

A multi-scale analysis of breeding site characteristics of the endangered fire salamander (*Salamandra infraimmaculata*) at its extreme southern range limit

Lior Blank · Leon Blaustein

Received: 4 July 2013 / Revised: 29 October 2013 / Accepted: 25 November 2013 / Published online: 7 December 2013
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Abstract Understanding species' distributions often requires taking into consideration the characterization of the environment at different spatial scales. The habitat characteristics of the endangered fire salamander, *S. infraimmaculata*, have received little attention. In this study, at this species' most peripheral and xeric limit (Mt. Carmel, Israel), we examined predictors of the larval distribution of *S. infraimmaculata* at aquatic-breeding sites at both local and landscape scales. We investigated the predictive power of environmental variables using two methods: generalized linear models and conditional inference trees (CTREE). Both multi-model approaches yielded similar results. At the local site scale, hydroperiod predicted breeding site use. At the landscape scale, *Salamandra* presence was best predicted by proximity to other breeding sites. In addition, our study indicates that sites selected for breeding are far from roads and agricultural fields. Overall, this study demonstrates that ultimately, both local and landscape scale predictors are necessary to understand properly a species' habitat requirements and thus can help in planning future management around the breeding sites.

Keywords Conditional inference trees · Generalized linear models · Land-use · Scale

Introduction

Many amphibian species require both terrestrial and aquatic habitats, making them particularly vulnerable to changes in their environment (Wells, 2007). Understanding breeding site use of threatened species provides vital scientific information that is key for setting up conservation plans.

Understanding species' distribution patterns often requires characterizing the environment at multiple spatial scales. Studies conducted at a single spatial scale may overlook species–environment relationships that operate at finer or coarser scales (Allen & Starr, 1982; Blank et al., 2013a). Examining species–environment relationships at different spatial scales is particularly important for amphibians because they have different environmental requirements at different life history stages. The local site scale is important as the place of oviposition or larviposition and larval growth until metamorphosis (Wells, 2007). Various predictors have been shown to be associated with an amphibian's occurrence at this scale, including biotic features (such as macrobenthos and periphyton assemblages) (Blaustein et al., 1996), tree cover (Skelly et al., 2005; Manenti et al., 2009), maximum water depth (Fuller et al., 2011), sulfate concentration (Egea-Serrano et al., 2006), water permanence (Denoël et al.,

Handling editor: Lee B. Kats

L. Blank (✉) · L. Blaustein
Institute of Evolution and Department of Evolutionary and
Environmental Biology, Faculty of Natural Sciences,
University of Haifa, 3498838 Haifa, Israel
e-mail: liorblank@gmail.com

2009), and pH (Denoël et al., 2009). The landscape scale is important as individuals migrate for various reasons. Gravid females may spread their progeny spatially and temporally between breeding sites (Segev et al., 2011), individuals disperse to new regions, move across terrestrial landscapes to forage, and find places for estivation and hibernation (Wells, 2007). However, with some exceptions (e.g., Hamer et al., 2002; Boyero, 2003; Bosch et al., 2004; Denoël et al., 2009), most studies that characterize habitat requirements of breeding sites have focused only on one spatial scale. McGarigal & Cushman (2002) and Stephens et al. (2004) identified that only a small number of studies were performed at the landscape level and the majority of the studies were patch-based. Ultimately, both local and landscape scale studies are necessary to understand properly the suitable habitat requirements of a species (Denoël & Lehmann, 2006).

In this study, we investigated environmental variables that predict the larval distribution of the fire salamander, *S. infraimmaculata*. This species is considered endangered in Israel (Dolev & Perevolotsky, 2004) and near endangered worldwide (Papenfuss, 2008). This conservation status highlights the importance of studying this species' habitat requirements. *Salamandra* populations in Israel occupy the southernmost, and most xeric habitats of this genus worldwide (Degani, 1996; Blank & Blaustein, 2012).

The habitat characteristics of *S. infraimmaculata* have received little attention. At the site scale, Goldberg et al. (2011) found that *S. infraimmaculata* larvae utilize water bodies over a wide range of temperatures, oxygen concentration, conductivity, pH, and ammonium. *S. infraimmaculata* was also shown to be tolerant over a wide nitrate range (Peleg, 2010). These studies only looked at breeding sites (and not unoccupied sites) and thus were not able to model the relative importance of each variable for site occupancy. At a broader scale, Blank & Blaustein (2012) used ecological niche modeling to predict the habitat requirements of *S. infraimmaculata*, and found that soil type was the most important predictor of the distribution, and that *S. infraimmaculata* presence was also associated with areas of high elevation. However, this study (Blank & Blaustein, 2012) only looked at broad-scale predictors. Segev et al. (2010) found that *S. infraimmaculata* population size was larger at permanent breeding sites than at ephemeral sites. However, a thorough study examining different

predictors of *S. infraimmaculata* distributions at both local and broad scale has not been conducted.

The aim of this study was to survey water bodies in the *S. infraimmaculata*'s most peripheral region, Mt. Carmel, Israel, to identify the environmental factors associated with this salamander at two scales: site and landscape. In addition, we examined the effect of land-use on site occupancy.

Methods

Study region

Mount Carmel is a mountain belt in northern Israel, covering an area of 240 km² with an altitude range of 40–546 m above sea level (asl) (Fig. 1a). Mt. Carmel's climate is eastern Mediterranean; it is characterized by relatively cool, wet winters and hot, dry summers (Kutiel, 2012). The area receives approximately 600 mm rainfall annually, mainly between November and March. Most stream systems on Mt. Carmel are ephemeral. The only exceptions are short sections of a few streams that are fed by springs throughout the year. Pools within these intermittent streams, as well as rain-filled rock pools not associated with these streams can serve as breeding sites for amphibians. The vegetation of Mt. Carmel is typical eastern Mediterranean shrubland, composed largely of a complex of oak, pine, and pistacia.

Amphibian sampling

Salamandra infraimmaculata breeding habitats in northern Israel are patchily distributed (Blank & Blaustein, 2012). In Israel, *S. infraimmaculata* females emerge from their summer estivation site beginning with the fall or winter rains, gravid with developed larvae. Larvae remain in pools for at least 2–3 months in the breeding site until metamorphosis (Degani, 1996). We constructed a list of 55 diverse water bodies (pools, ponds, ancient wine presses, and wells) in Mt. Carmel. We learned of the occurrence of these water bodies (without consideration to the presence or absence of fire salamander larvae) based on previous surveys done in the area and interviews with the Nature and Park Authority rangers. The survey took place between November 2009 and April 2010. Although hydroperiod for a given pool should vary among years due to year-to-year variation in rainfall, a

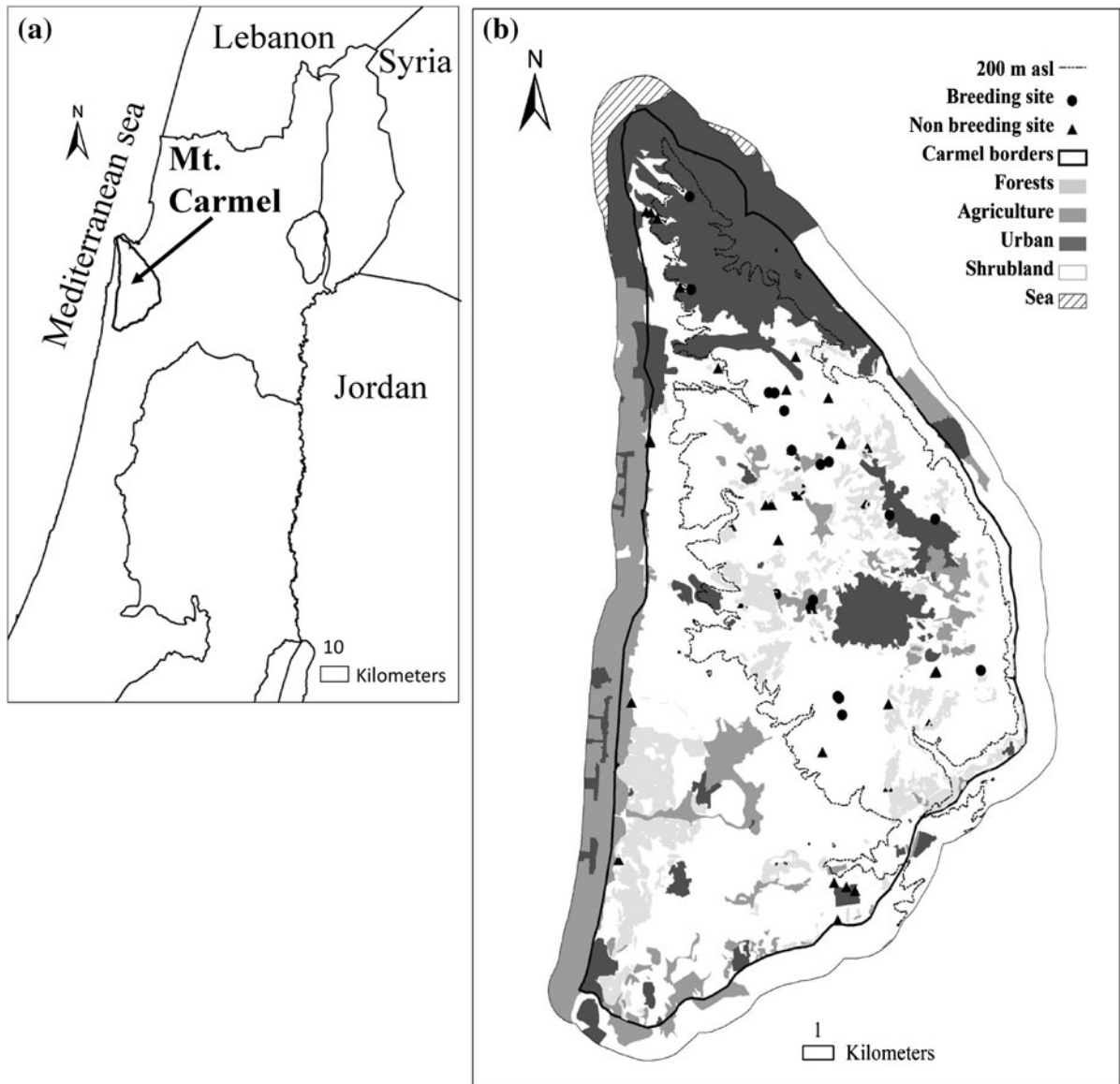


Fig. 1 a Location of the study area, Mt Carmel, in northern Israel. b Location of the sampling sites on Mt. Carmel and land-use categories

comparison of many pools should yield a strong rank correlation across years (Gomez-Garcia et al., 2009). Tavernini (2008) found that no significant differences in hydrochemical features between years, even when each pool showed a wide range of annual variability in water features. At each site, we checked for the occurrence of *S. infraimmaculata* larvae (Fig. 1b). Each site was visited four times spanning most of the season in which larvae of this species occur in temporary habitats. Some sites were visited only three times as they were dried by the third visit. After the

third visit there were no significant rain events that could lead to the accumulation of water in these sites. Moreover, *S. infraimmaculata* females do not larviposit as late as after this third visit (Degani, 1996). All sites were surveyed by both sweeping a dip net (haphazardly, with the number of sweeps per pond increasing with pond size) plus visual inspection by the same observer. The surveyed water bodies are relatively small and usually have clear water. Therefore, visual inspection increases reliable estimations of presence/absence of larvae in the water. Larvae were

Table 1 The 13 environmental variables assessed in the analyses and mean and range (in parentheses) of each variable for all sites sampled and for the subset of sites in which *Salamandra* larvae were present

Variables	Abbreviations	Units	All sites Mean (range)	Breeding sites Mean (range)
Local				
Maximum depth	MaxDepth	cm	55 (5–220)	68 (8–220)
Site area	Area	m ²	66 (0.2–785)	63 (0.62–400)
Percent shading by tree canopy	Shading	%	16 (0–100)	15 (0–100)
Water duration during breeding season	Hydroperiod		3.5 (1–4)	3.9 (3–4)
Landscape				
Mean solar radiation	Radiation	Mj/cm ² /a	2.7 (2.07–3.06)	2.7 (2.3–2.9)
Aspect to north or south	Northness	degrees	76 (0–180)	77 (0–165)
Slope		degrees	9 (0–23)	8 (0–15)
Elevation		meters asl	288 (35–515)	352 (290–490)
Nearest breeding site	NBS	meters	1,969 (27–8,545)	944 (65–4,752)
Land-use				
Distance to nearest road	distRoad	meters	575 (5–2,198)	729 (11–1,940)
Distance to nearest urban area	distUrbn	meters	705 (0–3,028)	767 (0–2,010)
Distance to nearest forest	distForest	meters	797 (0–4,928)	838 (0–4,872)
Distance to nearest agriculture field	distAgri	meters	2,898 (28–5,274)	3,670 (1,250–5,258)

identified at the breeding site and immediately returned after identification.

Environmental predictor variables

The environmental variables considered in our model (listed in Table 1) were based on our a priori rankings of their importance: four variables at the site scale, five variables at the landscape scale, and four land-use variables. Below, we provide descriptions of these variables, how they were measured, and a priori justification in choosing these variables.

Site scale variables

We classified the hydroperiod of each site into one of four rank categories according to latest date that it held water: December = 1, January = 2, March = 3 and holding water after March = 4. Hydroperiod can have a strong influence on larval development and survival (Sadeh et al., 2011). Permanent sites support larger adult populations of *S. inframaculata* (Segev et al., 2010). Longer hydroperiod often leads to greater body size at metamorphosis (Jakob et al., 2002) which may enhance survival and fecundity (Semlitsch et al.,

1988). Thus, we hypothesized that occupancy will be higher in ponds with a longer hydroperiod.

We used the largest area for a breeding site over all sampling periods in our analysis. We measured various pool dimensions in the field and calculated pool surface area using the most appropriate geometric shape. We expected that larger sites will have higher probability to contain *Salamandra* larvae because in general, breeding site size is correlated to effective population size (Wang et al., 2011) and migrating individuals should be more likely to encounter larger sites.

Maximum depth was the deepest point within each site found during all four visits. Deeper sites are more likely to retain water for a longer time and *Salamandra* females have been shown experimentally to deposit more young into deeper pools (Segev et al., 2011). We hypothesized then that deeper sites would be favorable for breeding.

Percent shading from trees, estimated visually from the edge of the ponds, was the proportion of the open water covered by tree canopy. Some amphibians prefer shaded sites while other prefers more sunny sites (Skelly et al., 2005; Van Buskirk, 2005). In our region, which is relatively xeric and hot, we hypothesized that *S. inframaculata* would prefer more shaded sites; minimal larval development time is long

(2–3 months; Sadeh et al., 2011) and pond desiccation is expected to be slower under shade.

Landscape scale variables

We derived most landscape variables from the digital elevation model (DEM) at 33-m resolution using ArcGIS (ESRI, Redlands, CA, USA). These variables were calculated for each site and include: slope, elevation, aspect, and mean solar radiation. Aspect is represented by angular data (0° – 360°). Potential direct incident radiation is symmetrical about the North–South axis. Sites located in East- or West-facing slopes will receive more or less the same amount of daily radiation. 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). To convert it to a linear scale representing the North–South axis, we subtracted all the values greater than 180 from 360. The North–South component of aspect is a variable in the range of 0° – 180° , where North = 0° , South = 180° , and East = West. Thus, we termed this variable “northness”. Mean solar radiation ($\text{Mj}/\text{cm}^2/\text{a}$) was estimated by simulation modeling based on clear sky insolation and exposure of different slopes. Estimates were made using the Solar Analyst extension on ArcView (McCune et al., 2002). In addition, we calculated the Euclidean distance to the nearest breeding site (NBS) using the ArcGIS spatial analyst distance function.

Steepness of a region significantly influences runoff: steep-sloped regions provide relatively little area where water can accumulate and to create potential breeding sites. Thus, we hypothesized that breeding sites would be mainly on moderate slopes and plateaus.

Elevation is an important factor limiting the persistence of many amphibian species (Bradford et al., 2003; Pineda & Halffter, 2004). In Israel, there are no records of *S. inframaculata* below 150 m asl (Blank & Blaustein, 2012; Blank et al., 2013b). Therefore, we hypothesized that breeding sites will be positively associated with elevation and there would be a clear low elevation threshold for the occurrence of the species.

The amount of solar radiation on the surface has been identified as an important factor that shapes the ecological conditions at a site (Geiger, 1965). Together with slope and aspect, radiation affects the

soil moisture, soil and near-surface air temperature and thus habitat preference of invertebrates (Nevo, 1995; Davies et al., 2006). Desiccation is a primary factor that could prevent amphibian larvae from reaching metamorphosis (Ryan, 2007). High temperature causes faster desiccation of water bodies and thus can have prominent impacts on species that use ephemeral habitats (Blaustein et al., 1999). Pools exposed to high solar radiation can also reach temperatures that are fatal for temporary pool organisms (Blaustein et al., 1999). In addition, for some species of amphibians, increasing temperature during larval development may result in reduction in time to metamorphosis and/or a decrease in size at metamorphosis (Voss, 1993; Morand et al., 1997). Shorter larval periods can result in metamorphosis at a smaller size (Sadeh et al., 2011) which can affect fitness and survival (Beck & Congdon, 2000). In addition, ponds that are more exposed to the sun have higher temperatures and, often, higher productivity (Werner & Glennemeier, 1999; Skelly et al., 2002). At moderate temperature ranges, habitats are likely to be favorable for amphibians, since they allow for higher growth rates and better survivorship of eggs and larvae (Skelly et al., 1999; Werner & Glennemeier, 1999). Thus, we did not have a clear single a priori hypothesis as to whether *S. inframaculata* would prefer sites that are exposed to lower radiation and are facing mainly to the North or alternatively, whether they would prefer sites that were exposed to higher radiation and facing to the South.

Salamandra inframaculata females can spread their progeny among different breeding sites (Segev et al., 2011) and there is some movement between breeding sites (Bar-David et al., 2007). However, this movement is mostly restricted to several hundreds of meters with a maximum distance detected of 1,280 m (Bar-David et al., 2007). Thus, we hypothesized negative relationship between occupancy and the distance between breeding sites.

Land-use variables

We calculated the minimal distance from each site to four land-uses: urban areas (cover 16.8% of the study area), agricultural fields (6.5%), forests (10%), and roads (road density in the study area is $0.00095 \text{ m}/\text{m}^2$). The remaining 66.7% of the area is collectively referred to as “shrubland” on digitized maps, is actually covered

by a heterogeneous mosaic of garrigue (low stature shrubs, up to 1 m height), maquis (tall shrubs, between 1 and 2 m height) and scrub forest (medium-sized trees) (Dufour-Dror, 2002). Because the biotic and abiotic features of the different types of vegetation formations could influence salamanders differently, and because the digital differentiation of the various habitats was not available, shrubland was not considered in our models. The first two variables and roads were manually digitized from high-resolution (1 m pixel size) aerial ortho-rectified images acquired in 2008. Forest data were provided by the Forest Authority of Israel. Distances to these land-use features were calculated using the ArcGIS spatial analyst distance function. Most pond-breeding amphibians depend on two types of habitat: breeding site for reproduction and different wetland and/or terrestrial habitat for foraging, hibernating, and/or migrating (Wells, 2007). Thus, proximity of breeding habitat to preferred terrestrial habitat might play a key role in the determination of occupancy of a breeding site. We hypothesized that *S. infraimmaculata* would select sites that would be closer to forests. The positive effect of the proximity of breeding ponds to the forests for some other amphibian species has been shown previously (Denoël & Ficetola, 2008; Silva et al., 2012). Forests positively affect many amphibian populations by insuring that conditions for feeding, moisture, shelter, and hibernation are present for all terrestrial life stages. However, little is known about the terrestrial phase of *S. infraimmaculata* and whether forest is a preferred habitat for adults or juveniles. As mentioned previously, the extent of movement of *S. infraimmaculata* adults is on the magnitude of several hundreds of meters (Bar-David et al., 2007).

Previous studies, which show variation in amphibian responses to urban areas, do not project a clear prediction as to how *S. infraimmaculata* might respond to this variable. For example, Knutson et al. (1999) found that most anurans they surveyed were negatively associated with the presence of urban area because of land-use transformation and wetland contamination. Segev et al. (2010), with a small number of breeding sites in their study, found a positive correlation between urban cover and *S. infraimmaculata* population size but suggested that this is because human settlements were purposely established close to permanent springs.

Agricultural areas are likely unfavorable to amphibians possibly due to nutrient or pesticide

contamination of ponds (Beja & Alcazar, 2003). Therefore, we hypothesized that *S. infraimmaculata* too, would show a positive relationship between occupancy and distance to agriculture land-use.

Roads are a dominant factor affecting amphibians for two main reasons. First, roads pose high mortality risk for individuals trying to cross the roads (Fahrig & Rytwinski, 2009; Garriga et al., 2012, T. Oron, personal communication), and second, avoidance from roads restrict migration and dispersal of adults and juveniles (Ray et al., 2002). In addition, pollution from road runoff was identified as a significant threat to aquatic habitats, and can impact population size and species presence (Dorchin & Shanas, 2010; Harless et al., 2011). In Israel, tens of *S. infraimmaculata* individuals have been observed killed on roads at a single site (T. Oron, personal communication). Thus, we hypothesized a positive relationship between occupancy and distance to roads.

Statistical analyses

All statistical analyses were carried out with R 2.7.2 (R Core Development Team). We tested all the variables for multicollinearity by examining cross-correlations among variables (Graham, 2003, see Table 2). Cross-correlations between the variables belonging to the same scale group were lower than 0.65. The dependent variable was binary, with values of 1 for breeding sites (sites with at least one larva observed in one of the visits) and values of 0 for non-breeding sites (no larvae detected).

The final predictive habitat suitability model was estimated using two methods in order to get more robust prediction. Logistic regression is a widely used method for predicting species habitat requirements. Recently, data-driven methods, such as Classification and Regression Trees (CART), have been used to identify habitat selection by species (Jha & Vandermeer, 2010; Gonzalez-Mirelis & Lindegarth, 2012). Advocates for tree-based methods suggested that they allow the construction of interpretable decision rules that can be applied in management programs and conservation plans. In addition, in tree-based methods, there is no need to use link parameters to describe the relationship between the predictor variables and the model. In addition, assumptions of linearity in linear models or in GLMs are not required for tree-based regression methods.

Table 2 Summary of the generalized linear models (GLM) and conditional inference tree (CTREE) examining predictors of breeding site used by *Salamandra infraimmaculata*

Variables			AICc	AICw	R_N^2
GLM					
Local					
Hydroperiod			67.35	0.384	0.2
Hydroperiod	MaxDepth		69.35	0.141	0.21
Area			69.68	0.138	0.0003
Landscape					
NBS	Radiation		65.91	0.123	0.28
NBS	Radiation	Northness	66.06	0.114	0.32
NBS	Elevation		66.31	0.101	0.27
Land-use					
distRoad	distAgri		64.46	0.360	0.31
distRoad	distAgri	distUrban	65.1	0.262	0.34
distRoad	distAgri	distForest	66.76	0.114	0.31
CTREE					
Local					
Hydroperiod			67.35		0.2
Landscape					
NBS	Radiation	Elevation	66.67		0.3
Land-use					
distRoad	distAgri	distForest	66.96		0.31

For the GLM method only the three models with the lowest AICc are presented. For variables abbreviations see Table 1. The AIC values for the GLM models and the CTREE models were calculated separately and separately for each scale

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

In the first method, we used logistic regression in the framework of GLMs to relate the environmental variables to the binary-dependent variable. Multi-model inference based on the Akaike Information Criterion (AIC) was used to rank the importance of variables (Burnham & Anderson, 2002; Saltz, 2011). We used the package “glmulti” to facilitate multi-model inference based on every possible first-order combination of the predictors in each scale (16 models for the local scale and for the land-use and 32 models for the landscape scale) (Calcagno, 2010). Comparing every possible model is not recommended as a model selection method (Burnham & Anderson, 2002). However, this approach can be a useful for assessing differences among models in case meaningful a priori model selection is not possible due to limited knowledge of species–habitat relationships (Doherty et al., 2012). The coefficients associated with each variable and their relative importance's were assessed using a multi-model average. To get a better understanding of the independent

contributions of each variable, we applied hierarchical partitioning (Nally & Walsh, 2004) using the package “Hier.part” (Nally & Walsh, 2004).

In the second approach, we used inference trees (CTREE) with a P value-based stopping criterion using the package “party” (Hothorn et al., 2006). In brief, in the first step, the algorithm selects the input variable that has the strongest association with the observations using a P value. A binary split is performed on this input variable. Testing and splitting is repeated for all covariates, recursively. A split was established when the P value was <0.05 . This process continues and the remaining predictor variables are recursively tested until no statistical support is found for additional splits. Similar to model selection using GLM, this method also identifies the important predictors, but in contrast to GLM, it also provides critical thresholds for the occurrence of the species, which can be used for management decisions (Moning & Muller, 2008).

Tree-based methods are hierarchical in nature and thus are able to demonstrate variables that are important only under special conditions. The role of each variable depends on the context, that is, the preceding factors located above it. This allows for identifying non-linear relationships and interactions between the variables. Because of this ability, the tree method helps in better portraying the relationships between variables. Tree-based output, the tree diagram, shows the probability of the events and illustrates the structure of the variables and their interactions, which would be difficult to model by logistic regression. Thus, we believe it makes the findings easier to interpret.

We did not use occupancy modeling because one of the assumptions of occupancy models is that sites are closed during the survey period (the “closure assumption”) (Rota et al., 2009). According to this assumption, the occupancy or non-occupancy state of a site cannot change between visits to the site. However, two situations might violate this assumption: non-occupied sites in the beginning of the season might become occupied later on as the females spread their progeny along the season. And second, as metamorphosis can minimally take 2–3 months, an occupied site might become non-occupied as larvae metamorphose and leave the site. Violation of the closure assumption would lead to positive bias in estimates of occupancy. Gu & Swihart (2004) showed that biological data containing false absences lead to biases when estimating the parameters for species distribution models. They recommend incorporating multiple sampling periods into presence–absence sampling protocols. Related work suggests that when larvae of *Salamandra salamandra*, a closely related species to *S. infraimmaculata* (Steinfartz et al., 2000), are present, the single-visit detection probability exceeds 90% (Manenti et al., 2009; Ficetola et al., 2011a). Thus, with three to four surveys, the cumulative detection probability is expected to be very high (Ficetola et al., 2011b).

Model assessment and validation

We assessed the performance of species distribution models according to their calibration and discrimination (Pearce & Ferrier, 2000). Calibration measures show how well the predicted occurrence probabilities agree with the observed frequencies. Discrimination refers to the model’s ability to discriminate between occupied and non-occupied sites. To evaluate model

calibration, we used Program R with multiple packages. We calculated R_N^2 values (Nagelkerke, 1991) using the package “PredictABEL” (Kundu et al., 2011). Model performance was evaluated using the “Area under the curve” (AUC). The AUC can range between 0.5, which indicates a model predictive ability no better than the null model, and 1.0, which indicates perfect discrimination (Swets, 1988). A model providing excellent prediction has an AUC >0.9, a fair model has an AUC between 0.7 and 0.9, while a model with AUC below 0.7 is considered poor (Swets, 1988). Furthermore, we calculated sensitivity (true positive rate) and Cohen’s kappa. A Cohen’s kappa value <0.4 indicate a poor classification performance, 0.4–0.75 is good, and >0.75 is excellent (Landis & Koch, 1977). All model assessments and validation were carried out with the “PresenceAbsence” package (Freeman, 2007).

Results

Habitat suitability models

Of the 55 sites monitored, we found that 20 of them served as breeding sites for *S. infraimmaculata*. Tables 2 and 3 show the results of the GLM analysis calculated independently for site scale, landscape scale and for land-use. On the local scale, the most important variable according to the multi-model average was hydroperiod with a relative importance of 0.955 (Table 3); pools of longer hydroperiod were more likely to contain *Salamandra* larvae. This variable was also selected in the two best GLM models (Table 2). Hydroperiod also had the highest independent contribution in the hierarchical partitioning analysis (Fig. 2). In the CTREE model, longer hydroperiod was also selected as the only important predictor (Fig. 3). According to the CTREE result, a hydroperiod that continued after March increases the probability of the site being used for breeding.

In the landscape scale analysis, NBS and radiation were included in the two best GLM models (Table 2). They also had the highest importance value according to the multi-model average with 0.886 and 0.571, respectively (Table 3). In the hierarchical partitioning, in addition to these variables, elevation also had a substantial independent contribution (Fig. 2). These three predictors were also selected in the CTREE modeling (Fig. 3). According to the CTREE analysis,

Table 3 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 ^a	Importance weight ^b
Local			
Area	−0.0003	0.0000	0.269
MaxDepth	0.00103	0.0000	0.280
Hydroperiod	1.49888	0.59	0.955
Intercept	−6.132	8.55	1
Landscape			
Slope	0.019	0.002	0.308
Northness	−0.003	0.0000	0.388
Elevation	0.002	0.0000	0.432
Radiation	2.073	6.18	0.571
NBS	−0.001	0.0000	0.886
Intercept	−5.946	41.78	1
Land-use			
Shading	−0.0007	0.0000	0.248
distForest	0.0000	0.0001	0.238
distUrbn	−0.0003	0.001	0.388
distRoad	0.001	0.001	0.818
distAgri	0.001	0.0003	0.989
Intercept	−3.596	1.225	1

^a Unconditional variance incorporates model uncertainty and thus provides a better reflection of the model coefficient (Burnham & Anderson, 2002)

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

occupied breeding sites were located within a maximum distance of about 1,200 m from another breeding site, and were characterized by relatively high radiation (>2.7 Mj/cm²/a) and high elevation (>177 m asl).

Regarding land-use, “distance to agricultural field” and “distance to road” were selected in the three best GLM models (Table 2). These two variables were the most important variables according to the multi-model average, with a relative importance of 0.989 and 0.818, respectively (Table 3). Occupied breeding sites were located far from these two entities. According to the hierarchical partitioning, distance from agricultural field was the variable with the strongest influence on *S. infraimmaculata*, followed by distance to road (Fig. 2). These results were congruent with the CTREE analysis: breeding sites far from agricultural fields (>~3,100 m), forests (>125.3 m) and roads (>415 m) were preferred (Fig. 3).

Model evaluation

The models for all three groups of variables explained between 20 and 31% of the overall variance (Table 2). AUC values ranged between 0.674 at the local scale and 0.805 for land-use, which indicate poor and fair models, respectively (Table 4). Cohen’s kappas were classified as good at all three variable groups. Sensitivity remained quite constant and ranged between 0.55 and 0.7.

Next, we compared the validation of the two modeling approaches (Table 4). The model selected by CTREE included more predictors than when using GLM in the landscape scale and for land-use. However, the R_N^2 , AIC, AUC, kappa and sensitivity remain fairly constant between the two methods.

Discussion

The statistical analysis performed in this study looked at each predictor at a specific scale, allowing for the species–environment relationships to be ascertained at different scales, separately. Despite their different statistical approaches, GLM and conditional inference tree approaches were consistent in identifying the best predictors at each scale, indicating that the results are robust. Our results show that the important predictors for site occupancy for breeding by *S. infraimmaculata* were hydroperiod at the site scale, NBS and to some degree, elevation at the landscape scale, and distances from agriculture fields and roads when considering land-use. However, the R_N^2 and AUC values suggest that using additional breeding sites and other variables may identify unexplained variance.

Breeding site scale

Many amphibian species exhibit plasticity in the rate of larval development (Rowe & Dunson, 1995). However, each species requires a minimum hydroperiod to complete metamorphosis. Thus, hydroperiod was found to be one of the most important factors determining habitat suitability for a given amphibian species (Snodgrass et al., 2000; Skidds & Golet, 2005). Similarly, we found hydroperiod to be a strong predictor for *S. infraimmaculata*. In fact, the ability to hold water for a few months during the breeding season was more important than the other habitat

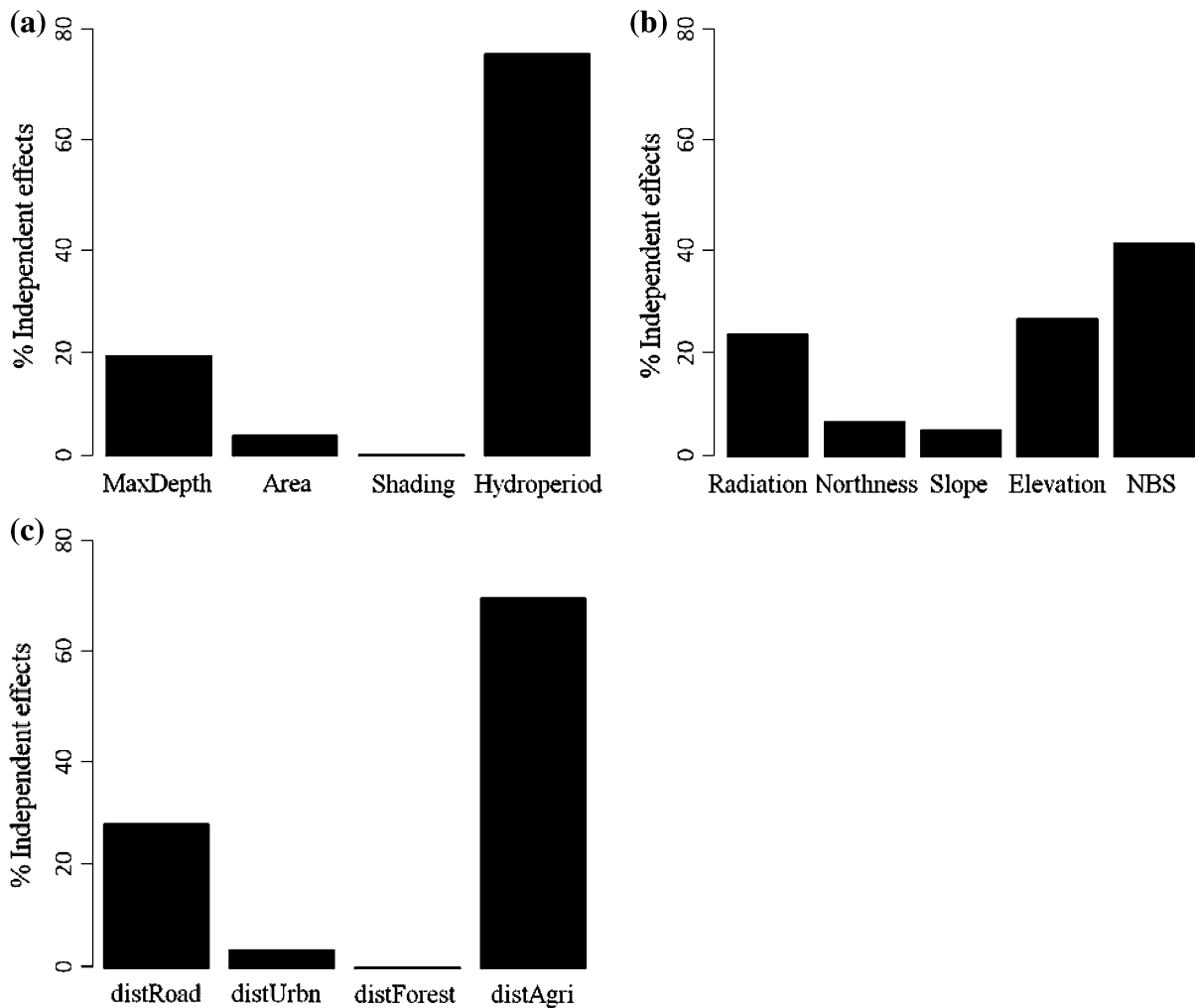


Fig. 2 The independent contribution of each variable to model fit as determined by hierarchical partitioning for **a** local and **b** landscape scales, and **c** land-use. For variables abbreviations, see Table 1

characteristics: depth, shading, and site area. Compared to many organisms with complex life histories that use ponds for the larval stage, larval development periods are relatively long for *Salamandra*, taking more than 2 months (e.g., Eitam et al., 2005; Sadeh et al., 2011). In some studies, water depth was found to be a predictor for the presence of caudates species (Joly et al., 2001); however, some species are known to select shallow water bodies for breeding (Beja & Alcazar, 2003). Apparently, *S. infraimmaculata* is a generalist in terms of size and depth of the breeding site. Segev et al. (2011) found that *S. infraimmaculata* females would larviposit in both very shallow and deeper pools but adjusted the number of larvae

according to volume. Presence of tree canopy, which could allow more allochthonous input, reduce maximum temperatures and evaporation rates, was unimportant in predicting the presence of *Salamandra* larvae. However, *S. infraimmaculata* larvae can persist in sites with relatively high water temperature (Blaustein et al., 1996). In addition, we found that in our study region, about 70% of the sites that were not shaded at all retained water after March.

Landscape scale

Bar-David et al. (2007) found that almost 90% of recaptured *S. infraimmaculata* where in a Euclidian

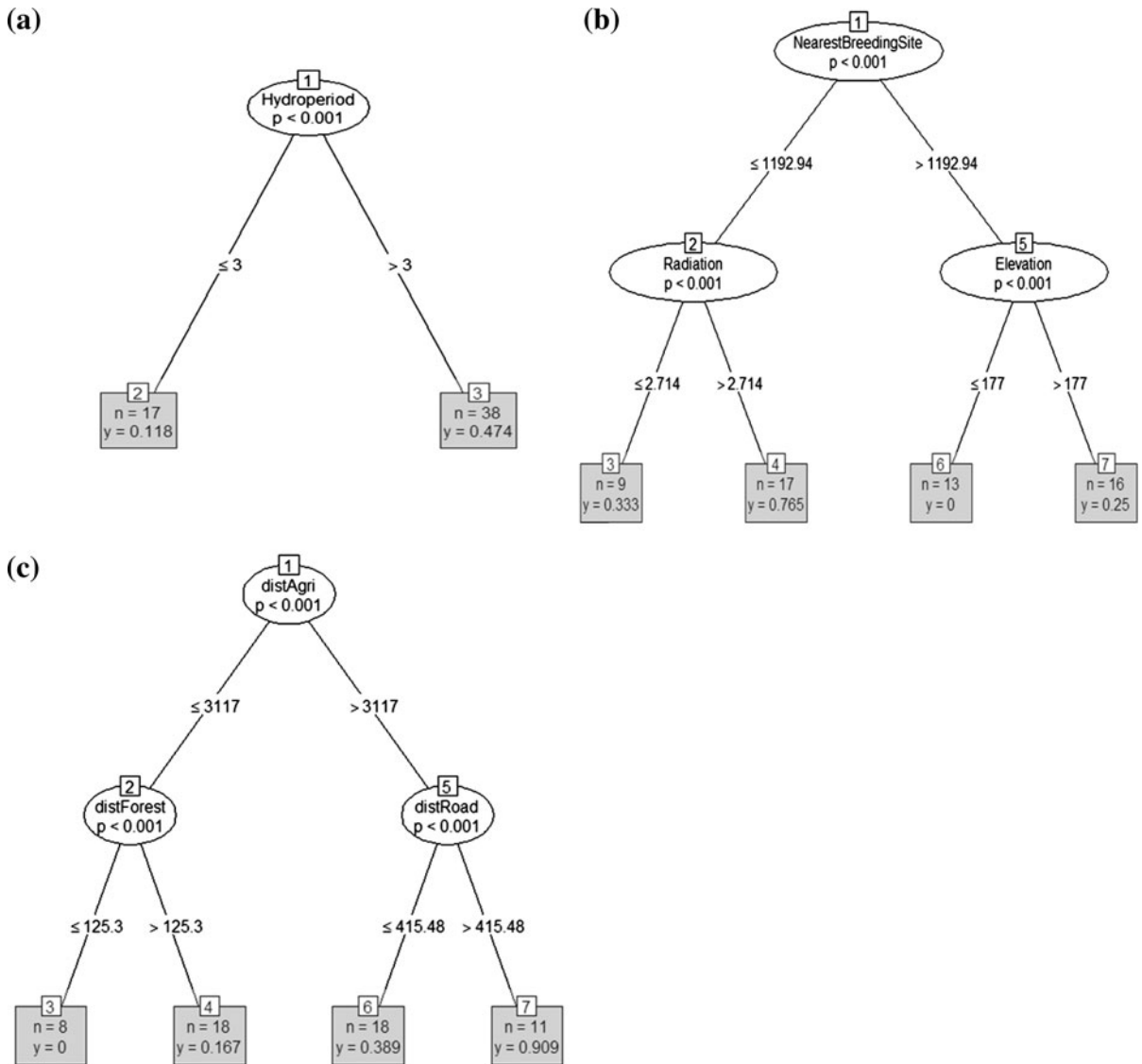


Fig. 3 Conditional inference tree plots, visualizing the distribution of the dependent variables with the significance value in each terminal node. The explanatory variables appearing in these diagrams are those showing the strongest association to the response variable. Values on lines connecting explanatory variables indicate splitting criteria; for example, the first split in diagram c separated sites that were in a distance $\leq 3,117$ m from agriculture field (left split) from sites in a

distance $> 3,117$ m (right split). Numbers in boxes above the explanatory variable indicate the node number. As we descend in the tree the importance of the variable to the process decreases. The upper variable is the most important. The effect of all the variables leading to the terminal node is collective. The P value in the nodes denotes the significance level used for a split to take place. n the number of sites classified in that node, y the predicted presence. For variables abbreviations see Table 1

distance of less than 200 m from where they were captured originally. Segev et al. (2011) found that gravid fire salamanders will spread their larval complement spatially and temporally throughout the breeding season. The result of the limited movement ability and the split clutch strategy is the increased

probability of a water body becoming a breeding site if it is close to other breeding sites, a conclusion supported by our study.

Radiation was found to be an important variable in the GLM, hierarchical partitioning, and the CTREE analyses. Radiation affects a number of conditions

Table 4 Characteristics and accuracy measures of the best GLM model, and conditional inference tree (CTREE) in each scale

Method	GLM			CTREE		
	Local	Landscape	Land-use	Local	Landscape	Land-use
AUC	0.674 ± 0.005	0.79 ± 0.065	0.805 ± 0.064	0.674 ± 0.005	0.79 ± 0.11	0.8 ± 0.06
Kappa	0.55 ± 0.11	0.495 ± 0.12	0.46 ± 0.12	0.55 ± 0.11	0.48 ± 0.12	0.46 ± 0.12
Sensitivity	0.65 ± 0.11	0.7 ± 0.1	0.55 ± 0.11	0.65 ± 0.11	0.65 ± 0.11	0.55 ± 0.11

All values are with ±standard deviation

such as soil moisture, soil temperature and near-surface air temperature (Nevo, 1995; Davies et al., 2006) and rate of desiccation that is a fundamental factor for amphibians using aquatic sites for breeding. In addition, it was shown that in some amphibians, increasing temperature may result in reduction in time to metamorphosis and/or a decrease in size at metamorphosis (Voss, 1993; Morand et al., 1997). Larval survival might be affected as well as fitness via metamorphosis at a smaller size (Sadeh et al., 2011).

Elevation was the second important predictor in the hierarchical partitioning. Congruent with this latter result, Blank & Blaustein (2012) found that *S. infraimmaculata* was positively associated with elevation. All breeding sites in the Mt. Carmel region are not lower than 200 m asl. In addition, all known breeding sites in other regions in Israel are above 150 m (Blank & Blaustein, 2012; Blank et al., 2013b). In addition, in other regions breeding sites are also found at higher elevations than the maximum elevation of Mt. Carmel (Goldberg et al., 2009). So far, there is no clear understanding of the mechanism driving the relationship between *S. infraimmaculata* occurrence and elevation. Lower human impact on higher elevation could potentially be an explanation. However, in our study region it is not likely as most of the region population is concentrated in the city of Haifa (77% of the population) and the Carmel city that resides in the middle of the study area (6.5%). Both of these cities are located on the central ridge of Mt. Carmel covering a large proportion of the highest parts of the region.

Land-use

Because of the movement between land and water habitats, and between breeding sites, amphibians can be highly sensitive to land-use such as agriculture and human-made structures such as roads (Fahrig &

Rytwinski, 2009; Garriga et al., 2012). Our study indicates that roads are landscape elements that negatively affect *S. infraimmaculata* occurrence. A large number of studies have shown that roads and traffic have negative effects on amphibians (for a review see Fahrig & Rytwinski, 2009). This negative effect may include the direct effects of mortality and habitat fragmentation (Fahrig & Rytwinski, 2009; Garriga et al., 2012). Currently, significant threats to populations of *S. infraimmaculata* in Israel are likely posed by anthropogenic activities such as habitat destruction and loss, and road traffic. Tens of dead individuals were collected on road in the past few years (T. Oron, unpublished data).

Our results suggest that agricultural fields, and to some extent also forests, are unsuitable habitat for *S. infraimmaculata* adults. To the best of our knowledge, the relationship between *S. infraimmaculata* breeding sites and agriculture and forest land cover was not studied. Beja & Alcazar (2003) found that the intensification of agricultural land-use was strongly and negatively correlated to amphibian abundance, with marked reductions in the occurrence of almost all studied species. This effect may be due to nutrient contamination, mainly high nitrate and phosphate loadings, and to pesticides. Nutrient contamination was found to be associated with reduction of amphibian populations in other agricultural landscapes (Bishop et al., 1999). In addition, agricultural areas may also negatively impact amphibians by destroying specific habitat features. For example, some burrowing amphibians are capable of digging their own burrows but many others use existing burrows constructed by small mammals. Soil compaction can occur from heavy machinery used in agriculture, and may destroy burrows (Rothermel & Luhring, 2005).

In contrast to our findings, the positive effect of the proximity of breeding ponds to the forests for some other amphibian species has been shown previously

(Denoël & Ficetola, 2008; Silva et al., 2012). Forest might be unfavorable for different reasons ranging from they been potentially more popular for human recreational activity and thus more disturbed environment or they have been a more exposed environment to predators as the subcanopy vegetation is not developed due to the shade from the trees.

An alternative interpretation of the land-use predictors is that they reflect the availability and condition of habitat used by adults. In our study region, most of the cover is garrigue, maquis or park woodland and one or more of these habitats are possibly favored by adults.

Concluding remarks

Both terrestrial and aquatic features are important for a site to be suitable for breeding. Our models indicate that sites holding water during most of the winter and early spring are preferred for breeding. *S. inframaculata* may be capable of assessing and choosing such sites for larviposition based on hydroperiod or the pattern may occur through pond fidelity (Warburg, 1994).

At the broader scale, our study strongly suggests the importance of the distance between breeding sites. This finding may indicate that favorable environmental conditions are clustered along the landscape. It may also indicate the higher probability of colonization of a specific breeding site from nearby breeding sites. Populations of many aquatic-breeding amphibians are small and are vulnerable to local extinction (Carlson & Edenhann, 2000; Trenham et al., 2003). There is evidence that these animals rely on dispersal and colonization for regional persistence (Carlson & Edenhann, 2000; Trenham et al., 2003). Our study also implies that sites selected for breeding would be far from roads and agricultural fields. Overall, this study demonstrates that ultimately both local and landscape scales predictors are necessary to properly understand species-specific suitable habitat requirements.

Acknowledgments This study was funded by the Israel Science Foundation grant 961-2008 awarded to Leon Blaustein, Deutsche-Israel Project DIP 10 awarded to Leon Blaustein, Alan R. Templeton, Sebastian Steinfartz and Arne Nolte, and a scholarship provided by the Israel Council for Higher Education awarded to Lior Blank. We thank Alan R. Templeton, Juha Merilä, Iftah Sinai, Arik Kershenbaum, Asaf Sadeh, and Ori Segev for fruitful discussion and Arik Kershenbaum for comments on the

manuscript. Field surveys of *S. inframaculata* larvae were conducted with permission from the Israel Nature and Parks Authority (permit 2009/36565).

References

- Allen, T. F. H. & T. B. Starr, 1982. Hierarchy: Perspectives for Ecological Complexity. University of Chicago Press, Chicago.
- Bar-David, S., O. Segev, N. Peleg, N. Hill, A. R. Templeton, C. B. Schultz & L. Blaustein, 2007. Long-distance movements by Fire Salamanders (*Salamandra Inframaculata*) and implications for habitat fragmentation. *Israel Journal of Ecology and Evolution* 53: 143–159.
- Beck, C. W. & J. D. Congdon, 2000. Effects of age and size at metamorphosis on performance and metabolic rates of Southern Toad, *Bufo terrestris*, metamorphs. *Functional Ecology* 14: 32–38.
- Beja, P. & R. Alcazar, 2003. Conservation of Mediterranean temporary ponds under agricultural intensification: an evaluation using amphibians. *Biological Conservation* 114: 317–326.
- Bishop, C. A., N. A. Mahony, J. Struger, P. Ng & K. E. Pettit, 1999. Anuran development, density and diversity in relation to agricultural activity in the Holland River watershed, Ontario, Canada (1990–1992). *Environmental Monitoring and Assessment* 57: 21–43.
- Blank, L. & L. Blaustein, 2012. Using ecological niche modeling to predict the distributions of two endangered amphibian species in aquatic breeding site. *Hydrobiologia* 693: 157–167.
- Blank, L., R. Linker & Y. Carmel, 2013a. A multiscale analysis of herbaceous species richness in a Mediterranean ecosystem. *Journal of Plant Ecology* 6: 113–121.
- Blank, L., I. Sinai, I. Bar-David, N. Peleg, O. Segev, A. Sadeh, N. M. Kopelman, A. R. Templeton, J. Merilä & L. Blaustein, 2013b. Genetic population structure of the endangered fire salamander (*Salamandra inframaculata*) at the southernmost extreme of its distribution. *Animal Conservation* 16: 412–421.
- Blaustein, L., J. Friedman & T. Fahima, 1996. Larval Salamandra drive temporary pool community dynamics: evidence from an artificial pool experiment. *Oikos* 76: 392–402.
- Blaustein, L., J. E. Garb, D. Shebitz & E. Nevo, 1999. Microclimate, developmental plasticity and community structure in artificial temporary pools. *Hydrobiologia* 392: 187–196.
- Bosch, J., L. Boyero & I. Martinez-Solano, 2004. Spatial scales for the management of amphibian populations. *Biodiversity and Conservation* 13: 409–420.
- Boyero, L., 2003. Multiscale patterns of spatial variation in stream macroinvertebrate communities. *Ecological Research* 18: 365–379.
- Bradford, D. F., A. C. Neale, M. S. Nash, D. W. Sada & J. R. Jaeger, 2003. Habitat patch occupancy by toads (*Bufo punctatus*) in a naturally fragmented desert landscape. *Ecology* 84: 1012–1023.
- Burnham, K. P. & D. R. Anderson, 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New York.

- Calcagno, V., 2010. glmulti: an R Package for easy automated model selection with (generalized) linear models. *Journal of Statistical Software* 34: 1–29.
- Carlson, A. & P. Edenharn, 2000. Extinction dynamics and the regional persistence of a tree frog metapopulation. *Proceedings of the Royal Society of London Series B: Biological Sciences* 267: 1311–1313.
- Davies, Z. G., R. J. Wilson, S. Coles & C. D. Thomas, 2006. Changing habitat associations of a thermally constrained species, the silver spotted skipper butterfly, in response to climate warming. *Journal of Animal Ecology* 75: 247–256.
- Degani, G., 1996. *Salamandra salamandra* at the Southern Limit of its Distribution. Laser Pages Publication, Kazrin.
- Denoël, M. & G. F. Ficetola, 2008. Conservation of newt guilds in an agricultural landscape of Belgium: the importance of aquatic and terrestrial habitats. *Aquatic Conservation: Marine and Freshwater Ecosystems* 18: 714–728.
- Denoël, M. & A. Lehmann, 2006. Multi-scale effect of landscape processes and habitat quality on newt abundance: implications for conservation. *Biological Conservation* 130: 495–504.
- Denoël, M., G. F. Ficetola, R. Cirovic, D. Radovic, G. Dzukic, M. L. Kalezic & T. D. Vukov, 2009. A multi-scale approach to facultative paedomorphosis of European newts (Salamandridae) in the Montenegrin karst: distribution pattern, environmental variables, and conservation. *Biological Conservation* 142: 509–517.
- Doherty, P. F., G. C. White & K. P. Burnham, 2012. Comparison of model building and selection strategies. *Journal of Ornithology* 152: 317–323.
- Dolev, A. & A. Perevolotsky, 2004. The red book: vertebrates in Israel. Israel Nature and Parks Authority and The Society for the Protection of Nature in Israel, Jerusalem, Israel.
- Dorchin, A. & U. Shanas, 2010. Assessment of pollution in road runoff using a *Bufo viridis* biological assay. *Environmental Pollution* 158: 3626–3633.
- Dufour-Dror, J., 2002. A quantitative classification of Mediterranean mosaic-like landscapes. *Journal of Mediterranean Ecology* 3: 3–12.
- Egea-Serrano, A., F. J. Oliva-Paterna & M. Torralva, 2006. Breeding habitat selection of *Salamandra salamandra* (Linnaeus, 1758) in the most arid zone of its European distribution range: application to conservation management. *Hydrobiologia* 560: 363–371.
- Eitam, A., L. Blaustein & M. Mangel, 2005. Density and inter-cohort priority effects on larval *Salamandra salamandra* in temporary pools. *Oecologia* 146: 36–42.
- Fahrig, L. & T. Rytwinski, 2009. Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and Society* 14: 21.
- Ficetola, G. F., R. De Manenti, F. Bernardi & E. Padoa-Schioppa, 2011a. Can patterns of spatial autocorrelation reveal population processes? An analysis with the fire salamander. *Ecography* 35: 693–703.
- Ficetola, G. F., L. Marziali, B. De Rossaro, F. Bernardi & E. Padoa-Schioppa, 2011b. Landscape–stream interactions and habitat conservation for amphibians. *Ecological Applications* 21: 1272–1282.
- Freeman, E. 2007. PresenceAbsence: An R Package for Presence–Absence Model Evaluation. USDA Forest Service, Rocky Mountain Research Station, 507 25th street, Ogden, UT, USA.
- Fuller, T. E., K. L. Pope, D. T. Ashton & H. H. Welsh Jr, 2011. Linking the distribution of an invasive amphibian (*Rana catesbeiana*) to habitat conditions in a managed river system in Northern California. *Restoration Ecology* 19: 204–213.
- Garriga, N., X. Santos, A. Montori, A. Richter-Boix, M. Franch & G. A. Llorente, 2012. Are protected areas truly protected? The impact of road traffic on vertebrate fauna. *Biodiversity and Conservation* 21: 2761–2774.
- Geiger, R., 1965. *The Climate Near the Ground* Harvard University Press. Massachusetts, Cambridge.
- Goldberg, T., E. Nevo & G. Degani, 2008. Breeding site selection according to suitability for amphibian larval growth under various ecological conditions in the semi-arid zone of northern Israel. *Ecologia Mediterranea* 35: 65–74.
- Goldberg, T., E. Nevo & G. Degani, 2011. Genetic diverseness and different ecological conditions in *Salamandra infraimmaculata* larvae from various breeding sites. *Animal Biology Journal* 2: 37–49.
- Gomez-Garcia, D., J. Azorin & A. J. Aguirre, 2009. Effects of small-scale disturbances and elevation on the morphology, phenology and reproduction of a successful geophyte. *Journal of Plant Ecology* 2: 13–20.
- Gonzalez-Mirelis, G. & M. Lindegarth, 2012. Predicting the distribution of out-of-reach biotopes with decision trees in a Swedish Marine Protected Area. *Ecological Applications* 22: 2248–2264.
- Graham, M. H., 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84: 2809–2815.
- Gu, W. & R. K. Swihart, 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biological Conservation* 116: 195–203.
- Hamer, A. J., S. J. Lane & M. J. Mahony, 2002. Management of freshwater wetlands for the endangered green and golden bell frog (*Litoria aurea*): roles of habitat determinants and space. *Biological Conservation* 106: 413–424.
- Harless, M. L., C. J. Huckins, J. B. Grant & T. G. Pypker, 2011. Effects of six chemical deicers on larval wood frogs (*Rana sylvatica*). *Environmental Toxicology and Chemistry* 30: 1637–1641.
- Hothorn, T., K. Hornik & A. Zeileis, 2006. Unbiased recursive partitioning: a conditional inference framework. *Journal of Computational and Graphical Statistics* 15: 651–674.
- Jakob, C., A. Seitz, A. J. Crivelli & C. Miaud, 2002. Growth cycle of the marbled newt (*Triturus marmoratus*) in the Mediterranean region assessed by skeletochronology. *Amphibia-Reptilia* 23: 407–418.
- Jha, S. & J. Vandermeer, 2010. Impacts of coffee agroforestry management on tropical bee communities. *Biological Conservation* 143: 1423–1431.
- Joly, P., C. Miaud, A. Lehmann & O. Grolet, 2001. Habitat matrix effects on pond occupancy in newts. *Conservation Biology* 15: 239–248.
- Knutson, M. G., J. R. Sauer, D. A. Olsen, M. J. Mossman, L. M. Hemesath & M. J. Lannoo, 1999. Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, USA. *Conservation Biology* 13: 1437–1446.

- Kundu, S., Y. S. van Aulchenko, C. M. Duijn & A. C. J. W. Janssens, 2011. PredictABEL: an R package for the assessment of risk prediction models. *European Journal of Epidemiology* 26: 261–264.
- Kutiel, H., 2012. Weather conditions and forest fire propagation: the case of the Carmel fire, December 2010. *Israel Journal of Ecology & Evolution* 58: 113–122.
- Landis, J. R. & G. G. Koch, 1977. The measurement of observer agreement for categorical data. *Biometrics* 33: 159–174.
- Manenti, R., G. F. Ficetola & F. De Bernardi, 2009. Water, stream morphology and landscape: complex habitat determinants for the fire salamander *Salamandra salamandra*. *Amphibia-Reptilia* 30: 7–15.
- McCune, B., D. Keon & R. Marris, 2002. Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science* 13: 603–606.
- McGarigal, K. & S. A. Cushman, 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications* 12: 335–345.
- Moning, C. & J. Muller, 2008. Environmental key factors and their thresholds for the avifauna of temperate montane forests. *Forest Ecology and Management* 256: 1198–1208.
- Morand, A., P. Joly & O. Grolet, 1997. Phenotypic variation in metamorphosis in five anuran species along a gradient of stream influence. *Comptes Rendus de l'Académie des Sciences-Series III-Sciences de la Vie* 320: 645–652.
- Nagelkerke, N. J. D., 1991. A note on a general definition of the coefficient of determination. *Biometrika* 78: 691–692.
- Nally, R. M. & C. J. Walsh, 2004. Hierarchical partitioning public-domain software. *Biodiversity and Conservation* 13: 659–660.
- Nevo, E. 1995. Asian, African and European biota meet at 'Evolution Canyon' Israel: local tests of global biodiversity and genetic diversity patterns. *Proceedings: Biological Sciences* 262:149–155.
- Papenfuss, T. 2008. *Salamandra infraimmaculata*. In IUCN 2008. Red List of Threatened Species. <http://www.iucnredlist.org/details/59466>.
- Pearce, J. & S. Ferrier, 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling* 133: 225–245.
- Peleg, N. 2010. Studies on the conservation of the fire salamander *Salamandra infraimmaculata* in Israel. PhD thesis. University of Haifa, Haifa, Israel.
- Pineda, E. & G. Halffter, 2004. Species diversity and habitat fragmentation: frogs in a tropical montane landscape in Mexico. *Biological Conservation* 117: 499–508.
- Ray, N., A. Lehmann & P. Joly, 2002. Modeling spatial distribution of amphibian populations: a GIS approach based on habitat matrix permeability. *Biodiversity and Conservation* 11: 2143–2165.
- Rota, C. T., R. J. Fletcher Jr, R. M. Dorazio & M. G. Betts, 2009. Occupancy estimation and the closure assumption. *Journal of Applied Ecology* 46: 1173–1181.
- Rothermel, B. B. & T. M. Luhring, 2005. Burrow availability and desiccation risk of mole salamanders (*Ambystoma talpoideum*) in harvested versus unharvested forest stands. *Journal of Herpetology* 39: 619–626.
- Rowe, C. L. & W. A. Dunson, 1995. Impacts of hydroperiod on growth and survival of larval amphibians in temporary ponds of central Pennsylvania, USA. *Oecologia* 102: 397–403.
- Ryan, T. J., 2007. Hydroperiod and metamorphosis in small-mouthed salamanders (*Ambystoma texanum*). *Northeastern Naturalist* 14: 619–628.
- Sadeh, A., N. Truskanov, M. Mangel & L. Blaustein, 2011. Compensatory development and costs of plasticity: larval responses to desiccated conspecifics. *PLoS One* 6: e15602.
- Saltz, D., 2011. Statistical inference and decision making in conservation biology. *Israel Journal of Ecology and Evolution* 57: 309–317.
- Segev, O., N. Hill, A. R. Templeton & L. Blaustein, 2010. Population size, structure and phenology of an endangered salamander at temporary and permanent breeding sites. *Journal for Nature Conservation* 18: 189–195.
- Segev, O., M. Mangel, N. Wolf, A. Sadeh, A. Kershenbaum & L. Blaustein, 2011. Spatiotemporal reproductive strategies in the fire salamander: a model and empirical test. *Behavioral Ecology* 22: 670–678.
- Semlitsch, R. D., D. E. Scott & J. H. K. Pechmann, 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. *Ecology* 69: 184–192.
- Silva, F. R., T. A. L. Oliveira, J. P. Gibbs & D. C. Rossa-Feres, 2012. An experimental assessment of landscape configuration effects on frog and toad abundance and diversity in tropical agro-savannah landscapes of southeastern Brazil. *Landscape Ecology* 27: 87–96.
- Skelly, D. K., E. E. Werner & S. A. Cortwright, 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. *Ecology* 80: 2326–2337.
- Skelly, D., L. Freidenburg & J. Kiesecker, 2002. Forest canopy and the performance of larval amphibians. *Ecology* 83: 983–992.
- Skelly, D. K., M. A. Halverson, L. K. Freidenburg & M. C. Urban, 2005. Canopy closure and amphibian diversity in forested wetlands. *Wetlands Ecology and Management* 13: 261–268.
- Skidds, D. E. & F. C. Golet, 2005. Estimating hydroperiod suitability for breeding amphibians in southern Rhode Island seasonal forest ponds. *Wetlands Ecology and Management* 13: 349–366.
- Snodgrass, J. W., M. J. Komoroski, A. L. Bryan & J. Burger, 2000. Relationships among isolated wetland size, hydroperiod, and amphibian species richness: implications for wetland regulations. *Conservation Biology* 14: 414–419.
- Steinfartz, S., M. Veith & D. Tautz, 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.
- Stephens, S. E., D. N. Koons, J. J. Rotella & D. W. Willey, 2004. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. *Biological Conservation* 115: 101–110.
- Swets, J. A., 1988. Measuring the accuracy of diagnostic systems. *Science* 240: 1285–1293.
- Tavernini, S., 2008. Seasonal and inter-annual zooplankton dynamics in temporary pools with different hydroperiods. *Limnologica* 38: 63–75.
- Trenham, P. C., W. D. Koenig, M. J. Mossman, S. L. Stark & L. A. Jagger, 2003. Regional dynamics of wetland-breeding frogs and toads: turnover and synchrony. *Ecological Applications* 13: 1522–1532.

- Van Buskirk, J., 2005. Local and landscape influence on amphibian occurrence and abundance. *Ecology* 86: 1936–1947.
- Voss, S. R., 1993. Relationship between stream order and length of larval period in the salamander *Eurycea wilderae*. *Copeia* 1993: 736–742.
- Wang, I. J., J. R. Johnson, B. B. Johnson & H. B. Shaffer, 2011. Effective population size is strongly correlated with breeding pond size in the endangered California tiger salamander, *Ambystoma californiense*. *Conservation Genetics* 12: 911–920.
- 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.
- Wells, K. D., 2007. *The Ecology and Behavior of Amphibians*. University of Chicago Press, Chicago, IL.
- Werner, E. E. & K. S. Glennemeier, 1999. Influence of forest canopy cover on the breeding pond distributions of several amphibian species. *Copeia* 1999: 1–12.