Population size, structure and phenology of an endangered salamander at temporary and permanent breeding sites

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ABSTRACT

The fire salamander, *Salamandra infraimmaculata*, is listed as an endangered species in Israel and Israeli populations represent the genus' worldwide southern-most limit. This endangered classification was based largely on limited mark-recapture data and on using the Lincoln index whose assumptions of equal catchability, time homogeneity and a closed population are unlikely kept for salamander populations. We estimated population size at five breeding sites in northern Israel – two permanent and three temporary breeding sites – for up to three years using a non-parametric procedure that allows the probabilities of recapture to vary both with time and with individual animal. We also compared breeding phenology and population size structure at these same sites. Population estimates at some breeding sites were larger than previously thought. Adult population size was not correlated with the size of the water body, but instead, sites with permanent water bodies had significantly larger populations. First arrival date to the breeding site of individuals on consecutive years was positively correlated at all sites suggesting that some individuals breed consistently early while others breed consistently late. Activity abundance was correlated with daily rainfall at a permanent site but not at an adjacent temporary site. Instead, activity abundance at the temporary breeding site was synchronised with pool inundation, which did not occur during the first rains. Males remained longer than females at all breeding sites. This study provides clear management implications both in terms of determining the vulnerability of specific populations, and in suggesting that permanent breeding sites are much more likely to support larger populations.

Introduction

A key but elusive parameter for evaluating species' conservation status or extinction threat level is population size (IUCN 2001). Populations sizes are often estimated using the Lincoln index even in cases where the assumptions of this index cannot be met. Violations of the assumptions of a closed population and of equal catchability over individuals and time may cause over- and under-estimates of population size, respectively (Bohlin & Sundström 1977; Lindeman 1990; Arntzen 2002).

Populations of the fire salamander, *Salamandra infraimmaculata*, in Israel represent the southern-most edge of the genus' range (Warburg 2007). Although *S. infraimmaculata* is considered endangered in Israel (Dolev & Prevolotzky 2004) and near endangered worldwide (Papenfuss et al. 2008), population size estimates using mark-recapture are scarce (Degani 1996). Mark-recapture studies are needed on this species to better evaluate its endangered status. Moreover, mark-recapture studies can be an important tool in elucidating the factors that affect carrying capacity, which is essential information to protect an endangered species. Although there is increasing recognition of the importance of quality and quantity of terrestrial habitat for conservation of amphibians (Loredo et al. 1996; Semlitsch 1998; Skelly et al. 1999; Porej et al. 2004; Schmidt et al. 2005), quality and quantity of aquatic habitat can certainly be the limiting factor for amphibian populations.

One factor that might affect adult population size is breeding pond size. Small ponds may produce fewer recruits than could otherwise be supported by the terrestrial environment. Such recruitment limitation could occur if small ponds are of poorer quality and less preferred than larger ponds. Small ponds could be of poorer quality as the result of stronger and negative density-independent processes (e.g., per capita immigration rates are lower in small ponds) or density-dependent processes (e.g., larval survival may be lower in small ponds if small ponds have greater larval densities) affecting the number of recruits. Furthermore, we have observed that *Salamandra* is more likely to choose to larviposit in a larger pond and deposit more larvae in larger ponds (unpublished data). A second factor is the ephemerality of

the aquatic breeding habitat. Desiccation is one of the primary factors that prevent amphibian larvae from reaching metamorphosis (Newman 1989; Ryan 2007). Habitat ephemerality is also an important selective force on life history traits of many temporary pool breeders (Blaustein & Schwartz 2001; Williams 2006) and on amphibians in particular (Semlitsch 1985; Wilbur & Alford 1985; Skelly 2001). Ecological and evolutionary responses of biota to ephemerality have been brought to the forefront of ecological science due to the threat of global climate change (Kareiva et al. 1993; Alford & Richards 1999; Gian-Reto et al. 2002). Changes in temperature and rainfall pattern may result in faster habitat desiccation and can thus have particularly large impacts on species that use ephemeral habitats (Blaustein et al. 2001; Araújo et al. 2006).

Additional constraints and factors are relevant for aggregate breeders like terrestrial salamanders. Their movement to, from and among breeding sites may be determined by the distance and habitat structure between aestivation sites and the breeding ponds, thus affecting the time of arrival to the breeding site. Different factors may constrain breeders at permanent versus temporary sites. Early breeders at permanent sites may be limited by the frequency and distribution of rainy nights suitable for terrestrial activity. However, temporary-site breeders also may be constrained by the timing of pond inundation (Griffiths 1997; Semlitsch et al. 1993) – i.e. due to percolation into dry soils, pools may not fill during the first rains after an extended dry season. Temporary Mediterranean winter ponds are characterised by high variation in hydroperiod and the unpredictability of annual pond filling (Jakob et al. 2003). Strategies to cope with this unpredictability mostly involve plasticity in the onset of breeding (Diaz-Paniagua 1998). We expected to find differences in breeding phenology between populations utilising permanent breeding sites and those utilising temporary sites. *Salamandra* species make for an excellent model organism to study intraspecific variation in breeding phenology in the context of site permanence because they breed in both permanent and temporary sites, because of their rather isolated populations and because of their remarkable plasticity in terms of life history, behaviour and morphology (Alcobendas & Castanet 2000; Weitere et al. 2004).

S. infraimmaculata is found in Turkey, Syria, Lebanon, and Israel (Steinfartz et al. 2000). They are found in three distinct geographic regions in northern Israel. Breeding adults show considerable pond fidelity with part of the breeding population returning to the same breeding site every year (Warburg 2006); however, there is some dispersal among breeding sites (Bar-David et al. 2007). Activity of adult *S. infraimmaculata* is largely restricted to rainy nights (which occurs mostly between late fall and late winter) when gravid females deposit larvae in a variety of aquatic habitats including springs, rock pools, quarry cisterns and wells (Degani 1996). The larvae are predaceous and cannibalistic, and exhibit strong density-dependent effects (Degani et al. 1980; Blaustein et al. 1996; Eitam et al. 2005; Segev & Blaustein 2007). Larvae of temporary breeding sites must metamorphose by early spring, while a fraction of the larvae in permanent sites continue to grow and metamorphose the following fall when the rains begin (Blaustein, pers. obs.).

In this study, we use mark-recapture data to assess the following adult population characteristics at three temporary and two permanent breeding sites: (1) Adult population size. We predicted that permanent sites would support larger adult populations (no loss of recruitment to desiccation) but that adult population size would also increase with pool size as we expect larger pools to be capable of supporting more larvae; (2) Within-season residence time at breeding site. If females leave the site after larvipositing and mating, then we would expect breeding activity to be largely at the beginning of the breeding season for

permanent sites, because there appears to be no advantage to depositing larvae late in a permanent pond (no risk of desiccation at the beginning, and delaying larviposition will increase the risk of cannibalism and intraspecific competition). However, for temporary sites, there are tradeoffs between desiccation risk occurring during the early part of the hydroperiod where rains are sporadic with risks of cannibalism and competition later (Crump 1983; Warburg 1994; Lawler & Morin 1993; Griffiths 1997; Lehtinen 2004), so we would thus expect greater temporal bet-hedging and thus a longer residence time at temporary breeding sites; (3) Among-season individual-specific timing in first appearance at breeding site. We predicted that permanent-site breeders will show reduced plasticity on first arrival date since there is no uncertainty regarding date at which the pond holds standing water; (4) Gender-related variation in site occupancy duration. We predicted that males will stay longer than females near the breeding site to increase female encounter rate as male *Salamandra* are capable of multiple copulations within a season (Steinfartz et al. 2006) while females are capable of long-term sperm storage and repeated usage (Sever 2002).

Methods

We studied five *S. infraimmaculata* populations (two permanent and three temporary breeding sites) for 2-3 seasons per site (Fig. 1; Tables 1, 2). We use the term "population" for the breeding aggregation around the sampled water body. Breeding sites were located at two geographic regions ~25 km apart in northern Israel: Mt. Carmel and the Lower Galilee. Adult *Salamandra* were monitored on rainy nights throughout the breeding season for a total of 43 nights (generally two sites were sampled on a given night) in which 670 captures were made over the entire study. We used visual search using head torches and kept duration (two person hours) and area searched ($\sim 1000\,\mathrm{m}^2$) constant among sites and censuses. As *Salamandra* are slow moving, virtually every salamander that was detected was caught. For each individual, we recorded a digital dorsal photo and gender. Individuals were then released at their capture site. Later in the laboratory, a hard-copy picture of every individual captured was compared with a photograph database of all previously caught individuals. The unique dorsal yellow spot pattern was used to make individual-specific identifications (Doody 1995; Warburg 2006).

We used the mark-recapture data to estimate adult population size using a non-parametric procedure developed by Chao et al. (1992), allowing probabilities of recapture to vary both with time (different probabilities of capture at the t different sampling times) and with individual animal (different individuals have different probabilities of capture). Given this general framework, Chao et al. (1992), provide three different bias corrections for dealing with these heterogeneities; we chose the model that gave the lowest variance. This procedure is especially appropriate for species like terrestrial salamanders that show high heterogeneity between individual capture probabilities (Grover 2000; Petranka & Murray 2001).

To examine the evidence for our hypothesis that permanent pools carry larger populations, we compared the natural log-transformed population values averaged over years between permanent and temporary breeding sites by a t-test. We also examined evidence that pool size may influence population size and considered the evidence that population size might be correlated with urban characteristics (Spearman rank correlation). Using Google Earth Pro, we estimated proportion of urbanised area, distance to nearest road and settlement, and total length of dirt and paved roads over a radius of 1.28 km radius (maximum
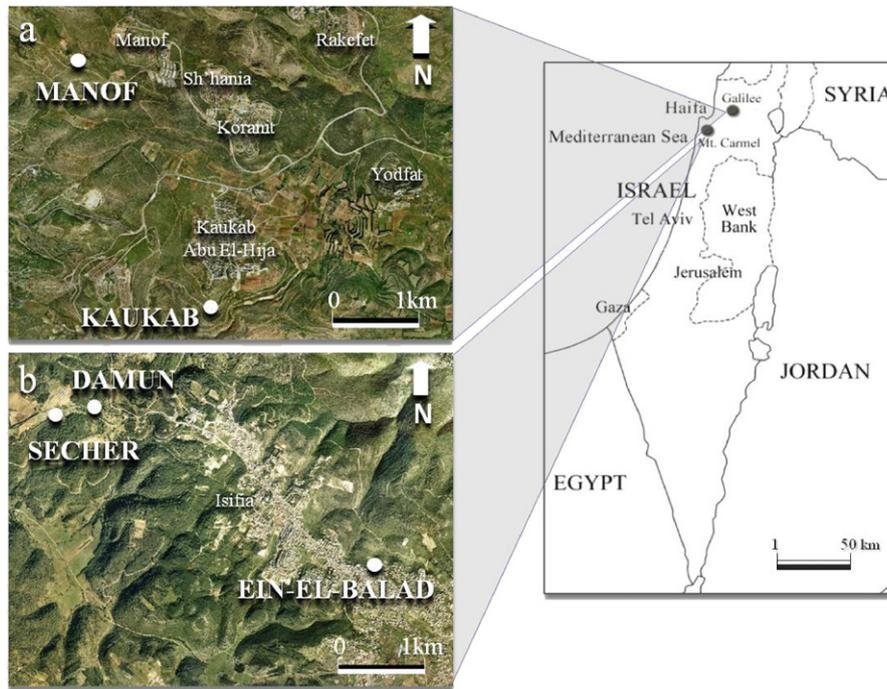
Fig. 1. Geographic maps of the study regions. On the aerial photos, *Salamandra infraimmaculata* breeding sites apear in capital letters and marked with dots while small letters signify nearby villages. The upper left hand (a) shows the Lower Galilee sites and the lower left hand map (b) shows the Mt. Carmel sites.

Table 1
Site ephemerality, location and description of the five breeding sites studied.

Ephemerality	Site	Description
Permanent	Ein-El-Balad	Spring-fed man-made pool (32º43′13″N; 35°04′17″E), ~20 m² surface area and ~1.2 m maximum depth.
	Kaukab	Spring (32°49′23″N; 35°14′51″E), two permanent rock pools, ~40 m apart; each ~15 m² surface area and ~0.8 m maximum depth).
Temporary	Secher	Large pool (32°44′04″N; 35°01′52″E), generally, but not always, dry in summer, ~400 m² and ~2 m max depth (See detailed site description at Segev & Blaustein 2007).
	Damun	Collection of temporary small volume and shallow rock pools (32°44′06″N; 35°02′00″E), (See detailed site description at Spencer et al. 1999).
	Manof	Collection of temporary rock pools (32°50′58″N; 35°13′52″E). *Salamandra* deposit larvae in two large (~40 m²), one medium (~15 m²).

Table 2
Yearly population size estimates, standard errors and number of samples at the two permanent and three temporary breeding sites. The year listed provides the beginning of the breeding season. For example, 2002 represents fall 2002 through spring 2003.

Site	2002	2003	2004	2005
Ein-El-Balad (permanent)				
Population Size	257.5	581.9	559.8	-
SE	39.5	117.9	184.9	-
Sampling Dates	15	8	6	-
Kaukab (permanent)				
Population Size	-	567.9	272.5	-
SE	-	136.7	95.4	-
Sampling Dates	-	6	4	-
Secher (temporary)				
Population Size	84.1	31.3	36.8	-
SE	20.3	11	15.4	-
Sampling Dates	15	8	5	-
Damun (temporary)				
Population Size	-	23.8	-	28
SE	-	24.2	-	21.3
Sampling Dates	-	3	-	3
Manof (temporary)				
Population Size	-	134.8	79.5	-
SE	-	70.2	53.5	-
Sampling Dates	-	6	4	-

dispersal distance detected to date by a *Salamandra* individual: Bar-David et al. 2007).

To determine if time of first appearance relative to conspecifics was consistent for specific individuals between years, we ranked all individuals that were caught on consecutive years for each year based on their first occurrence, and conducted Spearman-rank correlations across years. We also compared residence time between sites and years within the Carmel (Ein-El-Balad and Secher) and within the Galilee (Kaukab and Manof). When an individual was observed once, it was signed a value of 1, while for individuals with multiple captures, we used the interval between the first and last capture to estimate the minimal annual duration of stay at the breeding site.

We assessed whether breeding site activity (number of individuals observed on a given sampling night) at a permanent

(Ein El-Balad) and a temporary (Secher) breeding site during 2002 was correlated (Spearman rank). These two sites on Mt. Carmel are only ~5 km apart and were sampled on the same nights. We assessed the data for only these two sites on this one year due to insufficient sampling nights for the other sites and years.

Results

Population size

Estimated adult population sizes ranged considerably among breeding sites from > 500 to ~20 (Table 2). Based on 95 percent confidence intervals, there were no significant differences between population sizes across years within a site although there were many significant contrasts between sites within a year. Comparing sites averaged over years, population estimates could not be explained by the size of the breeding pools – either maximum pool volume (Pearson Correlation: r=-0.38; p=0.532; Fig. 2) or maximum surface area (Pearson Correlation: r=-0.37; p=0.542). Instead, the two permanent sites had considerably larger populations than the three temporary sites (t=4.33; df=3; p=0.027). Despite three orders of magnitude difference in pool volume, the three temporary sites show relatively small variation in population size (Fig. 2, Pearson Correlation: r=-0.074; p=0.953). A normalised test of mean differences on paired temporary sites sampled during the same year revealed no significant differences (p ⩾ 0.05 for all cases).

Average yearly population size was positively correlated with proportion of urbanised cover area (Spearman's Rho=0.9; p=0.037), negatively correlated with the distance to the nearest settlement (Spearman's Rho=-0.9; p=0.037) and tended to be, but not significantly, negatively correlated to road proximity (Spearman's Rho=-0.6; p=0.285) and to road length (Spearman's Rho=-0.7; p=0.188).

Residence timing and duration, phenology and synchronisation with rains

Specific individuals tend to consistently arrive either early or late to the breeding site. Individuals' first arrival date across seasons was positively correlated in all the breeding sites tested (we did not assess data from Damun site due to small sample size) (Table 3). Males stayed at the breeding site significantly longer than females with no site or site by sex interaction (Fig. 3; Table 4).

The number of active *Salamandra* at Ein-El-Balad was positively correlated with the daily amount of rain occurring on the census day throughout the season (Spearman Rho=0.708; p=0.002) (Fig. 4a). However, at the temporary Secher site, *Salamandra* numbers peaked on Nov. 12th, the first time during the rainy season that the pool had standing water. Aside from this peak, numbers at Secher were low throughout the rainy season
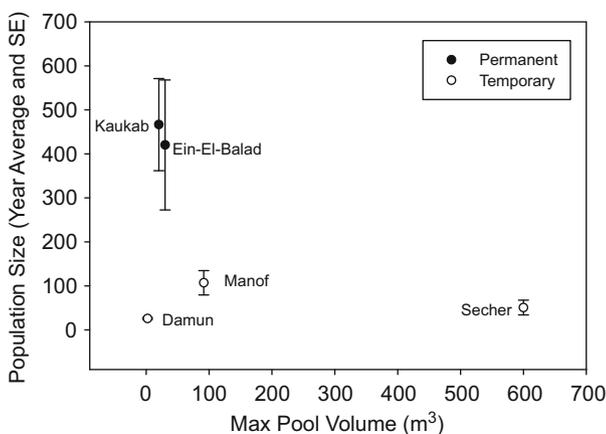
Table 3
Correlation analysis (Spearman rank) of individual breeders' first arrival date across consecutive seasons.

Site	Seasons Compared	N	Spearman Rho	p
Ein-El-Balad	2002-2003	38	0.437	0.0061
	2003-2004	30	0.51	0.004
Kaukab	2003-2004	34	0.527	0.0014
Secher	2002-2003	10	0.806	0.0049
Manof	2003-2004	6	0.871	0.0239

N = number of specific individuals found during both years.

showing no correlation with the daily rainfall (Spearman's Rho=-0.142; p=0.586) (Fig. 4b).

Discussion

Good population estimates for assessing the endangered status are uncommon for amphibians in general and rare for *Salamandra* species in particular (Miaud et al. 2001; Rebelo & Leclair 2003; Schmidt et al. 2005, 2007). For *S. infraimmaculata,* prior to our study, a long-term study of the Damun breeding site by M. R. Warburg (Warburg 1994, 2007; Bar-David et al. 2007), based on activity data, indicated a fluctuating, very small population; only 131 different individuals were detected over an 18 year period. This long-term study was influential in the local assessment that *S. infraimmaculata* was highly endangered in the Mt. Carmel region. Our own study also indicated a small population at this site. However, we have since found that populations at various breeding sites are linked by dispersal (Bar-David et al. 2007). Moreover, we have demonstrated that population size varies greatly among sites, ranging from hundreds (Kaukab, Ein-El-Balad) to tens (e.g., Damun).

We were also interested in explaining among-site variation in population size. We are limited in inferring what factors are important because of a small number of sites censused; careful censusing of numerous sites is problematic because rains at night are infrequent and unpredictable, long processing times, and the number of breeding sites, particularly permanent sites, are very limited. Nevertheless, our data strongly support our *a priori* hypothesis that permanent breeding sites support larger adult populations than temporary ones. Breeding site permanence may drive population dynamics at both pre-metamorphic larval stages and post metamorphic terrestrial stages and can have strong effects on both survival and reproductive fitness. Breeders at permanent sites can start the breeding season earlier since they do not depend on pool inundation as temporary sites breeders. Additionally, larvae developing at permanent sites are free from desiccation risks and may prolong their larval period and consequently metamorphose at a larger size, a trait that can have high selective value in amphibian species (see review by Altwegg & Reyer 2003). Pond volume differed among sites by several orders of magnitude, yet it did not show any importance in explaining the high variance in adult population size among these five breeding sites. Although greatly increasing the number of breeding sites checked is likely to reveal that breeding pond size can also be important, the overriding effects of pool permanence in this study suggest it to be most important. Quality and quantity of terrestrial habitat surrounding the breeding site should be important for the supporting populations of amphibians (Semlitsch 1998; Porej et al. 2004; Regosin et al. 2005). Urban cover, generally expected to be negatively correlated with amphibian population size, was *positively* correlated with *Salamandra* population size. This undoubtedly is confounded with pond permanence; historically, due to the paucity of water
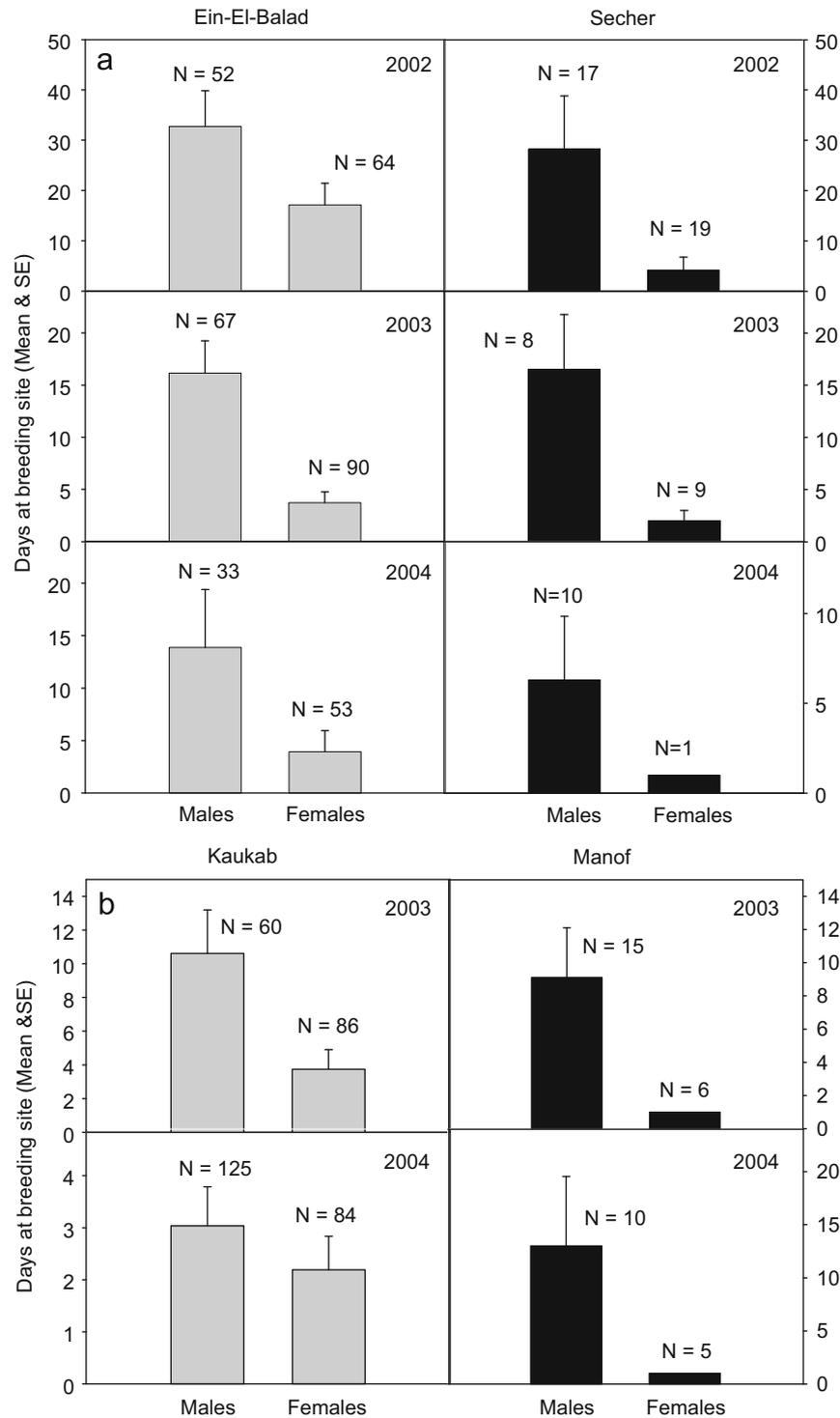

Fig. 2. *Salamandra infraimmaculata* average yearly population size estimates related to breeding pool maximum volume. Error bars are ± 1 standard error.

Fig 3. . Male and female breeding sites residence time. Sites are paired per year and with geographic region; (a) Carmel and (b) Lower Galilee. Error bars are one standard error. N=number of individuals.

sources that are available all year, human settlements were established close to permanent springs; large villages of Isifya and Kaukab exist close to Ein-El-Balad and Kaukab springs respectively, while no villages exist close to the temporary breeding sites. We suggest then that relatively larger *Salamandra* populations exist at the permanent sites not because of, but despite, the proximity to human settlements. We think it likely that the populations would be larger at the permanent sites were there no large urban settlements.

We found that males remain longer than females near the breeding site. This may reflect the species mating system and inter-sex conflicts as different selection pressures shape each gender's reproductive behaviour. *Salamandra* demonstrate multiple paternity (Steinfartz et al. 2006) – i.e., males are capable of multiple mating with different females during a single season (Adams et al. 2005). Females however are capable of long-term sperm storage and thus may not be limited by copulation every year to reproduce each year (Sever 2002).

Table 4
Analysis of variance assessing the influence of site, gender, year and gender by site interaction on breeders' residence time at the breeding site.

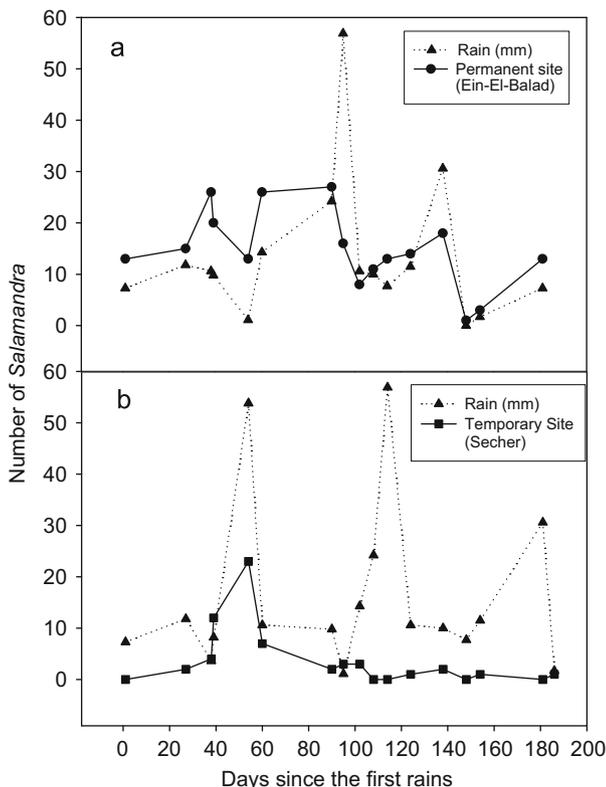| Geographic region	df	F	p
Carmel (Ein-El-Balad vs. Secher)			
Site	1	2.456	0.1178
Gender	1	11.638	0.0007
Year	2	11.42	< 0.0001
Gender*site	1	0.0125	0.9111
Galilee (Kaukab vs. Manof)			
Site	1	0.143	0.7055
Gender	1	8.907	0.003
Year	2	7.981	0.005
Gender*site	1	2.062	0.1518

Fig 4. . Temporal distribution of the numbers of *S. infraimmaculata* individuals censused across sampling dates and daily amount of rain at: (a) permanent site (Ein-El-Balad); and (b) temporary site (Secher) in the Carmel during 2002.

We found that individuals, in comparison to their conspecifics, were consistently early arrivers or late arrivers. The consistency in breeders' first arrival may be related to individual differences in orientation abilities or use of the same aestivation refuge year after year, resulting in individuals that use refuges closer to the breeding site consistently arriving earlier. This "refuge fidelity" may be prominent in habitats where high quality refuges are limited. Consistent ordered arrival to breeding site was shown for *Ambystoma maculatum* (Stenhouse 1985) but not for *Ambystoma talpoideum* (Semlitsch et al. 1993).

The temporal distribution of *Salamandra* across a breeding season may also be tied to breeding site permanence. At the temporary site, in contrast to the permanent site, salamanders seem to synchronise breeding-site activity with temporary pool filling (Jakob et al. 2003; Semlitsch et al. 1993) and the numbers observed was not correlated with daily amount of rain. This breeding strategy may maximise the duration of larval period and

reduces the probability for catastrophic mortality of entire larval cohorts due to early pool desiccation (Semlitsch 1987; Pechmann et al. 1991; Skelly 1996; Blaustein et al. 2001). Additionally, breeding shortly after pond-filling reduces inter-guild competition with other aquatic predators.

Conservation Management Implications

Small isolated populations are generally associated with higher probability of local extinction. The picture created by the long-term data of Warburg (1994, 2007) at the Damun site was alarming for two reasons: (1) it indicated a very low population size; and (2) it was assumed that due to strong pond fidelity (Warburg 2006), populations were isolated and thus more susceptible to local extinctions. Our information provides a somewhat more optimistic picture. First, although our estimated population size at the Damun site in recent years is within the range of that found by Warburg (1974–1999), other populations are several orders of magnitude greater. Degani (1996) has also demonstrated larger populations in Israel in the Galilee region. Second, we now know that breeding site populations on Mt. Carmel are linked as metapopulations by some among-site dispersal (Bar-David et al. 2007); which is also consistent with dispersal studies of another *Salamandra* species in Europe (Schmidt et al. 2005; Schulte et al. 2007).

Although some of the population sizes that we found are encouraging regarding conservation of this species, current activities in and around these sites raise considerable concern. The Kaukab site was stocked with *Gambusia* in 2002 which have since been decimating the larval cohorts (Segev et al. 2009). As it takes 4-5 years for *Salamandra* juveniles to become reproductively mature and join the adult population at the breeding site, we are likely to begin to see population declines if *Gambusia* is not removed. The Ein-El-Balad site, according to development plans for the nearby village of Isifya, will soon be encroached further. A wide dirt road built less than 5 m from the Manof site endangers the population as we have observed a number of roadkills (Segev and Blaustein, unpublished). Secher Pond is privately owned. It has been used for irrigation in the past and can be used for such purposes again.

The most significant information coming from our study regarding future management is the evidence that permanent ponds of similar size to temporary ponds will support a much larger adult population size of *Salamandra*. Over the past decade, numerous temporary ponds have been constructed to provide breeding sites for *Salamandra* within nature reserves. Our findings suggest that larger, more stable populations can be established if the ponds can be made to hold water year round.

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