Hydrobiologia
https://doi.org/10.1007/s10750-020-04302-1

PRIMARY RESEARCH PAPER

Relationships among breeding site characteristics and adult population size of the fire salamander, *Salamandra infraimmaculata*

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Received: 27 August 2019 / Revised: 27 April 2020 / Accepted: 15 May 2020

Abstract Effective amphibian conservation requires knowledge of both the aquatic and terrestrial phases of life. As extinction probabilities are a function of population size, it is crucial not only to understand the habitat requirement of the species but also to estimate its population size. In this work, we studied the endangered fire salamander, *Salamandra infraimmaculata*, and analyzed the population size at a total of 14 sites—eight temporary and six permanent. For identifying the local and landscape scales factors predicting *S. infraimmaculata*'s breeding sites we monitored 54 aquatic sites. We found that permanent sites support larger populations of adult salamanders. The breeding site characteristics analyses revealed that at the local scale water depth and shade were the most important factors and two regional variables were found to be important: proximity to another breeding site and elevation. This work provides two clear conservation implications permanent breeding sites will support much larger populations compared to temporary sites, particularly if close to other potential breeding sites, and both terrestrial and aquatic features are important for a site to be suitable for breeding.

Keywords Amphibian · Generalized linear models · Landscape · Scale

Introduction

Many amphibian species have been in danger of extinction in recent years (IUCN, 2018) and are known to be sensitive to diverse anthropogenic and environmental effects (Blaustein et al., 1994). In addition, there is extensive evidence for the effects of

Handling editor: Lee B. Kats

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10750-020-04302-1) contains supplementary material, which is available to authorized users.

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anthropogenic climate change upon the distribution and abundance of amphibian species (Milanovich et al., 2010; Blank et al., 2013b; Sutton et al., 2015). Water -breeding species are particularly vulnerable to environmental change because they rely on two components of the landscape: aquatic and terrestrial habitats (Denoël & Ficetola, 2008). Understanding these two components is of great importance, and might help in estimating the conservation status of species and aid in the formulation of conservation programs in light of predicted climatic changes (Pearson et al., 2014).

It has been previously shown that abiotic and biotic parameters might influence the occupancy of breeding sites by amphibians. For example, studies have shown that recruitment of amphibians is affected by hydroperiod, pool size, and predation (Marsh et al., 2005; Blank & Blaustein, 2014), soil temperature (Haan et al., 2007), proximity to roads (Mazerolle, 2004; Schmidt & Zumbach, 2008), stream morphology, and landscape cover (Manenti et al., 2009). Demographic processes such as survival and larvae recruitment, are affected by water loss in plethodontid salamanders (Pearson et al., 2014).

Extinction probabilities for wild populations are a function of population size and rate of decline (Caughley, 1994). Thus, it is crucial not only to understand the habitat requirement of the species but also to estimate its population size (Cushman et al., 2006; Álvarez et al., 2015). Segev et al. (2010), studied adult population size of Fire salamander populations, *Salamandra infraimmaculata* (Martens, 1885), in northern Israel at permanent and temporary breeding sites and found strong density-dependent effects, including cannibalism and increased competition due to limited resources (Blaustein et al., 1999; Sadeh et al., 2011; Degani, 2016). One goal of the current study is to expand the work of Segev et al. (2010) by performing mark/recapture studies to estimate adult population sizes associated with additional breeding sites. By expanding the number of sites with estimated adult population sizes, we strengthen our statistical power to investigate factors that could influence these local adult populations. Such factors are likely to vary over the diverse geographic areas inhabited by *S. infraimmaculata* in Israel (Sinai et al., 2019). Segev et al. (2010) only studied populations from Mt. Carmel and the Lower Galilee. This study includes sites from the Upper Galilee, so in combination with the earlier work of Segev et al. (2010), we now have a more complete sampling of the factors that could influence population size in the southernmost part of the range of *S. infraimmaculata*.

Because effective amphibian conservation requires knowledge of both the aquatic and terrestrial phases of life, our second goal focuses upon the factors that allow a site with an aquatic habitat to be used as a breeding site; that is, whether larvae can be found in the local aquatic habitat or not. Studies on *Salamandra infraimmaculata* in northern Israel are particularly important because this region is the southernmost periphery of species' distribution boundary and contains the most xeric habitat of this genus worldwide (Bar-David et al., 2007; Blank & Blaustein, 2012; Blank et al., 2013a). The fire salamander (*Salamandra infraimmaculata*) is classified as endangered (Dolev & Perevolotsky, 2004). Mount Carmel represents the southern-most region of *S. infraimmaculata* distribution and is geographically isolated by a valley from the populations in the more northern area of the Galilee mountains (Blank et al., 2013c; Kershenbaum et al., 2014; Sinai et al., 2019). These mountains extend into Lebanon and Syria (Steinfartz et al., 2000), as does the distribution of these salamanders (Fig. 1).

The fire salamander, like other complex life cycle organisms and aquatic-breeding amphibians, requires aquatic habitats for reproduction and for larval development and terrestrial habitats for juvenile and adult stages and dispersal. As habitat requirements differ among the two life stages, there is a need to recognize and quantify the type and degree of threats facing *Salamandra* in both aquatic and terrestrial habitats. Sinai et al. (2019) found that the area of the Lower Galilee was different from both the Carmel and the Upper Galilee in terms of precipitation, elevation, temperature and vegetation cover. These parameters are important to salamanders according to many studies (Blank & Blaustein, 2012, 2014; Caruso & Lips, 2013) and allow the adult and juvenile salamanders more moisture, shade and shelter than in arid and less humid regions like the Lower Galilee (Sinai et al., 2019). Amphibians are ectothermic and seem to be more vulnerable to warming and climate change than homeotherms. Ephemerality in temporary aquatic sites can be problematic in the Lower Galilee for salamanders' larval survival, especially given the prospects of global climate changes (Blaustein &

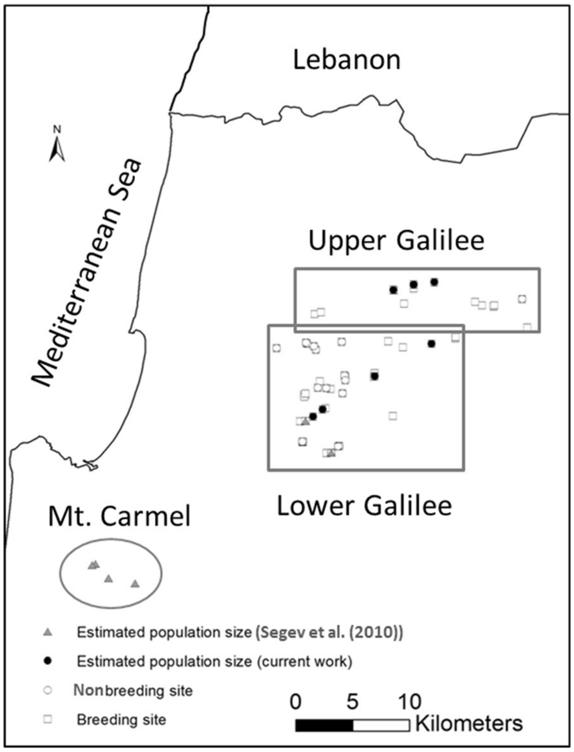

Fig. 1 Map of the study area

Wake, 1990), which can further reduce the water retention time of ponds (Givati & Rosenfeld 2013).

Characterizing the local and environmental factors associated with larval presence of *S. infraimaculata* in local aquatic habitats as well as adult population size at known breeding sites will help to estimate the species' survival potential and to develop long-term conservation programs. The specific goals of this study are to: [1] evaluate salamanders' adult population size in permanent (a pool which is not part of a stream system that holds water year-round) vs. temporary breeding sites, and [2] identify the local and landscape scales factors predicting *S. infraimmaculata*'s breeding sites.

Methods

Estimation of the size of adult salamander populations

For estimating adult population size we used mark-recapture methodology. During each visit to each breeding site, we searched for salamanders around the breeding site in the same-sized area and in a regular route, keeping a similar sampling effort (search time). We compared photos of captured individuals to identify recaptures from the individually unique spot pattern of each individual. We used a nonparametric procedure developed by Chao et al. (1992), which allows probabilities of recapture to vary both with time (different probabilities of capture at the different sampling times, *t*) and with individual animals (different individuals have different probabilities of capture). The general form of the estimator derived by Chao et al. (1992) is:

$$\hat{N} = \frac{D}{\hat{C}} + \frac{f_1}{\hat{C}}\hat{\gamma}^2$$

where D is the number of distinct animals captured in all the samples, $\hat{C}$ is an estimator of the sample coverage, f_i is the number of animals captured exactly i times in all the samples, and $\hat{\gamma}^2$ is an estimator of the square of the coefficient of variation in the catchability probabilities. Within this general framework, Chao et al. (1992) provided three different bias corrections for dealing with increasing deviations from an equal-catchability assumption in estimating the sample coverage, C:

$$\hat{C}_1 = 1 - \frac{f_1}{\sum_{k=1}^{t} kf_k}$$

$$\hat{C}_2 = 1 - \frac{f_1 - \frac{2f_2}{t-1}}{\sum_{k=1}^{t} kf_k}$$

$$\hat{C}_3 = 1 - \frac{f_1 - \frac{2f_2}{t-1} + \frac{6f_3}{[(t-1)(t-2)]}}{\sum_{k=1}^{t} kf_k},$$

where t is the number of samples taken at a site. We employed the bias correction that yields the least variance in the estimator of population size. This procedure is especially appropriate for species such as terrestrial salamanders, which show a high level of heterogeneity among individual capture probabilities (Segev et al., 2010). Segev et al. (2010) had estimated salamander population sizes at six sites in the Carmel and the Lower Galilee, and in this study we added eight additional sites in the Lower Galilee and the Upper Galilee.

Statistical analysis related to population size

We used a Kruskal–Wallis Test (SPSS) (Kruskal & Wallis, 1952) to test the null hypothesis of no difference in population sizes between permanent versus temporary sites.

Breeding site characteristics

Study site and data collection

We monitored 54 aquatic sites in the Lower Galilee and the Upper Galilee (Fig. 1). We learned of the occurrence of these water bodies (without consideration to the presence or absence of salamander larvae) based on previous surveys done in the area, interviews with the Nature and Park Authority rangers and following reports we got from the public resulting from an ad we circulated in villages in the area. In Israel, *S. infraimmaculata* females emerge from their summer (June–August) aestivation site in the fall (October–November) and then seek out aquatic-breeding sites for larviposition. Larvae remain in pools for about 2–3 months at the breeding site until metamorphosis (Degani, 1996). The survey took place between November and June in the years 2010–2013. All sites were monitored during the day for the occurrence of salamander larvae and each site was visited between 4 and 6 times. At every site, we visually inspected for the presence of salamander larvae and we used dip nets (dimensions of 200–400 μm) to further detect larvae when we did not visually find larvae. In most sites, we could recognize the larvae very easily because the water in the site was clear and the sites were relatively small and shallow. The same observer (IS) did all the measurements and sampling.

Environmental predictor variables

We measured four variables at each site (local variables) and six variables at the landscape scale (Table 1). Below, we provide a description of each variable, how it was measured, and the justification for choosing it.

Local variables

For characterizing site-scale properties of the breeding sites we measured four variables: [1] Maximum water depth - the deepest point in each site which was measured during all study years and all visits. We assume that deeper sites will retain water for a longer time and *Salamandra* females have been shown in experiments to deposit more larvae into deeper pools (Segev et al., 2011). We expect that deeper sites would be more favorable for breeding. [2] Shade—estimated visually once every year at each site. We classified the sites into three categories according to the proportion of the water surface covered by vegetation canopy or rocks above the water: no shade, half shade, full shade (e.g., in cave). Skelly et al. (2005) and Van Buskirk & Arioli (2005) have shown that shaded sites were preferred by some amphibian species while others prefer more sunny sites. Our study region is relatively xeric and hot, and thus we hypothesized that *S. infraimmaculata* would prefer more shaded sites in which desiccation is expected to be slower. [3] Vegetation NDVI (Normalized Difference Vegetation Index)—a simple indicator that can be used to analyze remote sensing measurements, and indicates whether the target being observed contains live green vegetation or not. For calculating NDVI we used radiometric and geometric corrected LANDSAT8 satellite imagery from February 2014 (Roy et al., 2014). NDVI is mainly related to canopy cover, water availability and net primary productivity (Peterman & Semlitsch, 2013), and may indicate higher levels of moisture, reduce water evaporation and can be linked to shelter availability. [4] Hydroperiod—measured in the beginning (November) and until the end (June) of each rainy session for 2 years. Each site was classified into one of five rank categories according to the number of month is held water: 0 = no observed standing water, 1 = standing water observed at a single visit, 2 = water observed during two visits, 3 = water observed in three visits, 4 = water observed in all four visits. As larval development periods until metamorphosis can take minimally 2–3 months (Degani, 1996; Eitam et al., 2005; Sadeh et al., 2011) many temporary site can still serve for breeding. Hydroperiod is known to influence larval development and survival (Sadeh et al., 2011). In addition, Segev et al. (2010) showed that adult populations size of *S. infraimmaculata* in permanent sites was larger. Thus, we expect that

Table 1 The 10 variables studied in this work and the mean and range of each variable for all sampled sites and for breeding sites

	Units	All sites; mean (range)	Breeding sites; mean (range)
Local			
Maximum depth	cm	0.8 (0.1–3.2)	0.8 (0.1–3.2)
Shade	Categories (0–2)	0.6 (0–2)	0.7 (0–2)
Hydroperiod	Categories (0–4)	2.1 (0–4)	2.2 (0–4)
NDVI		0.41 (0.18–0.62)	0.41 (0.18–0.58)
Landscape			
Elevation	Meters	378 (130–880)	418 (141–880)
Aspect	Degrees	88 (0–177)	95 (0–177)
Slope	Degrees	8 (0–31)	10 (0–31)
NBS	Meters	1103 (27–4528)	837 (27–3858)
distSett	Meters	571 (0–1507)	528 (0–1386)
distRoad	Meters	319 (0–999)	350 (25–999)

larvae occupancy will be larger in breeding sites with a longer hydroperiod.

Landscape variables

We quantified six variables for characterizing large-scale properties of the breeding sites: slope, elevation, aspect, distance of each breeding site to its nearest neighboring breeding site (NBS), distance from roads (distRoad), and distance from settlements (distSett).

Elevation, aspect and slope were calculated for each site using the Digital Elevation Model (DEM) with 33-m resolution using ArcGIS (ESRI, Redlands, CA, USA). Aspect is represented by angular data (0–360). To convert it to a linear scale on a North–South axis, we subtracted all the values greater than 180. The North–South component of aspect is a variable in the range of 0–180, where North = 0, South = 180, and West =East. In the northern hemisphere, North-facing slopes receive less radiation than South-facing slopes resulting in cooler temperatures and longer hydroperiods (Blaustein et al., 1999), thus we expect that breeding sites located on North-facing slopes will be preferred. Elevation is also a factor that might limit the persistence of amphibians (Bradford et al., 2003; Pineda & Halffter, 2004). In Israel there are no breeding sites of *S. infraimmaculata* below 150 m asl (Blank & Blaustein, 2012). Thus, we hypothesized that breeding sites will be positively associated with increased elevation. As for the slope variable, steepness influences runoff and we expect that on steep slopes water will accumulate less compared to moderate slopes, and thus the potential for the formation of breeding sites is lower. Thus, we hypothesized that breeding sites would be mainly on plateaus and moderate slopes.

NBS, distSett and distRoad are the Euclidean distances to the closest breeding site, settlement, and road, respectively. All three variables were calculated using the ArcGIS spatial analyst distance function (in meters). Settlements and roads were manually digitized from high-resolution (1 m pixel size) aerial ortho-rectified images acquired in 2014. Previous studies do not indicate a clear prediction as to how *S. infraimmaculata* might respond to proximity to settlements. For example, Segev et al. (2010), found a positive correlation between urban area and *S. infraimmaculata* population size. The authors proposed that this is because human villages were purposely established close to permanent springs. In contrast, Knutson et al. (1999) found that most anuran species they surveyed had negative relationships with the presence of urban areas due to land-use transformation and wetland contamination. Roads may have multiple effects on the abundance of amphibians: roads pose mortality risk when trying to cross the roads (Fahrig & Rytwinski, 2009; Garriga et al., 2012), they restrict migration and dispersal (Ray et al., 2002), and pollution from road runoff might pose a threat to aquatic habitats (Dorchin & Shanas, 2010; Harless et al., 2011). A small scale study on *S. infraimmaculata* found that sites selected for breeding are far from roads (Blank & Blaustein, 2014). Thus, we hypothesized a positive relationship between breeding site occupancy and distance to roads. As for NBS, Segev et al. (2011) found that *S. infraimmaculata* females can spread their larvae among different breeding sites and there is some movement between breeding sites (Bar-David et al., 2007). However, this movement is mostly limited to several hundreds of meters (Bar-David et al., 2007). Thus, we hypothesized an increased probability of a water body becoming a breeding site if it is near other breeding sites.

Statistical analysis of environmental variables on larval presence

We tested for multicollinearity by examining cross-correlations among variables when cross-correlations between the variables belonging to the same scale group were identified as lower than 0.7 and by calculating the variance-inflated factor (VIF) to verify that the VIF is lower than 10 (Neter et al., 1989) using the package ‘car’ (Fox et al., 2012) implemented in R studio 1.2.1335 (R Development Core Team, Vienna, Austria). We used logistic regression in the framework of GLMs to relate the environmental variables to the binary-dependent variable (larvae or no larvae in a site).We used multi-model inference based on the Akaike Information Criterion (AIC) to rank the importance of variables (Burnham & Anderson, 2002; Blank & Blaustein, 2014; Blank et al., 2019; Krasnov et al., 2019). We used the package ‘glmulti’ (Calcagno & de Mazancourt, 2010) (implemented in R studio 1.2.1335) to facilitate multi-model inference based on every possible first-order combination of the predictors in each scale. The coefficients associated with each variable and their relative importance were assessed using a multi-model average. We used a Mann–Whitney Test (SPSS) to test the null hypothesis that water depth is not different between permanent and temporary sites. We calculated for each site in each season the ratio between the number of times we found larvae and the number of visits. We then used a Mann–Whitney Test (SPSS) on these ratios to test the null hypothesis that water depth in permanent sites has no effect on these site-specific ratios (that is, on our ability to find salamander larvae in the breeding site during the rainy season). We also calculated the average ratio for temporary and permanent sites each season.

Results

Adult population size

We added six previously studied breeding sites (Segev et al., 2010) (Table 2) to eight new breeding sites surveyed in this study (Table 3). We made 164 visits during 106 nights (during some nights we visited two sites). During the study, we captured and photographed 586 adult salamanders and 297 different individuals.

The estimated population sizes ranged between small populations of about 20 individuals to more than 500 individuals in the largest populations (Tables 2, 3). Estimated population size in permanent sites was statistically significant larger compared to temporary sites (Kruskal–Wallis Test, $\chi^2 = 8067$, df = 1) (Fig. 2).

Breeding site characteristics

Environmental predictor variables

Of the 54 monitored sites, 13 sites were permanent and 41 were temporary (Table 1S). The authors monitored the permanent sites for many years and their permanency of these breeding sites is established. 35 sites were breeding sites (larvae present) (Table 1S), although 30 of these sites were not known to serve as breeding sites prior to this work.

On the local scale, the most important variable for being a breeding site or not, according to the multi-model average, was water depth (Depth) with a relative importance of 0.77 (Table 4). Specifically, deeper pools were more likely to contain Salamander larvae (Table 4). Water depth was also selected in the three best GLM models (Table 5). Water depth also had the highest independent contribution in the hierarchical partitioning analysis (Fig. 3).

In the large scale analysis, NBS and elevation were included in the three best GLM models (Table 5). Both NBS and elevation also had the highest importance value according to the multi-model average (0.73) (Table 4). In the hierarchical partitioning, in addition to these variables that had the highest independent contributions, slope and distRoad had a substantial independent (> 20%) contribution (Fig. 4).

Table 2 Yearly population size estimates, standard error and the number of sampling days. Adopted from (Segev et al., 2010)

Site		P/T	Average	2002	2003	2004	2005	2009	2010
Hik	Estimated population size	P	248					178.5 ± 39.7	9.7 ± 317.5
	Sampling days							5	5
Manof	Estimated Population size	T	106.1		134.8 ± 70.2	79.5 ± 53.5			
	Sampling days				6	4			
Damun	Estimated population size	T	25.9		23.8 ± 24.2		28 ± 21.3		
	Sampling days				3		3		
Ein Balad	Estimated population size	P	466.4	257.5 ± 39.5	581.9 ± 117.9	559.8 ± 184.9			
	Sampling days			15	8	6			
Kawkab	Estimated Population size	P	420.2		567.9 ± 136.7	272.5 ± 95.4			
	Sampling days				6	4			
Secher	Estimated Population size	T	50.7	84.1 ± 20.3	31.3 ± 11	36.8 ± 15.4			
	Sampling days			15	8	5			

P permanent, *T* temporary

Table 3 Yearly population size estimates, standard error and the number of sampling days of the current study

Site		P/T	Average	2013	2012	2011	2010
Eshchar	Estimated population size	T	40.8		28.3 ± 8.267	35.6 ± 9.12	58.7 ± 32.4
	Sampling days				10	8	8
Atsmon	Estimated population size	T	21.8			22.5 ± 21.32	21.1 ± 17.6
	Sampling days					9	7
Ein Camon	Estimated population size	P	256.2			286.265 ± 74.23	226.1 ± 83.4
	Sampling days					9	7
Haluz	Estimated population size	P	61.5		72.3 ± 26.0	53.775 ± 29.3	58.5 ± 58.3
	Sampling days				8	9	10
Harashim	Estimated population size	P	85.4		47.9 ± 14.5	179.6 ± 161.9	28.6 ± 11.6
	Sampling days				10	9	6
Sala	Estimated population size	T	20.3	5.7 ± 5.74	34.8 ± 21.86		
	Sampling days			10	13		
Manof s	Estimated population size	T	19.5	19.3 ± 7.9	19.6 ± 8.24		
	Sampling days			11	11		
Harashim south	Estimated population size	T	29.5		29.5 ± 12.87		
	Sampling days				9		

P permanent, *T* temporary

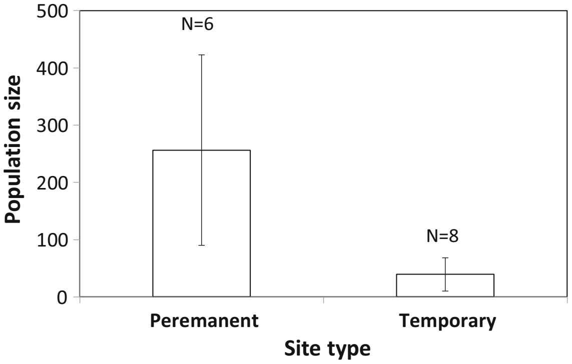

Fig. 2 The difference in the estimated population size between permanent and temporary sites (combined data from current study with that of Segev et al., 2010)

The average water depth and the type of site, permanent or temporary

The average water depth was lower in temporary sites than in permanent sites for all four studied seasons, and significantly lower in three out of the four study seasons (Fig. 5). The frequency of finding larvae in permanent sites was significantly larger than that in temporary ones (Fig. 6) in all four study seasons.

Discussion

Studying populations at the limit of a species' range is of great value, particularly for conservation planning of endangered species such as *S. infraimmaculata*, to determine the factors that are shaping population size and the geographic distribution (Gaston, 2003). One complication that has become increasingly important in light of predicted climate changes are that populations in the geographic margin of a species range may becoming less optimal. Hampe & Petit (2005) concluded that these marginal populations are disproportionately important for the survival and evolution of species. Nevertheless, these populations remain understudied despite having the highest chances for local extinction due to climate change (Cahill et al., 2013). In this study, we set out to better understand what factors support large adult population size and to identify the species–environment relationships at different scales.

In this study, we extend the work of Segev et al. (2010) by estimating additional local adult population sizes at a total of 14 sites that now cover most of the species' range in Israel. Our results support the results of Segev et al. (2010) and clearly show that the

Table 4 The estimated coefficients and the relative importance of each variable estimated across all fitted GLM models using a multi-model average approach

Variables	Estimate	Unconditional variance	Importance[a]
Local			
NDVI	− 0.31	3.35	0.25
Hydroperiod	0.07	0.04	0.3
Shade	0.66	0.44	0.66
Depth	0.0012	0.31	0.77
(Intercept)	0.31	0.89	1
Landscape			
distSett	− 0.0001	0	0.26
Aspect	0.001	0	0.28
Slope	0.06	0.005	0.57
distRoad	0.002	0	0.6
Elevation	0.003	0	0.73
NBS	− 0.0004	0	0.73
(Intercept)	− 1.037	2.15	1

[a] The importance weight for a predictor is the sum of Akaike weights of the models in which the predictor was present

Table 5 Summary of the generalized linear models (GLM)

Models					AICc	AICw	R^2_N
Local							
Depth	Shade				67.31	0.27	0.11
Depth					68.71	0.13	0.01
Depth	Hydroperiod	Shade			69.24	0.1	0.19
Landscape							
NBS	Elevation	distRoad	NBS		64.76	0.11	0.32
NBS	Elevation	Slope	distRoad	NBS	65.12	0.09	0.36
NBS	Elevation	Slope			65.86	0.06	0.29

Only the three models with the lowest AICc are presented

AICc Akaike Information Criterion with small sample correction, *AICw* model weight, R^2_N Nagelkerke's R^2 (Nagelkerke, 1991)

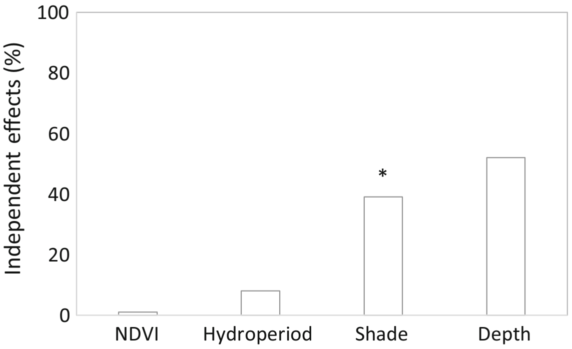

Fig. 3 The independent contribution of each local scale variable to model fit as determined by hierarchical partitioning. For abbreviations, see Methods section. *Statistically significant variables (P value < 0.05)

permanent sites support larger populations of adult salamanders. Breeding site permanency can enhance survival and fitness of both larvae and adults. Breeders at permanent sites have some obvious advantages. Females can larviposition earlier in the breeding season since they do not depend on rain water filling the sites. Additionally, larvae developing at permanent sites are free from desiccation risks. Sadeh et al. (2011) found that larvae can sense and respond to desiccation and can change their development rate, but this accelerated development might damage the larvae. Prolonging their larval period has another advantage as larvae can metamorphose at a larger size, a trait that can increase their adult fitness (Altwegg & Reyer, 2003).

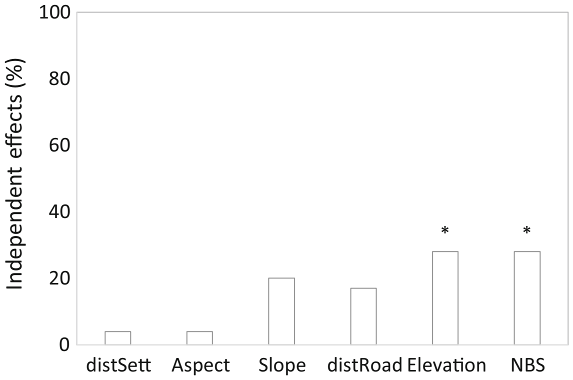

Fig. 4 The independent contribution of each large scale variable to model fit as determined by hierarchical partitioning. For abbreviations, see Methods section. *Statistically significant variables (P value < 0.05)

Our studies also focused on the factors that allow an aquatic site to become a breeding site (that is, the presence of larvae). Water depth was the most important factor in the GLM and hierarchical partitioning local analyses in predicting which sites become breeding sites. We also found that permanent sites are deeper compared to temporary sites. It seems that the water depth could be very significant in the future survival of the salamander populations especially for populations in the temporary sites on the border of the species distribution area.

Shade was also found to be important variable. Larval development periods are relatively long for Salamandra, taking more than 2 months (Eitam et al., 2005; Sadeh et al., 2011). It was previously found that

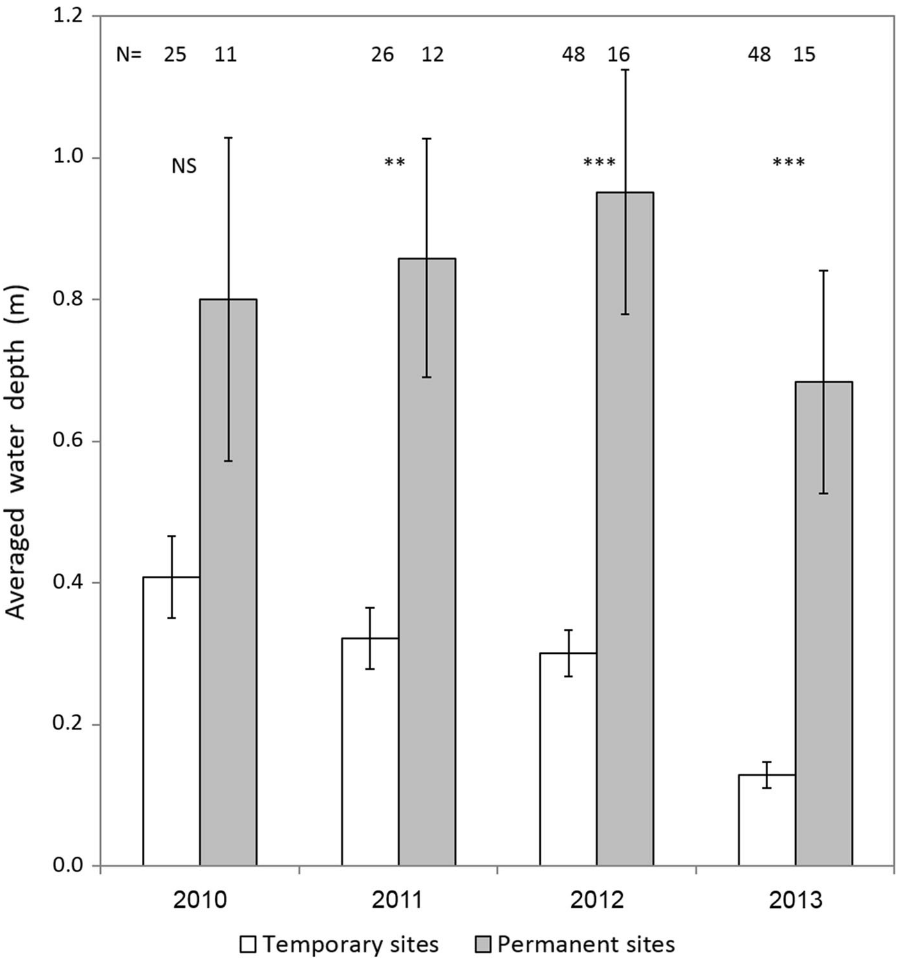

Fig. 5 The average water depth and the type of site, permanent or temporary. Significance determined by a Mann–Whitney Test with ** significant at the 0.01 level, and *** at the 0.001 level

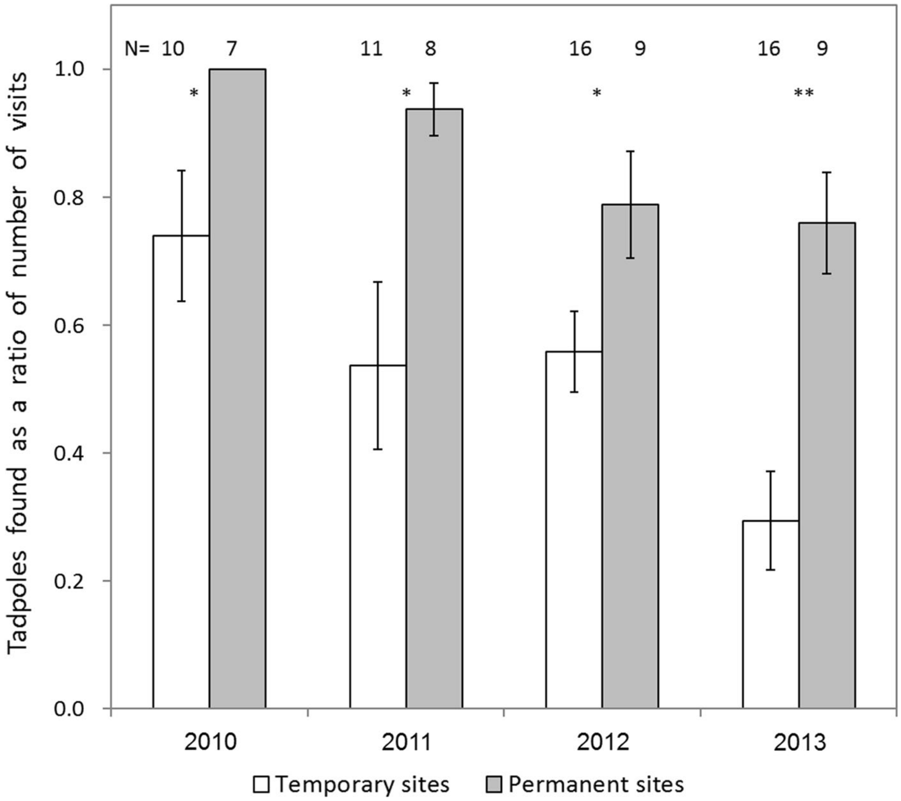

Fig. 6 difference of feasibility to find larvae in permanent or temporary sites (Mann–Whitney Test). Significance determined by a Mann–Whitney Test with * significant at the 0.05 level, and ** at the 0.01 level

water depth could predict the presence of caudate species (Joly et al., 2001). There are some species that prefer shallow water bodies for breeding (Beja & Alcazar, 2003). In that sense *S. infraimmaculata* is a generalist in terms of breeding site depth and *S. infraimmaculata* females were found to larviposition in both shallow and deeper pools (Segev et al., 2011). Shaded sites have lower temperatures and evaporation rates and this can increase the water holding capacity of sites and make them more attractive to salamanders.

Two regional variables were found to be important: distance from another breeding site and elevation. Short distance from another breeding site was the most influential variable that may contribute to functional stability of the site breeding capacity. A nearby breeding site could serve as a "backup" when one breeding site becomes damaged or dried (Cushman, 2006; Petranka, 2007). One or even a few nearby breeding sites is insufficient for amphibian survival to the long term, so the accepted strategies for preserving amphibian populations is to consider them at the level of metapopulations and often dig new breeding sites or sites clusters to be inhabited by individuals from the existing sites (Smith & Green, 2005; Marsh, 2008). Evidence about elevation is also important as salamander breeding sites have been found in the Carmel Mountain (Blank & Blaustein, 2012) and in Lebanon (Bogaerts et al., 2013)—both elevated regions. Elevation can affect the temperature, humidity and precipitation, which are important to a salamander's habitat.

Concluding remarks

This work highlights two aspects that might be important in the context of management and conservation. The first conclusion is that permanent breeding sites will support much larger populations compared to temporary sites. In light of the many threats that the *S. infraimmaculata* are facing on the edge of its distribution range such as climate change and accelerated development there is an advantage in constructing artificial sites that hold water year round. Our analyses also indicate that the most important regional variable for a breeding site was distance to another site. This makes sense in the context of a metapopulation in which some sites may only have a small population size or even go extinct on any given year. Such sites are important as back-up sites and sites of recolonization and can contribute greatly to metapopulation stability (Templeton et al., 2011). Constructing breeding sites that also support small size population might provide an important genetic reservoir for the species as whole, displaying unique adaptations that could play a disproportionate role in the long-term species survival and evolution. Conservation efforts should also focus on constructing breeding sites to support diverse populations sizes and carefully plan the locations of these sites to facilitate variation in gene flow between sites and in metapopulation stability that will enhance overall survival of the species.

Our second insight emphasizes that upon designing such breeding sites, one needs to take into account both the terrestrial and the aquatic features for a site to be suitable for breeding. Our models indicated that deeper and shaded sites are preferred for *S. infraimmaculata* breeding. At a broader scale, our study found the spatial context of site location is important. Sites in higher elevation and in proximity to other breeding sites were preferred. Overall, this study demonstrates that to properly understand species-specific suitable habitat and the drivers for population size, it is required to study both site and landscape scales predictors.

Acknowledgements This study was funded by ISF Grant 961-2008 awarded to Leon Blaustein, German-Israel Project Grant BL 1271/1-1 und STE 1130/8-1 awarded to Leon Blaustein, Sebastian Steinfartz, Arne Nolte and Alan Templeton. The Field collection of salamanders, experimentation, and their release were conducted according to the Nature and Parks Authority permit 2015/41180 and with accordance to the guidelines of the Animal Experimentation Ethics Committee at Haifa University permit number 033_b9947_6. We thank Antonina Polevikove and Shi Koren for her help with the field work.

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