the depth treatment locations were randomized

within each enclosure to avoid any potential spatial confounding effects. A terrestrial stone refuge was positioned in the center of each enclosure, equally distant from the 4 tubs. Each trial began by placing a single gravid female into an enclosure on the same night it was collected from its natural breeding site. Trials were conducted at the onset of the wet season to assure that gravid females were still carrying full or nearly full larval complement. We made daily counts of the number of larvae in each pool, leaving all larvae in the tubs where they were deposited. Each female was kept inside her enclosure for 2 weeks to allow the female to experience several rain events.
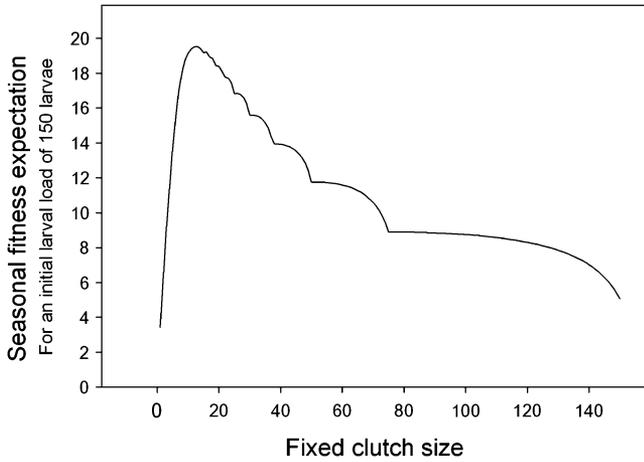
Figure 2
Female seasonal fitness expectation $W(l_0, h, 1, 1|c_f)$, as a function of fixed clutch size, c_f. The peak fitness at a small clutch size indicates a considerable benefit to spreading the larval load over many separate depositions.

After each 2-week trial, to eliminate possible chemical traces of the previous trial's larvae, all enclosure tubs were cleaned, dried, and refilled with aged tap water and rainwater for a new trial with a different female. The experiment utilized 15 gravid females (the maximum permitted by the Israel Nature Authority), and these 15 trials were completed over 10 weeks (18 October–29 December 2002). Each female and her deposited larvae were returned to their original site once the trial ended.

Statistical analysis

To consider the females' responses to pool depths, we compared the frequency of deposition events within each pool depth class regardless of number of larvae deposited in each event. We considered this for the first larviposition event of
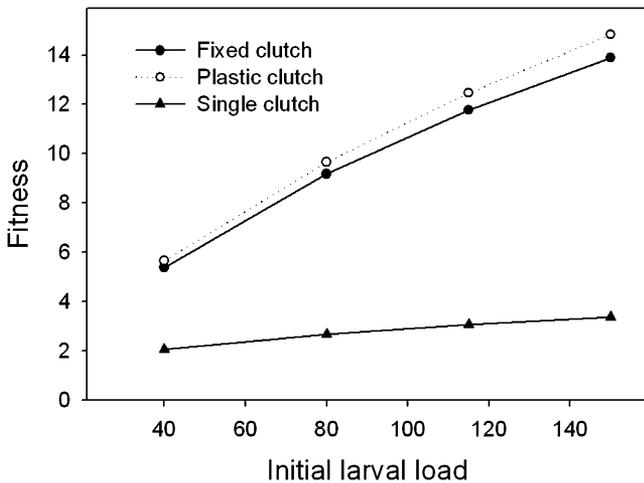

Figure 3
A comparison of expected accumulated maternal fitness for 4 initial larval loads, $l_0 = 40, 80, 115,$ and 150, over the entire breeding season for females employing 3 different larviposition strategies: 1) single clutch, $W(l_0, h, 1, 1|c_f = l_0)$, that is, deposition of the entire larval load into the first pool encountered; 2) fixed clutch size strategy, $W(l_0, h, 1, 1|c_f^*)$; and 3) plastic clutch size strategy, $F(l_0, h, 1, 1)$.
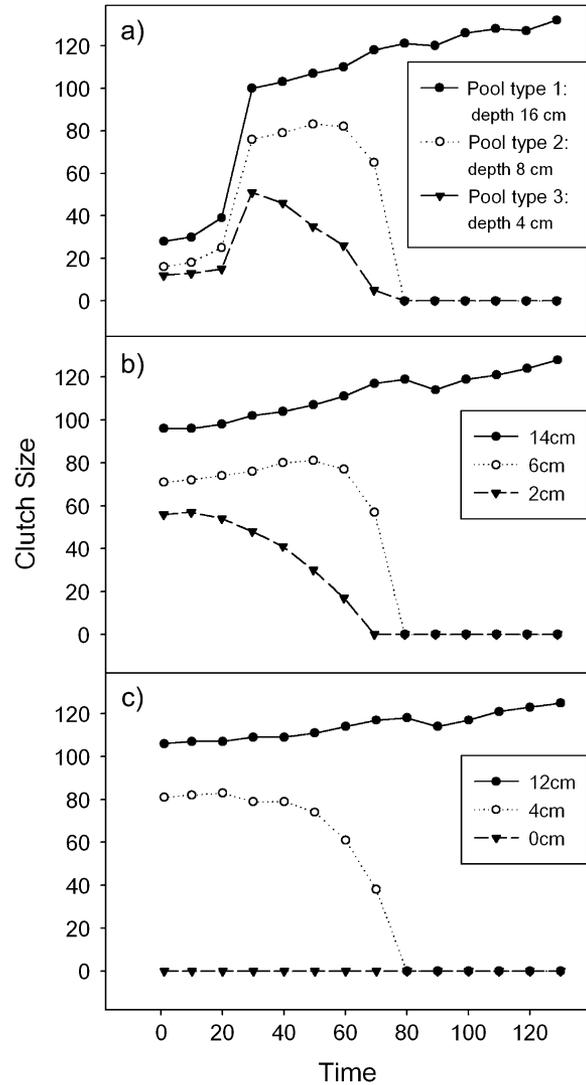

Figure 4
Distribution of optimal clutch size, $c^*(150, i, d, t)$, over time for different combinations of pool types, i, and current depths, d, at a constant load of $l = 150$ larvae. See "model predictions" for analysis.

each female only. We also compared the mean numbers of larvae deposited into each pool depth, both during each female's first larviposition and mean numbers accumulated throughout the experiment. The data for first larviposition would more closely approximate conditions of all else being equal in the tubs except for pool depth/volume, whereas the accumulated data also incorporate potential ideal-free distribution effects—for example, mothers might first choose deeper pools but then later deposit into shallower pools once larvae occupied the deeper pools. We found no effect of original breeding site on the number of larvae deposited either on the first night or overall during the females' entire stay within the enclosures. We thus give no further consideration to possible differences in behavior among sites.

The number of larvae in each depth class did not distribute normally. Therefore, we performed a Mann–Whitney U test to assess the effect of pool depth on the number of larvae deposited on the first trial night and throughout the females' stay within the enclosures. One of the 15 females participating in the experiment escaped from her enclosure following the
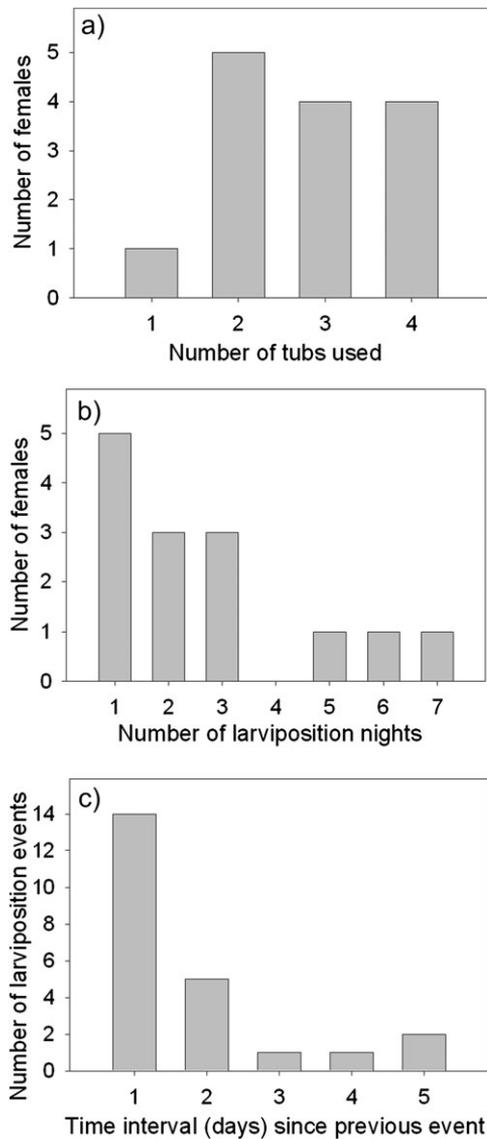

Figure 5
Spatial and temporal larviposition: (a) Number of tubs used per female throughout the experiment; (b) The total number of nights during which females larviposited; and (c) The distribution of sizes of time intervals between consecutive larviposition events by individual females that deposited on more than one night.

first night and was thus excluded from our analyses of temporal larval spread and accumulated number of larvae.

EXPERIMENTAL RESULTS

The average number of larviposition events per female was 4 (standard error [SE] = 0.65; range = 1–9). Eventually, 13 of 15 females (86%) larviposited in more than 1 tub, and 8 (53%) larviposited into at least 3 tubs (Figure 5a). These results indicate that *S. infraimmaculata* are capable of spreading their larvae spatially, across different pools. Nine of 14 females (64%) larviposited during more than a single night (Figure 5b), and in these females, the interval between consecutive larviposition events varied between 1–5 days (Figure 5c). These results show that *S. infraimmaculata* are capable of spreading their larvae temporally on discrete rain events. Females larviposited mostly during rainy nights: 20 of 24 (86%)
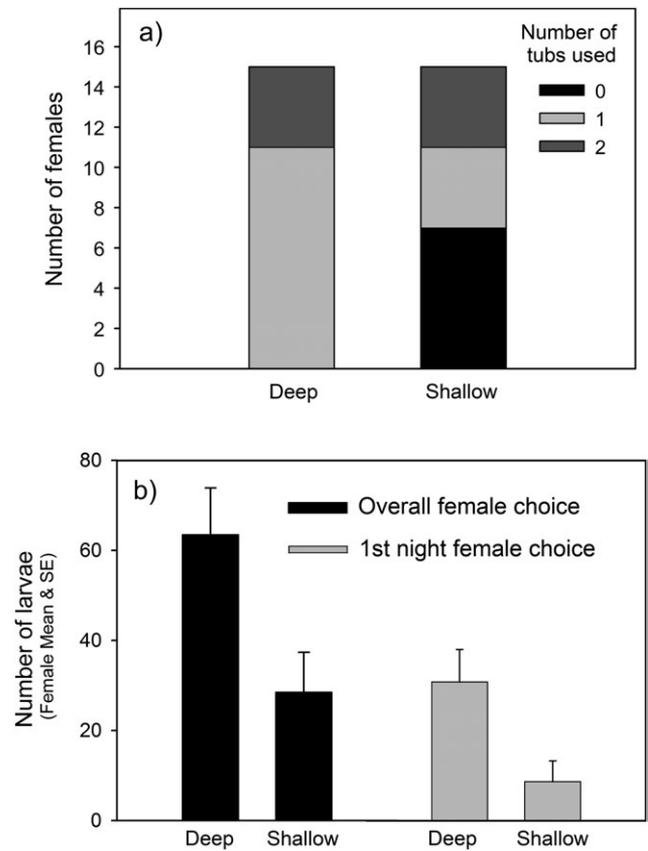

Figure 6
(a) Number of tubs used by depth type by females during their first larviposition events; (b) Mean accumulated number of larvae deposited per female in the deep (14 cm) versus shallow (4.5 cm) tubs during the entire experiment (black bars) and during each female's first larviposition event only (gray bars).

larviposition events occurred during rainy nights or not more than 48 h following a rain event (defined as $\geq$7.3 mm).

Considering each female's first larviposition event, when all 4 tubs in her enclosure still contained no larvae, 7 of 15 females (47%) completely avoided larviposition in either of the shallow tubs. Instead, at least one of each pair of the deep tubs was chosen for larviposition (Figure 6a). During each female's first larviposition event, significantly more larvae were deposited into the deep pools ($N = 14$; Mann–Whitney $U = 162$; $P = 0.003$; Figure 6b). Overall, during their entire stay within the enclosures, females deposited significantly more larvae into deep pools ($N = 14$; Mann–Whitney $U = 150$; $P = 0.017$; Figure 6b).

DISCUSSION

Our model predicted that gravid salamanders will spread their larval complement spatially and temporally throughout the breeding season and that their distribution of larvae will incorporate plastic responses in clutch size to perceived pool quality factors, specifically pool volume. The predictions of both temporal and spatial larval spread as well as the prediction of a plastic response to pool volume were supported by the results of our outdoor pool choice experiment.

Marsh (2001) highlights the need to distinguish spatial patterns resulting from individual behavior (e.g., habitat selection and dispersal), from changes in population demographics. In a set of natural ephemeral pools that vary in depth, pond

fidelity may be responsible for higher larval abundances in deeper pools if salamanders return yearly and deposit most or all of their progeny into sites where they were born (Rebelo and Leclair 2003; Warburg 2007)because females that consistently larviposit into shallow, short-lived pools will have fewer successfully metamorphosing descendants. However, field observations of small pools often containing fewer than 20 individuals (Segev O, unpublished data) as well as observations of long-range dispersing adults (Bar-David et al. 2007) that likely do not always return to their natal pond, do not support such a breeding strategy. Our model, consistent with theory for parasitoid insects (Mangel 1987), predicts that larval density-dependent effects are responsible for the spreading of larvae in time and space as an optimal resolution of the trade-off between current and future reproduction. It is increasingly acknowledged by biologists that the evolution of phenotypes is highly influenced and constrained by phylogenetic histories. Phylogenetic constraint may limit the spread of this strategy because only some clades/species are able to split the clutch load in amphibians (see Wells 2007). Embryo retention in the uterus for some or all development in *Salamandra* clade may have determined this pattern of larvae distributed along time and across space. The scope of our model and its predictions are limited to the effects of natural selection. Our experiment confirmed the females' ability of assessing pool depths, but still they used more than one pool, including inferior (shallow) ones, and spread their larvae among them.

The temporal distribution of rain combined with breeding pools' spatial distribution may dictate the interval between breeding bouts within a single breeding season. In our experiment, the temporal distribution of rain was primarily responsible for timing of larviposition. Our experiment confirms that gravid *S. infraimmaculata* are physiologically capable of delaying deposition long enough to utilize temporally distinct rain events, that is, temporally spread their larvae.

Greater accuracy in assessment of breeding patch qualities should be favored by natural selection when costly penalties exist for its over- and under-estimation (Godfray 1994). Assessment of patch quality has been treated extensively in the context of foraging theory (Valone and Brown 1989; Gotceitas and Colgan 1991; Vásquez et al. 2006). In breeding habitat selection, a large body of literature was devoted to the effects of biotic factors (mainly the presence of predators and competitors: see reviews in: Blaustein 1999; Skelly 2001; Vonesh and Blaustein Forthcoming), and several studies demonstrate that some species breeding in temporary waters can assess water-holding capacities (Spieler and Linsenmair 1997; Rudolf and Rodel 2005; Brown et al. 2008). Aquatic insects like mosquitoes and chironomids that do not submerge during egg deposition may, contrarily, lack the ability to assess water depth (Arav and Blaustein 2006; Mokany and Mokany 2006). Our study indicates that *S. infraimmaculata* can evaluate pool depth or volume, probably while swimming prior to larviposition initiation. The mechanism may involve sight, tactile cues received either by contact of the gravid female appendages with the pool floor or by sensing minute changes in water pressure while submerging. The evaluation of water loss rates in pools by changes in their water levels over repeated visits was previously suggested for 2 anurans, *Hoplobatrachus occipitalis* (Spieler and Linsenmair 1997) and *Phrynobatrachus guineensis* (Rudolf and Rodel 2005). Although not addressed in the current study, such dynamic pool quality assessment may be practiced by *S. infraimmaculata* females to gage water-holding capacity, rate of water loss, and hydroperiod. A mark–recapture study of *S. infraimmaculata* at breeding sites revealed high within-season recapture rate in breeding pools vicinity (Segev et al. 2010) that may be attributed to multiple pool sampling. Moreover,

observations of a breeding site containing numerous pools from the time of their first inundation revealed that females repeatedly visited the pools over a week before the first female deposited larvae (Sadeh A, personal observation). This species also exhibits fine-tuned dynamic responses to the presence of prior, cannibalistic, conspecific larvae in the pool (Sadeh et al. 2009).

Beyond its contribution to life-history and habitat selection theory, this study helps clarify the relationship between ecological concepts (such as the mechanisms that underline the spatiotemporal distribution of threatened organisms) and applied real-world problems facing natural resource managers (Jonzen 2008). For example, breeding habitat selection has consequences for the probability of colonization success in captive release, relocations, and translocation programs (Stamps and Swaisgood 2007). For amphibian conservation, it is generally unknown whether the terrestrial habitat or the breeding habitat serve as the limits to the population growth or whether a specific breeding site will provide for a source or sink population. Understanding habitat selection with respect to adjustment of progeny across pools and time, combined with an understanding density-dependent growth, can aid conservation planners in improving or expanding terrestrial versus aquatic habitat to achieve increased population size (Boyce and McDonald 1999).

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