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Microclimatic variation in multiple *Salamandra algira* populations along an altitudinal gradient: phenology and reproductive strategies

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Abstract. *Salamandra algira* is one of the southernmost species of the genus, and most of its ecology remains poorly known. We studied the microhabitat conditions of the sites occupied by several populations of *S. algira* along an altitudinal gradient, and the use of water bodies for reproduction. The microclimate conditions were analysed at six sites in northern Morocco: one site in Beni Snassen massif (*S. algira spelaea*), two in the Middle Atlas and central Rif mountains (*S. algira splendens*), and three in the western Rif mountains and Peninsula Tingitana (*S. algira tingitana*), where a viviparous population also occurs. The microclimate was characterized using temperature and relative humidity data loggers for a period of two years. We also measured the surface area and depth of the water bodies where we found *S. algira* larvae. Our results showed an autumn-winter reproductive period for all ovoviviparous populations studied. In most of the aquatic habitats examined, larvae appeared between November and March, although this period could extend to May at higher altitudes. Larval abundance and their size variability did not correlate with water body size or microclimate conditions. The decrease in the number of larvae per water body coincided with the existence of suitable conditions for post-metamorphic dispersal. *Salamandra algira* occurred in regions with moist conditions (annual average relative humidity greater than 64 %) and with mean annual temperatures of 13.6-18.6 °C, but populations were largely segregated along a gradient of humidity, with some showing higher and more constant values than others. The viviparous population occurs in a region with maritime influence and greater microclimate stability than the other sites studied.

Keywords. Viviparity, fire salamander, microhabitat, North Africa.

INTRODUCTION

Salamandra is a genus that occurs along the Western Palaearctic, appearing especially diversified in the Mediterranean region (Steinfartz et al., 2000). The southern boundaries of the geographic range of *Salamandra* species occur in northern Morocco and northern Israel, where they reach latitudes of 34°N–32°N (Warburg, 1986; Salvador, 1996). At these southern boundaries, *Salamandra* populations are associated with evergreen forests at low-medium altitudes (below 2000 m a.s.l.), occurring in isolated areas, in some cases at low densities (Escoriza and Comas, 2007; Warburg, 2007). The distribution of *Salamandra algira* Bedriaga, 1883 extends from north-western of Morocco to the north–eastern tip of Algeria (Stuart et al., 2008), but is discontinuous, and some populations are separated from one another by major geographical barriers, such as the semiarid Moulouya valley (Escoriza et al., 2006a). Little is known about the phenology and habitat preferences of *S. algira*, except for scattered observations of its activity and presence (Doumergue, 1901; Pasteur and Bons, 1959; Schleich et al., 1996; Martínez-Medina, 2001; Beukema et al., 2013; Escoriza et al., 2013).

Numerous studies have examined the ecological niche of the amphibians on the basis of bioclimatic mod-

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els, although this type of analysis can produce a false estimation of the species' fundamental niche (Araújo et al., 2013). These models at coarse resolution may overestimate the exposure to climate variation that a species experiences, owing to the buffering effect of the microhabitat on temperature (Scheffers et al., 2014). This fact is especially relevant in terrestrial salamanders, whose occurrence is strongly dependent on microclimatic gradients that show rapid variation at fine spatial resolution (Peterman and Semlitsch, 2013). In the case of the genus *Salamandra*, microhabitat conditions have a significant effect on its occurrence, because *Salamandra* species show strong site fidelity and move in relatively small territories, covering distances up to 1300 m (Bonato and Fracasso, 2003; Bar-David et al., 2007; Schulte et al., 2007). The activity of terrestrial salamanders is strongly controlled by two environmental parameters, relative humidity (RH) and air temperature (Spotila, 1972). Salamanders show increased surface activity at relatively low temperatures (although not below 0° C) and high air humidity (Welsh and Lind, 1995; Helfer et al., 2012). This activity is critical for their survival because it is related to foraging, reproductive migration and post-metamorphic dispersal (Baldauf, 1952; Feder and Londos, 1984; Liebgold and Jaeger, 2007).

The surface activity of the salamander species (such as *Salamandra infraimmaculata* and *Lycisalamandra helverseni*) that inhabit southern Mediterranean regions occurs mainly between autumn and early spring (Degani and Warburg, 1978; Polymeni, 1994). It is possible that the reproductive activity of *S. algira* also occurs during late autumn, winter, and early spring, because most observations of adults and larvae reported in the literature have been recorded during this period (Doumergue, 1901; Pasteur and Bons, 1959; Martínez-Medina et al., 1997; Escoriza et al., 2006a). Given that *S. algira* occupies elevations of 100–2010 m a.s.l. in Morocco (Bons and Geniez, 1996), we anticipated that local climatic conditions would cause differences in the onset of reproductive activity and larval occurrence. We analysed the effects of hydroperiod on larval development and abundance, because this factor has a significant impact on the larval stages of other species of salamander (Semlitsch and Wilbur, 1988; Rowe and Dunson, 1995). This analysis of environmental conditions should also provide new data on the conditions in which the viviparous population of *S. algira* inhabits. In other ectothermic vertebrates, this parity mode has evolved independently in several species that appear in cold regions (Pyron and Burbrink, 2014). In the case of the genus *Salamandra,* viviparity is a reproductive strategy that presumably also evolves under harsh environmental conditions, such as extreme temperatures and the absence of surface water (Veith et al., 1998; Velo-Antón et al., 2007). However, there is not necessarily a relationship between these conditions and the development of viviparous reproductive strategies (Dopazo and Korenblum, 2000; García-París et al., 2003). In northern Morocco, the only known viviparous population of *S. algira* occurs in a mountain range near the coast, on a limestone substrate that lacks surface water bodies (Martínez-Medina et al., 1997; Martínez-Medina, 2001).

In this study, we characterized the microclimate at six sites along the distribution of *S. algira* in northern Morocco, analysing the relationships between environmental variables, reproductive mode (viviparous *vs.* ovoviviparous), and larvae presence. First we determine whether a microclimatic gradient exist among these populations of *S. algira*. Then we assessed whether larvae presence and their development correlate with environmental conditions on a small spatial scale.

MATERIALS AND METHODS

The study was conducted in northern Morocco (Fig. 1). Climatic data were obtained in areas inhabited by six isolated populations of *Salamandra algira.* Population 1 (northern tip of Tingitana Peninsula, Fig. 1), represents a population of *S. algira tingitana*, which is viviparous. Populations 2 and 3 (north-western Rif) represent a different lineage from population 1. These two populations (2 and 3) are located at different altitudes (Table 1). Populations 4 (central Rif) and 5 (Middle Atlas) correspond to two lineages of *S. algira splendens,* separated geographically by a river valley. Population 6 represents *S. algira spelaea,* a population genetically closer to the Algerian populations than to the

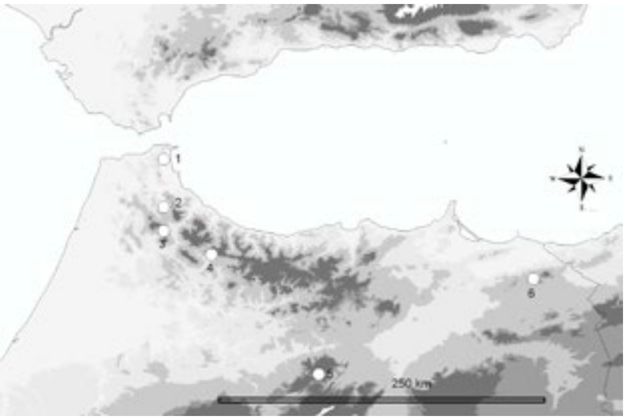

Fig. 1. Study area and sites (white circles). 1) northern tip of Tingitana Peninsula, viviparous population of *S. algira tingitana*, 2) north western Rif, low altitude population of *S. algira tingitana,* 3) north western Rif, high altitude population of *S. algira tingitana* 4) central Rif, *S. algira splendens*, 5) Middle Atlas, *S. algira splendens,* 6) Beni Snassen, *S. algira spelaea.*

Table 1. Geographic and altitudinal location of the studied sites, relative position in the microclimatic gradient and intra-annual microclimate variation. CCA scores: scores obtained in the first axis of the canonical correspondence analysis, based on the variables of annual temperature / relative humidity (RH). PERM: P values obtained by PERMANOVA comparing the values of annual temperature / RH of one site against the rest. AD: average dissimilarities, dispersion of the values of annual temperature / RH per site.

	Lat / Long	Altitude (m a.s.l.)	CCA scores	Permutation P	AD
North Peninsula Tingitana	35.8º N, 5.4º W	328	0.80	0.001	0.72
Western Rif (low)	35.4º N, 5.4º W	113	0.30	0.002	1.03
Western Rif (high)	35.2º N, 5.4º W	1006	-0.18	0.86	1.24
Central Rif	35.0º N, 5.0º W	1488	-0.87	0.001	1.30
Middle Atlas	34.0º N, 4.1º W	1470	-0.32	0.001	1.63
Beni Snassen	34º N, 2º W	860	0.40	0.001	0.95

other populations occurring in Morocco (Escoriza and Comas, 2007). We installed a HOBO® Pro V2 data logger temp / RH at each of these localities, near one or more water bodies where we had previously found larvae, during the two-year period (March 2010 to March 2012). These data loggers were programmed to record temperature and RH with a two-hour periodicity, with an accuracy of about ± 0.21 °C and ± 2.5 %, respectively. The data loggers were placed at ground level, in areas sheltered from the sun, oriented north, and approximately 100 m from the nearest water body. Environmental parameters were measured at the local scale because the presence and density of amphibian species in forest habitats can show significant variations with very fine spatial resolution (Stoddard and Hayes, 2005; Olson et al., 2007). We found no water body containing the larvae of population 1 (viviparous), so in this case the data logger was placed where we observed adults.

Each site was sampled in September, November, January, March, and May, because we expected to find greater reproductive activity in autumn, winter and springtime, based on previous surveys and the literature (see above). The water bodies surveyed were temporary ponds and springs. At two localities (western Rif, high altitude site, and Middle Atlas) we included two water bodies, because they were found nearby but show important variation in their surface area. This makes a total of seven surveyed aquatic habitats, a sufficient number to draw ecological conclusions in descriptive and time-sequenced studies of aquatic communities (Ruhí et al., 2013). We measured the surface area of the water body and its average depth, as a proxy for hydroperiod (Brooks and Hayashi, 2002). The surface area of each water body was estimated on the basis of the maximum length of the longitudinal and transverse axes, assuming an elliptical shape. In water bodies larger than 100 m^2, the surface area was obtained using a Garmin Dakota 100 GPS unit. Average depth was defined as the mean value of five successive measurements from the shore to the centre. The number of larvae was determined from a minimum of 10 dip nets in ponds with a surface area of less than 50 m^2 and from up to 60 dip nets in ponds over 1,000 m^2 in an attempt to include all possible mesohabitats (from shallow water to deep zones). We also measured the length of the larvae, since the variability in their size (standard deviation of larval length), could indicate the existence of sequential episodes of larval depositions, i.e., greater variability in size may be associated with the existence of several larval cohorts in the same pond. The total length of larvae was measured to the nearest 0.1 mm using a digital calliper and larvae were released afterwards.

The positions of the studied sites according to the temperature and RH gradients were examined with a canonical correspondence analysis (CCA) conducted with the vegan package (Oksanen et al., 2012) of the software R (R Development Core Team, 2011). The existence of significant differences between the climatic conditions, when one site was compared with the rest, was established with permutational multivariate analysis of variance (PERMANOVA; Anderson, 2005). We also assessed the variability in the microclimate conditions per site using a permutational analysis of multivariate dispersions (PERMDISP; Anderson, 2004). PERMDISP provides an estimate of the dispersion of the data around a centroid, based on a statistic of average dissimilarities (AD). This statistic can be interpreted as a proxy for microclimate stability per site (i.e., greater AD indicates greater instability in the microclimatic conditions). Because of computational limits, the statistics in these analyses were calculated for a random sample of 400 measures per site. The presence of larvae in the water bodies and the standard deviations of larval size were correlated with environmental variables, specifically with the water body size (surface area of the water body x average depth), the temperature at 12:00 h (local time), and the number of days per month with optimal conditions for activity (optimal days, OD). The size of the water body was studied to determine the possible effects of this variable on larval abundance and development. Air temperature at 12:00 h is related to water temperature and therefore to the rate of variation in larval size (Petranka, 1984). The value of air temperature included in the analysis corresponds to that measured on the 15th day of the month. OD is the number of days per month on which air temperature was within the range of 4.0-14.9 °C and RH was above 80 % for at least two hours. These parameters correspond to the surface activity intervals described for other southern Mediterranean *Salamandra* species (Degani, 1996; García-París et al., 2004; Rebelo, 2008). Therefore, this analysis examined the possible correlation between environmental conditions and larval abundance, which could be result of variations in adult surface activity. This correlation was assessed with the RELATE routine based on Euclidean distance matrices (Clarke et al., 2008), after applying Bonferroni's correction. These analyses were performed with the PRIMER v6.1.11 package (Primer-E Ltd., Plymouth).

RESULTS

The studied populations occurred within a mean annual temperature range of 13.6-18.6 °C, at a mean annual RH exceeding 64 % (Fig. 2). The CCA provided a high eigenvalue for the first axis (eigenvalue = 0.40, explained variance = 88 %), indicating that this axis represents a strong environmental gradient, whereas the second axis described a weaker gradient (eigenvalue = 0.05, explained variance = 12 %). On the first axis, RH contributed more (biplot score = 0.66) than temperature (biplot score = 0.14). The CCA scores for each site on the first axis are shown in Table 1. The site of viviparous *S. algira tingitana* showed the highest CCA score (i.e., highest RH values), whereas the site in the central Rif had the lowest score. The PERMANOVA analysis revealed that most of the studied populations occupied a distinct position on this gradient (Table 1). The sites occupied by these populations showed variable microclimatic stability: the site of the viviparous population had the lowest AD values (i.e., greatest microclimatic stability), whereas both populations of *S. algira splendens* (located at higher altitudes) had the highest AD values (i.e., lowest microclimatic stability; Table 1). Our data reveal the existence of suitable conditions for surface activity between November and April at all sites, although these conditions may extend from October to May at higher altitudes (Fig. 3). This period coincided with the appearance of larvae in all surveyed water bodies during November, although at one site larvae were detected from September (Table 2). The presence of larvae in the water bodies extended until the month of March, and in May, larvae were only observed in one water body. The standard deviation of larval size (i.e., size variability) was greatest in January and the maximum mean larval size was observed in March (Table 2). In all the cases, larval abundance and size variability did not correlate significantly with the size of the water body, OD, or air temperature (Table 3).

DISCUSSION

Our results indicated an autumn-winter reproductive period for all the ovoviviparous populations of *Salamandra algira* examined. At the beginning of this period, there was an increase in the suitable conditions for activity in this species, which possibly correlate with the onset of reproductive activity. Winter breeding activity is usually found in circum-Mediterranean populations of the genus *Salamandra* (Degani and Warburg, 1995; Rebelo and Leclair, 2003), possibly in response to higher autumn-winter precipitation and the occurrence of mild temperatures. The first larval cohort was found in November, and the larvae were small and uniformly sized. The increase in size heterogeneity observed in January may be attributable to the co-occurrence of several larval cohorts (produced by several episodes of larval deposition) within a single pond. In most of the water bodies examined, there was a reduction in the number of larvae and their size variability in March, which indicated the end of new larval recruitment, the metamorphosis of the first cohorts, and the possible exist-

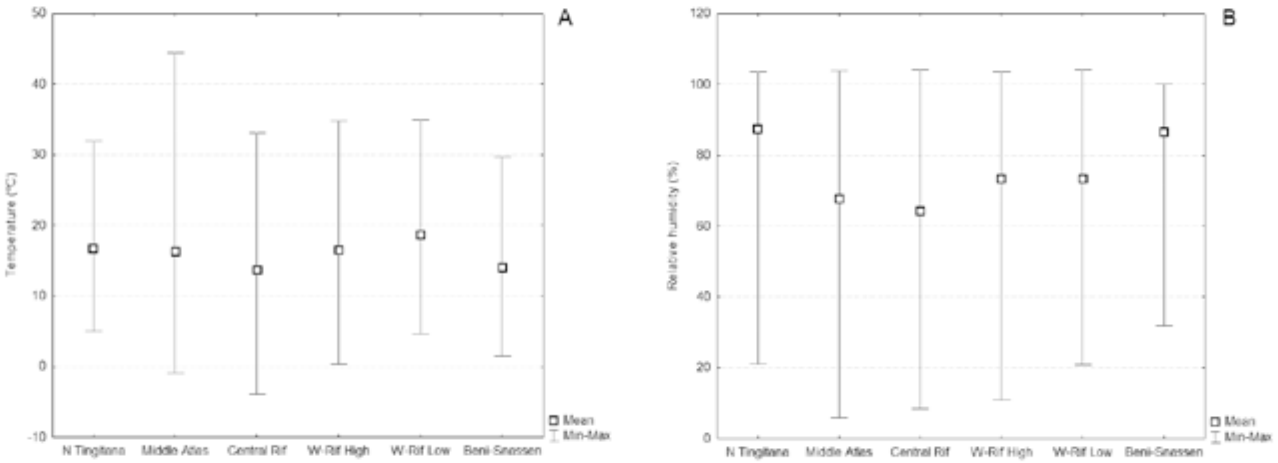

Fig. 2. Plot of mean temperatures (A) and relative humidity (B). Northern tip of Tingitana Peninsula (N Tingitana), Middle Atlas, Central Rif, Western (W) Rif High, Western (W) Rif Low and Beni-Snassen.

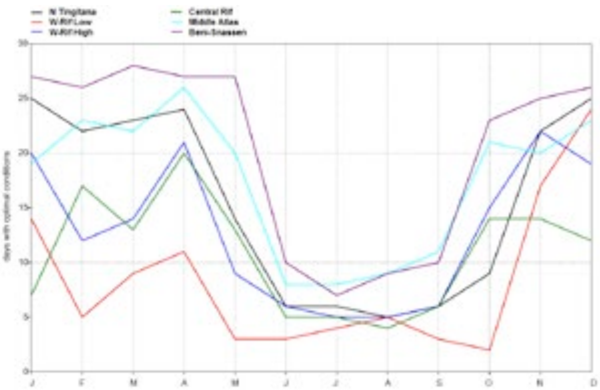

Fig. 3. Days with optimal conditions per site, number of days per month in which environmental conditions are suitable for surface activity (air temperature between 4-14.9 °C and relative humidity > 80 %). Northern tip of Tingitana Peninsula, black (N Tingitana); Middle Atlas, aquamarine; Central Rif, green; Western (W) Rif High, blue; Western (W) Rif Low, red; Beni-Snassen amethyst.

ence of an increasing cannibalistic pressure exerted by the larger larvae (Escoriza et al., 2006b). This decline in larval abundance was not correlated with water body size or microclimatic conditions. As in other salamander species, there is a minimum time period required for metamorphosis, which may be related to water temperature and available trophic resources rather than to the hydroperiod (Maret and Collins, 1994; Díaz-Paniagua et al., 2005; Ryan, 2007). This result also suggested that, in some populations, although there were suitable conditions for adult activity, individuals did not breed in late winter / early spring. However, at one site, large larvae were detected in mid-September, possibly caused by an episode of larval deposition during late spring and the persistence of the larvae in the water body during the summer (Escoriza et al., 2006b). Metamorphosis occurred at larval lengths of 62-69 mm. At all sites, the decline in the number of larvae per water body (probably due to the beginning of larval metamorphosis) coincided with the existence of suitable air temperature / RH conditions for post-metamorphic dispersal (temperatures of 4-14 °C and 80 %-100 % RH). At sites located at higher altitudes, activity may cease for a few days in the month of January, when temperatures drop below 2 °C. At lower altitudes, conditions were possibly suitable for activity throughout the winter.

Table 2. Data measured on five sampling occasions during one year period at seven aquatic habitats that correspond to different populations of *Salamandra algira*. W: Western. At two sites (W Rif high and Middle Atlas) two water bodies were sampled.

		W Rif (low)	W Rif (high)	W Rif (high)	Central Rif	Middle Atlas	Middle Atlas	Beni Snassen
Number of *S. algira* larvae	September	0	0	0	0	0	2	0
	November	4	5	14	9	6	19	7
	January	3	5	13	13	7	19	4
	March	0	1	1	0	5	12	1
	May	0	0	0	0	0	3	0
Average total length of larvae (mm)	September	0	0	0	0	0	56.5	0
	November	43.4	38.8	40.9	40.9	42.3	35.0	34.6
	January	52.3	55.5	47.3	48.9	43.1	40.1	41.9
	March	0	62.9	69.2	0	56.2	51.1	64.9
	May	0	0	0	0	0	53.9	0
Standard deviation of total length of larvae	September	0	0	0	0	0	0.7	0
	November	4.2	3.5	3.6	3.8	3.4	7.4	3.2
	January	5.2	2.9	3.9	8.9	11.5	8.0	5.3
	March	0	0	0	0	5.0	2.8	0
	May	0	0	0	0	0	1.9	0
Surface area × average depth	September	0	0	0	2	0	0.7	0
	November	24	28	9	2	10	0.7	0.1
	January	69	28	4	2	13	1	0.1
	March	60	28	4	2	3	0.7	0.1
	May	32	21	3	2	0.6	0.7	0.1
Air temperature (°C) at 1200 h	September	25.6	28.3	28.3	19.8	27.5	27.5	21.1
	November	15.9	14.4	14.4	7.0	12.9	12.9	9.7
	January	11.0	7.7	7.7	3.5	7.6	7.6	7.4
	March	18.6	18.5	18.5	16.5	17.9	17.9	15.4
	May	26.8	25.8	25.8	17.8	20.8	20.8	18.1

Table 3. P values obtained correlating distance matrices of SD (standard deviation of total length of larvae) and N (number of *S. algira* larvae per water body) with water body size (surface area x average depth), T (air temperature at 12:00 h) and OD (days with optimal conditions per month). W: Western. At two sites (W Rif high and Middle Atlas) two water bodies were sampled.

	W Rif (low)	W Rif (high)	W Rif (high)	Central Rif	Middle Atlas	Middle Atlas	Beni Snassen
SD / water body size	1	1	1	1	0.49	1	1
SD / T	0.63	1	0.42	0.42	0.91	0.07	0.42
SD / OD	1	0.77	1	1	1	1	1
N / water body size	1	1	0.49	1	0.42	1	1
N / T	1	0.49	0.49	0.42	0.28	0.28	0.56
N / OD	0.42	0.35	0.21	1	1	1	1

Our results indicated that the examined populations were largely segregated along a gradient of humidity, with some populations showing higher and more constant values of RH than others. This suggests a variation in the suitability of environmental conditions across sites, which may be related to variations in adult density, as described for other species (Degani and Warburg, 1978). However, in the Beni Snassen massif, where *S. algira* is extremely localized (Escoriza and Comas, 2007), local microclimate conditions were very suitable for this species. This could be an effect of the spatial resolution at which the data were obtained. The discontinuous vegetation cover in the Beni Snassen massif (Tobi et al., 2000) could cause rapid spatial changes in environmental parameters when the buffering effects of vegetation are lost (Rykken et al., 2007). This fact would explain the confinement of this population to a few favourable areas.

The viviparous population occupied a climatic niche distinct from that occupied by the other studied populations of *S. algira*, with more stable microclimatic conditions throughout the year. Similarly, based on macroclimatic niche models, Beukema et al. (2010) also found that these localities showed a lower annual thermal range when compared with those occupied by ovoviviparous populations. This microclimate stability arise from the particular conditions of the Gibraltar Strait region, with its constantly high air humidity (Mejías et al., 2007). This population inhabits a calcareous massif with poor vegetation cover (Martínez-Medina et al., 1997). A dense vegetation cover reduces the oscillation of air temperature and soil moisture (Rittenhouse et al., 2008), and for this reason the occurrence of terrestrial salamanders is usually related to the structure of vegetation (Herbeck and Larsen, 1999). However, as in other coastal populations of salamanders (Diller and Wallace, 1994), the constant air humidity may reduce the salamanders' dependence on the buffering effects of vegetation cover.

Our data offered new insights into the ecology of a little-known salamander species that is distributed in relict populations in northern Morocco. These data suggest a link between the presence of *S. algira* and high moisture levels. Environmental moisture is most stable in mature forests with a closed canopy and dense shrub cover, but may change dramatically with perturbation of the plant cover. In recent decades, there has been a significant loss of forest areas in northwest Africa (Zaimeche and Sutton, 1997) with the spread of agriculture, and this loss has reached 42 % of the surface area in the Rif mountains (Taïqui, 1997). Proper protection of these forests, with consequent preservation of their unique microclimatic environments, will be essential for the survival of most populations of *S. algira*.

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