ISRAEL JOURNAL OF ECOLOGY & EVOLUTION, Vol. 53, 2007, pp. 143–159

LONG-DISTANCE MOVEMENTS BY FIRE SALAMANDERS (*SALAMANDRA INFRAIMMACULATA*) AND IMPLICATIONS FOR HABITAT FRAGMENTATION

Shirli Bar-David,[a,b,]* Ori Segev,[a] Nir Peleg,[a] Naomi Hill,[a] Alan R. Templeton,[c] Cheryl B. Schultz,[a,d] and Leon Blaustein[a]

[a]*Institute of Evolution and Department of Evolutionary and Environmental Biology, Faculty of Sciences, University of Haifa, Haifa 31905, Israel*

[b]*Mitrani Department of Desert Ecology, Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Sede Boqer 84990, Israel*

[c]*Department of Biology, Washington University, St. Louis, Missouri 63130-4899, USA*

[d]*School of Biological Sciences, Washington State University, Vancouver, Washington 98686, USA*

ABSTRACT

Dispersal may be particularly important for the regional persistence of metapopulations that experience local extinctions. Some amphibian species are structured as metapopulations. Long-term persistence of these species should depend on natural connections between local subpopulations through dispersal. We explored movement distances of fire salamander adults (*Salamandra infraimmaculata*), a locally endangered species, on Mt. Carmel, northern Israel, and investigated the implications of movement for persistence of populations.

During the breeding seasons (November–March) of 1999–2000 and 2002–2006, capture–recapture surveys were conducted around four breeding sites and along unpaved roads connecting them. Out of 300 adult salamander captures, 72 cases were recaptures. Most of the recaptures were in the same site as the initial capture. In eight cases (11%), however, salamanders were recaptured at least 400 m away from the first site. The maximum direct distances between capture–recapture sites (1100–1300 m) were greater than previously documented and indicated potential connectivity between breeding sites.

We then examined the potential implications of habitat fragmentation, i.e., isolation of a breeding site, on population persistence by calculating local extinction risks of one of the sites assuming it is an isolated population. Parameters were based on 18 years of count-based data. The high probability of local extinction found by the analysis highlights the severe consequences of fragmentation. Hence, we conclude that it is important to preserve the terrestrial habitats and promote landscape connectivity between breeding sites, in addition to the aquatic sites, in order to enable individual movements between sites and the possibility of a rescue effect.

*Author to whom correspondence should be addressed. E-mail: shirlibd@bgu.ac.il
Accepted December 2007.

Keywords: Population persistence, amphibians, metapopulation, dispersal, connectivity between breeding sites, Israel, capture–recapture

INTRODUCTION

Dispersal is an important life history trait with direct consequences on gene flow and population dynamics and persistence (Colbert et al., 2001). Dispersal between populations may reduce local extinction rates through a "rescue effect" (Brown and Kodric-brown, 1977), by reproduction in the populations into which they disperse, and by increasing genetic diversity. Moreover, dispersers may recolonize areas following local population extinction and can live and reproduce in small areas of suitable habitat that would be insufficient to support a viable isolated local population (Templeton et al., 2001).

Dispersal may be particularly important for the regional long-term persistence of populations that are structured as a metapopulation (Hanski and Gilpin, 1997) and experience local extinctions due to stochastic processes. A metapopulation is defined as a set of breeding patches connected by occasionally dispersing individuals. Each patch, when isolated, has a substantial extinction probability. Thus, the long-term persistence of the metapopulation depends on dispersal and colonization and occurs only at the regional level (Smith and Green, 2005).

Some amphibian species populations are structured as metapopulations (Smith and Green, 2005). Moreover, many studies of amphibian populations have documented high local extinction rates due to droughts and other factors (reviewed by Marsh and Trenham, 2001). Consequently, the long-term persistence of these species should depend on natural connections between local subpopulations through dispersal.

Traditionally, amphibians were believed to have strong breeding site fidelity and low dispersal rates (Blaustein et al., 1994). However, recent studies demonstrate that amphibians do exhibit a wide range of dispersal strategies, and there are species that can move distances much greater than previously thought (Marsh and Trenham, 2001; Trenham et al., 2001; Funk et al., 2005; Smith and Green, 2005; Cushman, 2006). These movements may include directional dispersal followed by establishment, migration between breeding sites (e.g., Funk et al., 2005), and temporary migration between critical habitat elements (e.g., between breeding sites and terrestrial habitats, as in the case of the spotted salamanders (*Ambystoma maculatum*) and American toads (*Bufo americanus*) (Rothermel, 2004)).

Although amphibians depend on both aquatic and terrestrial habitats for their population viability, conservation efforts aiming to protect these species historically focused on protecting wetlands and mostly neglect terrestrial habitats (Semlitsch, 1998; Rothermel, 2004; Sztatecsny and Schabetsberger, 2005). If dispersal between breeding sites plays an important role in amphibian dynamics, then habitat fragmentation (e.g., roads and urbanization) may increase extinction rates (Funk et al., 2005; Marsh et al., 2005; Cushman, 2006) because dispersal can be strongly influenced by the environmental matrix (Templeton et al., 2001, but see Marsh et al., 2004). Thus, historical conservation efforts would not be sufficient for protecting amphibian populations at the landscape level (Semlitsch, 1998; Rothermel, 2004; Funk et al., 2005). A better understanding of the role of dispersal in different amphibian species is needed as a basis for developing protection measures (Trenham and Shaffer, 2005) and for defining the proper "conservation unit", i.e., the landscape components that should be protected.

Dispersal data that allow reliable estimates of dispersal parameters are lacking for most amphibians species (Smith and Green, 2005; Cushman, 2006). Salamanders as a group may not move very far. However, there is high variation among species in the maximum distance recorded, ranging from several meters (e.g., *Rhyacotridon cascade*, Smith and Green, 2005) to several kilometers (e.g., *Taricha rivularis*, Smith and Green, 2005; for further discussion see: Semlitsch, 1998; Trenham et al., 2001; Marsh and Trenham, 2001; Rothermel, 2004; Trenham and Shaffer, 2005).

Information on movement patterns of the fire salamander, *Salamandra infraimmaculata* (Steinfartz et al., 2000), and on its role in population structure and persistence should contribute to conservation measures aimed to protect this locally endangered species. In this study, we first investigated movement distances of fire salamanders among and around breeding sites on Mt. Carmel, northern Israel, using capture–recapture data. The movement distances may include any type of movements from a breeding site: dispersal to summer burrows (temporary migration), dispersal between breeding sites, foraging forays, or unidirectional movement followed by establishment. We compared these movement distances to the direct distances between breeding sites in the area as an indication of potential connectivity between the sites through migration or dispersal. We then explored the potential implications of isolation of the breeding sites, caused by habitat fragmentation, on population persistence by calculating local extinction risks in one of the breeding sites, assuming it is an isolated population.

METHODS

1. THE SPECIES

Salamandra infraimmaculata (also referred to as *Salamandra salamandra infraimmaculata* (Degani et al., 1999)) is found throughout much of the Near East (Steinfartz et al., 2000), but is classified as an endangered species in Israel (Dolev and Perevolotsky, 2004). The species is found in several areas of northern Israel. Mt. Carmel is the southern limit of its range worldwide (Degani, 1996). *S. infraimmaculata* adults return to breeding sites in the autumn and winter when the rains begin. Females larviposit in a variety of aquatic habitats including small springs, large ponds, rock pools, pools in wadis (summer-dry streams), quarry cisterns, and wells (Degani, 1996). Larvae remain in temporary pools for a minimum of 2–3 months, then metamorphose and leave the water. After reaching reproductive maturity (approximately 3–5 years old), *S. infraimmaculata* return to pools to breed (Warburg, 1994). Little is known about the terrestrial, nonbreeding stage of *S. infraimmaculata*. Adults and juveniles are assumed to crawl into the burrows or crevices in the ground, under rocks, or into small caves during the hot, dry season. The range of movement distances from the breeding sites to the summer habitats is unknown, as is the range of the potential long-distance movements of dispersing individuals. The conventional wisdom is that the fire salamanders have strong breeding site fidelity (Warburg, 1994). We know of no dispersal assessments of *S. infraimmaculata*. In "homing" experiments, *S. infraimmaculata* individuals returned to the original site in which they were captured when the displacement distance was up to 400 m away from the site where they were released (Degani, 1996). A recent study (Schmidt et al., 2007) suggested high migration activity of *Salamandra salamandra salamandra*, however, it was based on demographical analysis and not on empirical data of movement patterns.

2. THE STUDY AREA

Mt. Carmel, located in northern Israel (Fig. 1), is characterized by Mediterranean climate (Carmel and Stoller-Cavari, 2006). *S. infraimmaculata* breeding habitats in the Mt. Carmel region are patchily distributed, and many of the breeding sites are ephemeral. The study area (32°44′N, 35°00′E) covered ~15 km^2 on the top of Mt. Carmel, south of Haifa, between two settlements: Kibbutz Beit-Oren and the town of Isfiya (Fig. 1). Within this area, four breeding sites were studied (Fig. 1): (1) Sekher Pond, a semi-permanent pond; (2) Damun pools, a set of temporary natural rock pools (Spencer et al., 2002), approximately 400 m from Sekher Pond. At this site, *S. infraimmaculata* dynamics were extensively studied between the years 1973–1991 (Warburg, 1994); (3) Pine Club breeding site, which includes a man-made temporary water reservoir and temporary natural rock pools; (4) Ein Alon, a permanent natural spring.

Direct distances among the studied breeding sites range from 400 m to several kilometers. The direct distance from one breeding site to the closest site in its vicinity is up to 2 km (Fig. 1). Natural undisturbed habitat of Mediterranean woodland connects the Sekher and Ein Alon sites. However, a two-lane road runs between the Sekher, Damun, and the Pine Club sites (Fig. 1).

Mt. Carmel is subject to development pressure. The transformation of agricultural lands and woodlands into built-up areas—e.g., the growth of the city of Haifa in the north and the town of Isfiya in the east—is a process that leads to loss of natural habitats and to fragmentation. This process threatens biodiversity in the region, including the distribution of *S. infraimmaculata*.

3. CAPTURE–RECAPTURE

Adult salamanders were captured on rainy nights throughout the breeding season from October to March. The study was conducted during 5 breeding seasons: 1999–2000 and 2002–2006 (total of 61 nights—average of 12 nights per season). During the winter of 1999–2000, capture efforts were focused on Damun site and the ~17 km of unpaved forest roads within the study area. These roads pass near two of the studied sites (Damun and Ein Alon, Fig. 1). During 2002–2005, capture efforts were focused on the breeding sites (mainly Sekher and Damun, Fig. 1). Throughout the 2005–2006 season, all the sites and unpaved roads were explored for salamanders: on each night a couple of breeding sites or road segments were surveyed.

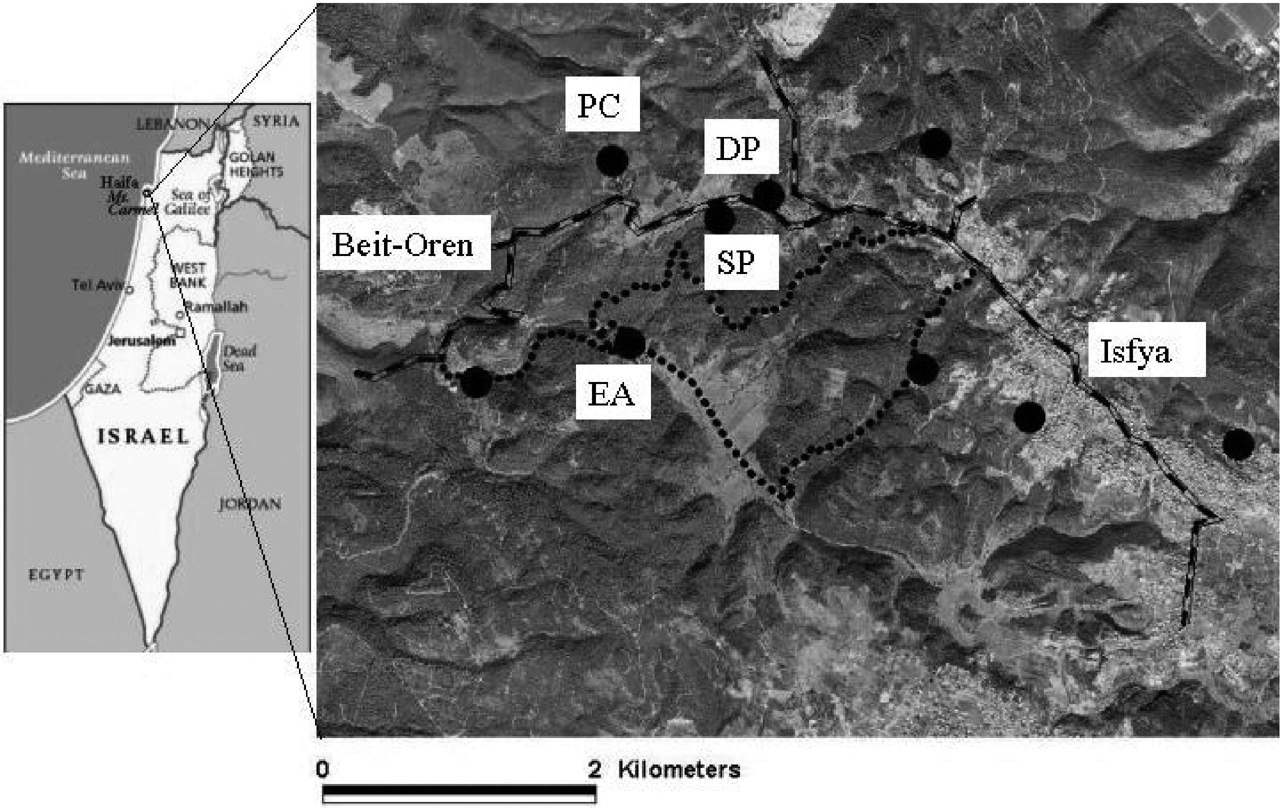

Fig. 1. Map of the study area. Dots, representing breeding sites of *S. infraimmaculata* in the studied area, are within the Mt. Carmel region. Capture–recapture study was conducted in four breeding sites: Sekher Pond (SP), Damun pools (DP), Pine Club (PC), and Ein Alon (EA); and along unpaved roads (dotted lines). Beit-Oren and Isfiya are a Kibbutz and a town, respectively, at the edges of the study area. Paved roads are represented by dashed lines.

During each survey, we searched for salamanders (using flashlights) in a constant area per site, for approximately one hour. The following parameters were collected on each adult salamander encounter: (1) digital dorsal photo, (2) sex (at the beginning of the season when distinction is clear), and (3) spatial position (the breeding site). Accurate spatial position (geographic coordinates) was measured by a GPS (Rikaline model 6021-×6; error of ± 5 m) or by a car odometer (error up to ± 50 m) for individuals encountered on the routes between the breeding sites. The captured individuals were immediately released at their capture site.

A photograph of each captured individual was compared with our photograph database. We used the unique dorsal spot patterns of each individual to identify the same individual at different recapture events (Warburg, 1994). At least two observers confirmed a recapture. Capture–recapture locations were then analyzed using Geographical Information System techniques (Arcview 3.1) and digitized aerial photos.

4. EXTINCTION RISKS

To assess the implications of isolation of a breeding site on population persistence, we examined the risk of extinction of the population in the Damun site, assuming for the analysis that it is an isolated population. The goal of this analysis was to provide a general estimate of extinction probabilities in order to suggest the potential effect of habitat fragmentation around one breeding site leading to isolation and hence to limitation of recolonization or rescue effect. We used long-term count data (population censuses over multiple years) of the Damun population collected by Warburg (1994) as the empirical basis for the analysis. The count data represent the cumulative number of different individuals captured on various searching occasions, in each breeding season (Warburg, 1994). We used the diffusion-approximation approach developed by Dennis et al. (1991) and described by Morris and Doak (2002, chapter 3). In this method, P, the probability of extinction in t years, is a function of the geometric mean of the population growth rate, μ, and the variance of the log population growth rate, σ^2, the initial population size (*), and an extinction threshold of population size (*). It is calculated as

$$P\left(t \middle| x_d, \mu, \sigma^2\right) = \Phi\left(\frac{-x_d - \mu t}{\sqrt{\sigma^2 t}}\right) + \exp\left(-2\mu x_d / \sigma^2\right)\Phi\left(\frac{-x_d - \mu t}{\sqrt{\sigma^2 t}}\right)$$

where Φ is the standard normal cumulative distribution function and x_d is the distance on a logarithmic scale from the parameters indicated above by a star: initial population size and an extinction threshold of population size.

Given the uncertainty about the current population size of the Damun population, we used a range of likely initial population sizes, between 20–60 individuals (see Warburg, 1994), to calculate the probabilities of extinction. We defined the extinction threshold as 2 individuals, since there were years in which the census counts (Warburg, 1994) indicated only few individuals, and yet the population did not become extinct.

This count-based analysis is based on several assumptions, which we assessed following Morris and Doak (2002, chapter 3), before carrying out analyses: (a) Density independence—there was no significant correlation between μ and the population size at each time step (linear regression, df = 17, $p = 0.19$). Hence we concluded that the applicability of the analysis is not likely to be violated by density dependence, at least over time periods of moderate length; (b) No temporal environmental trends—there was no significant change in μ over time (linear regression df = 17, $p = 0.96$) nor a temporal trend in σ^2 over time (linear regression df = 17, $p = 0.24$); (c) Only small to moderate environmental variation—the Mediterranean climate is relatively stable, and catastrophes are rare. With short-term count data, we lacked sufficient information to estimate the frequency and potential impact of rare catastrophes. Thus, if catastrophes do occur (e.g., a sequence of several years of drought) our assessment of extinction risk will likely underestimate the true risk; (d) No demographic stochasticity—data were not sufficient to include the potential impact of demographic stochasticity, and we therefore might underestimate extinction risk; (e) Observation error is minor (i.e., census counts represent the true population size of the entire population or a constant proportion of the population)—since we used published count-based data, we could not estimate observation error and its potential impact on simulation results. Observation error might lead to a pessimistic measure of viability over the short term (Morris and Doak, 2002); however, it might offset to some extent the potential underestimates mentioned above.

Given these uncertainties and the limitations of the count-based data, we were interested in general trajectories. These simulations were intended as an illustration of the types of phenomena that may be observed, and thus illustrate the potential importance of rescue effect through dispersal for population persistence.

RESULTS

1. CAPTURE–RECAPTURE

Out of 300 adult salamander captures, 72 cases were recaptures. More than half of the recapture events (51%) occurred after a time interval of from one to four years. One recapture event occurred after six years (Table 1). Most of the recaptures were in the close vicinity of the same breeding site as the former capture site, i.e., within 200 m of the pond (Table 1). In eight cases (11%), however, salamanders were recaptured at least 400 m away from the first location (Fig. 2): three males, two females, and three of undetermined sex. In three cases, the direct distance between recaptures was greater than 1100 m, with a maximum distance of 1280 ± 50 m (Fig. 2). Two recaptures were in different breeding sites (Table 1): one animal first captured in Sekher was recaptured in Ein Alon, and another first captured in Sekher was recaptured in Damun (Fig. 3). The latter was a detected road kill 30 m away from a rock pool of the Damun breeding site and 400 m away from Sekher, the original site of capture. The movement-distances curve (Fig. 2) that presents the distribution of distances between capture–recapture sites may include any type of movements from a breeding site: dispersal to summer burrows (temporary migration), dispersal between breeding sites, foraging forays, or unidirectional movement followed by establishment. This curve fits the general shape of a

Table 1
Number of capture–recapture events within and between seasons and sites. Adult salamanders were captured and documented on rainy nights throughout the entire breeding season from October to March, during 5 seasons: 1999–2000 and 2002–2006. Capture efforts were focused on four breeding sites and unpaved forest roads ("roads") between sites (Fig. 1)

Time interval between capture–recapture	Capture–recaptures within the same breeding site	Capture–recaptures in different breeding sites	1st capture along a road and recapture in a breeding site	Capture–recaptures along a road
Same season	34	1	0	2
After a year	13	0	0	0
After 2 years	11	1	1	0
After 3 years	4	0	2	0
After 4 years	1	0	1	0
After 5 years	0	0	0	0
After 6 years	0	0	0	1

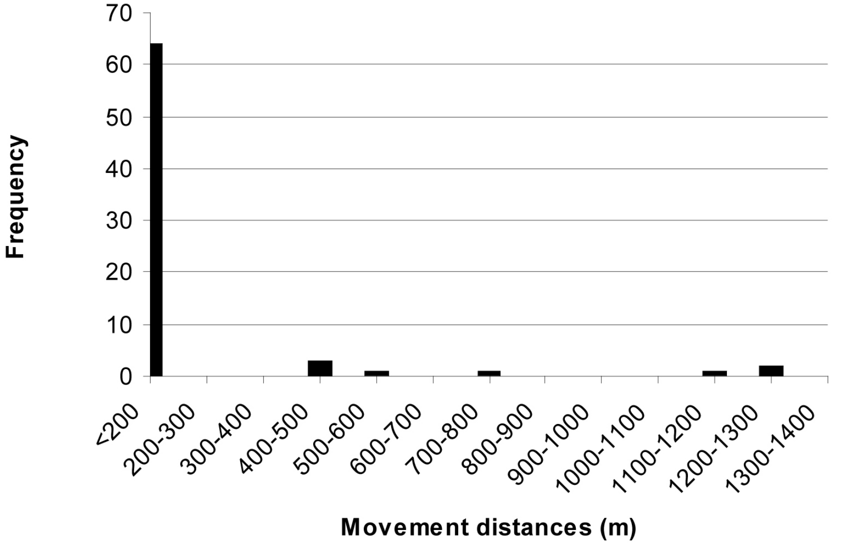

Fig. 2. Movement curve of *S. infraimmaculata* on Mt. Carmel. The frequency distribution of distances between capture and recapture of 72 recapture events.

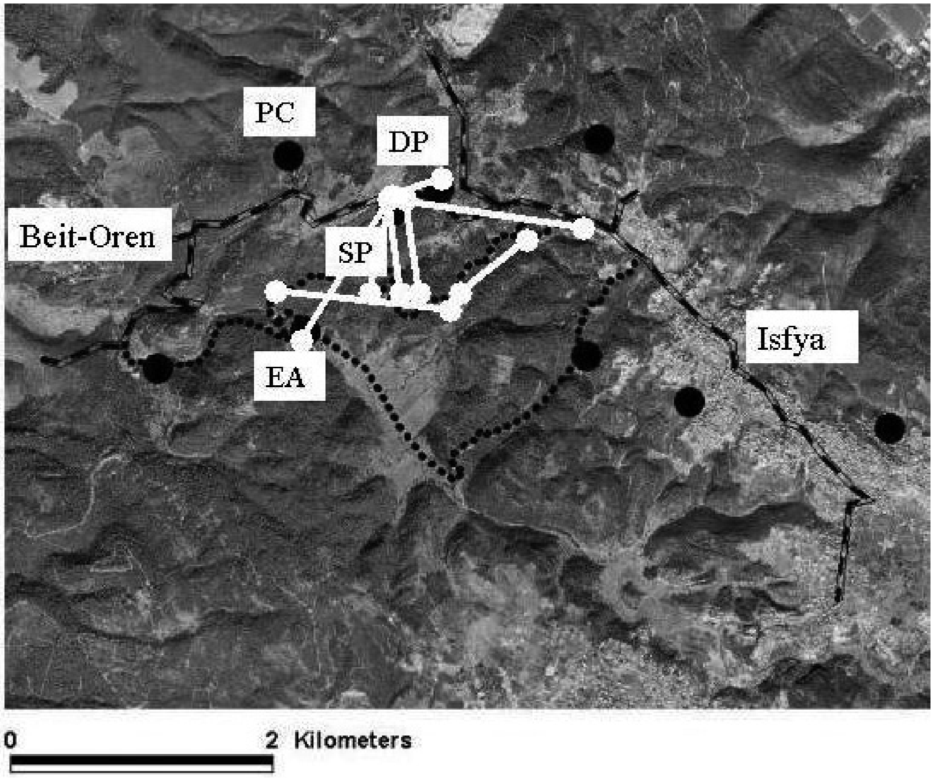

Fig. 3. Capture–recapture locations of long-distance movements. Capture–recapture locations of eight cases in which salamanders were recaptured between 400 and 1280 m (± 50 m) away from the initial capture. Each pair is represented by a straight connector (in white).

typical dispersal curve: at one end of the distribution there is an abundance of relatively short distance movements whereas at the other end there is a scarcity of relatively long-distance movements (Nathan et al., 2003).

The four breeding sites explored in our study (Fig. 1) are separated by no more than 1200 m. These distances are within the movement distances found in our study (Fig. 2). Hence, these sites, and other sites within these movement distances, are likely connected by dispersal (Fig. 4).

2. EXTINCTION RISKS

Based on 18 years of count-based data of adult salamanders at Damun reported in Warburg (1994), the population geometric growth rate, μ, is 0.019 (i.e., the population tends to increase). The variation in this parameter, σ^2, is 0.267. For a range of initial population sizes (between 20–60 individuals) and an "extinction threshold" of 2 individuals, the model predicted that the probability of extinction of this "single, isolated

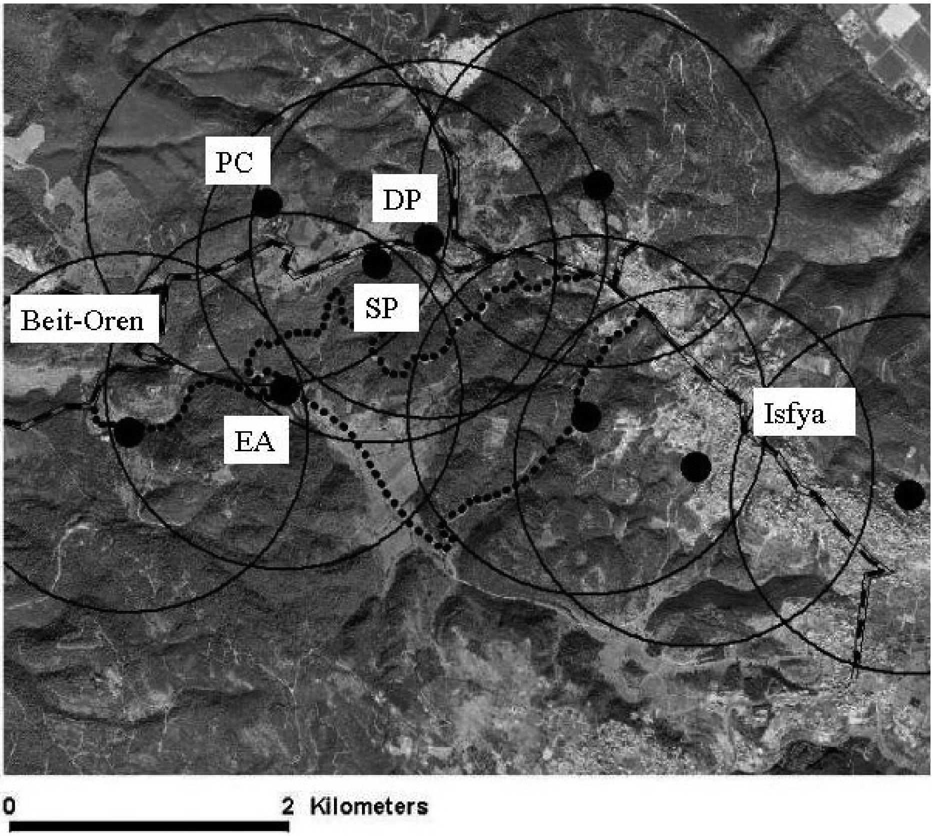

Fig. 4. Estimated ranges of potential connectivity by long-distance movements between breeding sites. Dots represent breeding sites of *S. infraimmaculata* in the studied area. Circles represent the ranges of potential movement distances from breeding sites (their radius = ~max recorded movement distance (1280 m)).

population" is at least 25 percent within 50 years and at least 40 percent within 100 years (Fig. 5a). For the lowest range of the initial population size (e.g., 20 individuals, Fig. 5b), the probability of extinction is at least 50 percent within 100 years.

Confidence interval analyses, following Morris and Doak (2002), yielded a 95% confidence interval for μ of –0.234 to 0.277, and for σ^2 of 0.148 to 0.618. Model projections based on calculation by 500 bootstrap samples from these ranges (Morris and Doak, 2002) generate rather broad confidence intervals for the probability of extinction risk (dotted lines, Fig 5).

DISCUSSION

Habitat fragmentation is considered as a major threat to amphibian populations (Semlitsch, 2003). An immediate effect of fragmentation is the mortality of individuals occur-

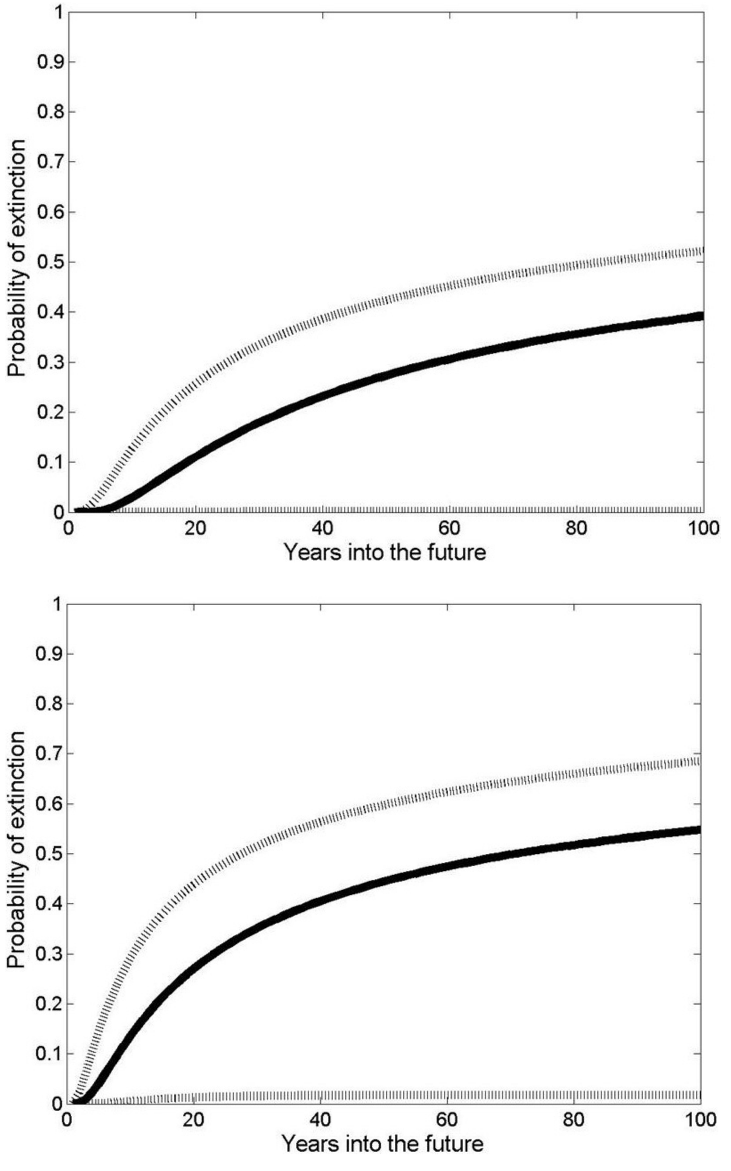

Fig. 5. Extinction time cumulative distribution function for the Damun salamander population. The risk of local extinction, for an initial population of salamanders of 60 individuals (a) and 20 individuals (b) to decline to an extinction threshold of 2 individuals, when $\mu = 0.019$ and $\sigma^2 = 0.267$ (solid lines). The analysis (Morris and Doak, 2002, chapter 3) was based on 18 years of count-based observation data (Warburg, 1994—Appendix 1). Dotted lines outline results for an approximate 95% confidence interval ($-0.234 < \mu < 0.277$ and $0.148 < \sigma^2 < 0.618$) as determined by a bootstrap procedure (calculated by 500 bootstrap samples, Morris and Doak, 2002).

ring in the destroyed or degraded habitats. Secondarily, the loss of landscape connectivity and the introduction of landscape barriers affect animal movement. The implications of these processes for amphibian populations are poorly understood (Dodd and Smith 2003), especially since the movement abilities of amphibian species were rarely directly tested and quantified (Smith and Green, 2005). Recent research suggests that the impact of habitat fragmentation increases with dispersal ability of amphibian species (reviewed by Cushman, 2006). Generally, in species with high dispersal abilities, dispersal among subpopulations is expected to increase population persistence through gene flow and rescue effect. Hence, habitat fragmentation, which induces isolation of subpopulations, is expected to increase extinction rates (Funk et al., 2005).

Movement data on *S. infraimmaculata*, collected in this multi-year capture–recapture study, indicate capability of long-distance movement. The maximum direct distances between capture and recapture sites (1100–1300 m) were found to be greater than movement distances of *S. infraimmaculata* previously documented in the literature (Degani, 1996). Although most of the recaptures were in the close vicinity of the first captures, usually near the breeding sites (indicating high fidelity), the distribution of movement distances (Fig. 2) implies that there is a strong likelihood that some individuals may complete long-distance movements beyond the maximum distance recorded in this work. These long-distance movements may increase connectivity and contribute to population persistence through rescue effect and re-colonization (Semlitsch, 2003; Smith and Green, 2005; Cushman, 2006).

Based on the movement capabilities of *S. infraimmaculata* found in this study, we suggest that its breeding sites in the study area are connected (Fig. 4). Hence, the spatial structure of the *S. infraimmaculata* individuals in the study area likely fits that of a metapopulation (rather than a set of isolated populations). However, further studies should be conducted to estimate the rate of dispersal of both adult and immature salamanders and how it might be affected by habitat type, topography, and connectivity between breeding sites.

Data on long-distance movements are usually scarce; thus accurate estimates of long-distance dispersal are difficult to obtain (Trakhtenbrot et al., 2005). Moreover, they are usually underestimated by capture–recapture studies since they are often artificially truncated by the size of the study area (Marsh and Trenham, 2001; Smith and Green, 2005). However, it should be mentioned that only efficient long-distance movement (i.e., a movement that is followed by establishment and breeding) would lead to a successful colonization and hence contribute to population persistence (Nathan et al., 2003). In the context of amphibian populations, long-distance movements might be particularly important for enabling connectivity to remote breeding sites. Due to high local extinction rates in many amphibian species, the regional population persistence is dependent on local rescue effects through dispersal and re-colonization (Marsh and Trenham, 2001).

Because this capture–recapture study focused on adult salamanders, our estimates of distance and frequency of long-distance movements are probably conservative; juveniles are thought to be the main dispersers in populations of herpetofauna (Marsh et al., 2004; Cushman, 2006; Templeton et al., 2007). Moreover, the study design, which focused primarily on a few specific breeding sites and ignored others, as well as possible routes between them, and the potential detection error, likely also lead to conservative estimations. Thus, movements between breeding sites are likely more frequent than measured in this study. Genetic studies conducted on individuals from these populations support high inter-pond dispersal (Peleg et al., 2007). The analysis indicates low average genetic differentiation between geographically close breeding sites (e.g., $Fst = 0.0165$ between Sekher and Damun sites). This suggests high connectivity between them.

Isolation of a breeding pond of *S. infraimmaculata* through habitat fragmentation might increase the probability of local extinction by limiting the probability of successful inter-pond movement (i.e., movement followed by establishment, spawning, or breeding) and hence the probability of a rescue effect and re-colonization (Cushman 2006). The risk of local extinction of the Damun population, found in our analysis, highlights the severe potential consequences of fragmentation on population persistence: the Damun population, if isolated, might become extinct, with high probability, within a few dozen years. This would have a direct effect on the dynamics of the *S. infraimmaculata* population on Mt. Carmel at the regional level. The rather broad confidence intervals of the model projections limit the accuracy of the extinction risk estimates. In this analysis, however, the general trajectories are emphasized in order to illustrate the types of phenomena that may be observed following population isolation.

To enable salamander movements over the landscape (i.e., movement between breeding sites and movement to terrestrial habitats), the conservation unit should include landscape components beyond the aquatic sites. It is important to maintain terrestrial buffers around breeding sites (Semlitsch, 1998; Porej et al., 2004; Regosin et al., 2005), and connections between them and suitable terrestrial habitats (Rothermel, 2004). Since the type and quality of the landscape occurring between habitat patches affect the number of successful immigrants (Smith and Green, 2005), it is important to maintain landscape connectivity and migratory links between breeding sites (Marsh and Trenham, 2001; Funk et al., 2005; Rubbo and Kiesecker, 2005).

Among the vertebrate animal taxa, amphibians are the group with the highest proportion of species threatened with extinction (Stuart et al., 2004; Beebee and Griffiths, 2005). Recent research suggests that roads can have a substantial negative effect on amphibian persistence by decreasing dispersal and increasing mortality (Dodd and Smith, 2003; Marsh and Beckman, 2004; Marsh et al., 2005; Cushman, 2006). In our study, roadkills of adult salamanders were found along a road near the Damun site (Fig. 1). One of these individuals was first captured at the Sekher site, indicating that it crossed the road while moving between the breeding sites (Fig, 1). To mitigate the negative effect of roads on dispersal and hence on species persistence, construction of underpasses for animals is a potential measure to be taken. However, the efficiency of these underpasses should be further explored for different amphibian species (Lesbarreres et al., 2004).

Given the temporary nature of many *S. infraimmaculata* breeding sites on Mt. Carmel, the patchy structure of the habitat, and the intense development pressure in this region, the regional population might be under threat. In such a highly disturbed landscape, further development in the area (e.g., paving new roads) might create dispersal barriers that would prevent migration and natural colonization from occurring. In this case, translocation of amphibians might be considered as an option for preserving the population (Marsh and Trenham, 2001). However, as has been suggested by Seigel and Dodd (2002), translocation is a complex issue, and amphibian translocations have potentially large costs in comparison to their possible benefits, so translocations could be particularly damaging to critically endangered species.

Another management strategy that may be considered in the context of landscapes undergoing habitat fragmentation is the creation of artificial winter pools. Artificial pools, when created within a suitable distances from occupied pools, may serve as an effective conservation tool by enhancing colonization and dispersal (Johnson and Semlitsch, 2003; Petranka et al., 2003; Semlitsch, 2003). For both management strategies, accurate information about dispersal is critical in estimating the potential connectivity between sites and suitable distances between pools.

Further study of *S. infraimmaculata* on Mt. Carmel is needed in order to gain additional insights on dispersal parameters, to estimate annual migration rates, and to explore the ways these parameters are affected by habitat fragmentation. Moreover, to gain a better understanding of metapopulation viability, the dynamics of each subpopulation around a breeding site should be explored: some might be sink or others source populations. Studies focused on exploring long-distance movement traits should cover large areas (e.g., studies that covered larger areas also tended to report longer maximum movement distances; reviewed by Smith and Green (2005)). In designing studies of amphibian dispersal, this consideration should be taken into account (Funk et al., 2005). Moreover, based on the capture–recapture events in our study, we suggest that research efforts should be focused not only around breeding sites, but also on potential migration routes between them. Also, since *S. infraimmaculata* individuals spend the majority of their lifetime in terrestrial habitats, research should include these habitat components and concentrate on inter-habitat movements (e.g., Rothermel, 2004). More precise details on dispersal traits will illuminate the potential threat of future urban and road development plans on the population's long-term persistence on the regional scale.

In summary, *S. infraimmaculata* was found to have greater movement ability than has been previously reported, and is apparently adapted to dispersal. Hence habitat fragmentation might endanger the population's long-term persistence, on both local and regional scales. It is therefore important to preserve the terrestrial habitats and landscape connectivity between breeding sites, in addition to the conventional protection of aquatic sites, in order to enable individual movements that are invaluable for population dynamics.

ACKNOWLEDGMENTS

We thank G. Emmer and the rangers of the Israel Nature and Park Authority (Mt. Carmel region), in particular A. Levi, for valuable help in fieldwork, and A. Silberbush, G. Degani, M. Warburg, and S. Steinfartz for constructive discussions. We also thank the GIS Department of the Jewish National Fund (Keren Kayemet Le'Israel) for providing aerial photos of the study area and H. Kutiel for providing long-term precipitation data. This research was supported by United States-Israel Binational Science Foundation grant 2002-365 awarded to L. Blaustein, M. Mangel, and A.R. Templeton. We are grateful for constructive comments on an earlier version of this manuscript made by D. Saltz, R. Nathan, B.P. Kotler, and two anonymous reviewers.

REFERENCES

Beebee, T.J.C., Griffiths, R.A. 2005. The amphibian decline crisis: a watershed for conservation biology? Biological Conservation 125: 271–285.

Blaustein, A.R., Wake, D.B., Sousa, W.P. 1994. Amphibian declines—judging stability, persistence, and susceptibility of populations to local and global extinctions. Conservation Biology 8: 60–71.

Brown, J.H., Kodricbrown, A. 1977. Turnover rates in insular biogeography—effect of immigration on extinction. Ecology 58: 445–449.

Colbert, J., Danchin, E., Dhondt, A.A., Nichols, J.D. 2001. Dispersal. Oxford University Press, New York.

Cushman, S.A. 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biological Conservation 128: 231–240.

Degani, G. 1996. *Salamandra salamandra* at the southern limit of its distribution. Laser Pages Publishing, Jerusalem, Israel, 154 pp.

Degani, G., Jackson, K., Dosoretz, K., Plotzki, Y. 1999. Molecular DNA variation in *Salamandra salamandra infraimmaculata* from different habitats. Israel Journal of Zoology 45: 239–246.

Dennis, B., Munholland, P.L., Scott, J.M. 1991. Estimation of growth and extinction parameters for endangered species. Ecological Monographs 61: 115–144.

Dodd, C.K., Smith, L.L. 2003. Habitat destruction and alteration, historical trends and future prospects for amphibians. In: Semlitsch, R.D., ed. Amphibian conservation. Smithsonian Books, Washington and London.

Dolev, A., Perevolotsky, A. 2004. The red book—vertebrates in Israel. Israel Nature and National Parks Authority and The Society for the Protection of Nature in Israel, Jerusalem, Israel.

Funk, W.C., Greene, A.E., Corn, P.S., Allendorf, F.W. 2005. High dispersal in a frog species suggests that it is vulnerable to habitat fragmentation. Biology Letters 1: 13–16.

Hanski, I.A., Gilpin, M.E. 1997. Metapopulation biology: ecology, genetics and evolution. Academic Press, San Diego, California.

Johnson, J.R., Semlitsch, R.D. 2003. Defining core habitat of local populations of the gray treefrog (*Hyla versicolor*) based on choice of oviposition site. Oecologia 137: 205–210.

Lesbarreres, D., Lode, T., Merila, J. 2004. What type of amphibian tunnel could reduce road kills? Oryx 38: 220–223.

Marsh, D.M., Trenham, P.C., 2001. Metapopulation dynamics and amphibian conservation. Conservation Biology 15: 40-49.

Marsh, D.M., Beckman, N.G. 2004. Effects of forest roads on the abundance and activity of terrestrial salamanders. Ecological Applications 14: 1882–1891.

Marsh, D.M., Thakur, K.A., Bulka, K.C., Clarke, L.B. 2004. Dispersal and colonization through open fields by a terrestrial, woodland salamander. Ecology 85: 3396–3405.

Marsh, D.M., Milam, G.S., Gorham, N.R., Beckman, N.G. 2005. Forest roads as partial barriers to terrestrial salamander movement. Conservation Biology 19: 2004–2008.

Morris, W.F., Doak, D.F. 2002. Quantitative conservation biology, theory and practice of population viability analysis. Sinauer Associates, Sunderland, MA.

Nathan, R., Perry, G., Cronin, J.T., Strand, A.E., Cain, M.L. 2003. Methods for estimating long-distance dispersal. Oikos 103: 261–273.

Petranka, J.W., Kennedy, C.A., Murray, S.S. 2003. Response of amphibians to restoration of a southern appalachian wetland: a long-term analysis of community dynamics. Wetlands 23: 1030–1042.

Peleg, N., Segev, O., Hill, N., Fahima, T., Tempelton, A.R., Blaustein, L. 2007. Genetic diversity and conservation of the endangered fire salamander on Mt. Carmel and the Lower Galilee (*Salamanadra salamandra*). Israel Journal of Ecology and Evolution 52: 159–204 (Abstract).

Porej, D., Micacchion, M., Hetherington, T.E. 2004. Core terrestrial habitat for conservation of local populations of salamanders and wood frogs in agricultural landscapes. Biological Conservation 120: 399–409.

Regosin, J.V., Windmiller, B.S., Homan, R.N., Reed, J.M. 2005. Variation in terrestrial habitat use by four poolbreeding amphibian species. Journal of Wildlife Management 69: 1481–1493.

Rothermel, B.B. 2004. Migratory success of juveniles: a potential constraint on connectivity for pond-breeding amphibians. Ecological Applications 14: 1535–1546.

Rubbo, M.J., Kiesecker, J.M. 2005. Amphibian breeding distribution in an urbanized landscape. Conservation Biology 19: 504–511.

Schmidt, B.R., Schaub, M., Steinfartz, S. 2007. Apparent survival of the salamander *Salamandra salamandra* is low because of high migratory. Frontiers in Zoology 4: 19.

Seigel, R.A., Dodd, C.K. 2002. Translocations of amphibians: proven management method or experimental technique? Conservation Biology 16: 552–554.

Semlitsch, R.D. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conservation Biology 12: 1113–1119.

Semlitsch, R.D. 2003. Amphibian conservation. Smithsonian Books, Washington and London.

Smith, M.A., Green, D.M. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography 28: 110–128.

Spencer, M., Schwartz, S.S., Blaustein, L. 2002. Are there fine-scale spatial patterns in community similarity among temporary freshwater pools? Global Ecology and Biogeography 11:71–78.

Steinfartz, S., Veith, M., Tautz, D. 2000. Mitochondrial sequence analysis of *Salamandra* taxa suggests old splits of major lineages and postglacial recolonizations of Central Europe from distinct source populations of *Salamandra salamandra*. Molecular Ecology 9: 397–410.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., Waller, R.W. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306: 1783–1786.

Sztatecsny, M., Schabetsberger, R. 2005. Into thin air: vertical migration, body condition, and quality of terrestrial habitats of alpine common toads, *Bufo bufo*. Canadian Journal of Zoology-Revue Canadienne de Zoologie 83: 788–796.

Templeton, A.R., Robertson, R.J., Brisson, J., Strasburg, J. 2001. Disrupting evolutionary processes: the effect of habitat fragmentation on collared lizards in the Missouri Ozarks. Proceedings of the National Academy of Sciences of the United States of America 98: 5426–5432.

Templeton, A.R., Neuwald, J.L., Brazeal, N.H., Robertson, R.J. 2007. Restoring demographic processes in translocated populations of collared lizards in the Missouri Ozarks through prescribed forest fires. Israel Journal of Ecology and Evolution 53: 179–196, this issue.

Trakhtenbrot, A., Nathan, R., Perry, G., Richardson, D.M. 2005. The importance of long-distance dispersal in biodiversity conservation. Diversity and Distributions 11: 173–181.

Trenham, P.C., Shaffer, H.B. 2005. Amphibian upland habitat use and its consequences for population viability. Ecological Applications 15: 1158–1168.

Trenham, P.C., Koenig, W.D., Shaffer, H.B. 2001. Spatially autocorrelated demography and interpond dispersal in the salamander *Ambystoma californiense*. Ecology 82: 3519–3530.

Warburg, M.R., 1994. Population ecology, breeding activity, longevity, and reproductive strategies of *Salamandra salamandra* during an 18-year long study of an isolated population on Mt. Carmel, Israel. Mertensiella 4: 399–421.