Breeding coloration, mating opportunities, activity, and survival in the lacertid lizard Psammodromus algirus

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Breeding coloration, mating opportunities, activity, and survival in the lacertid lizard *Psammodromus algirus*

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Díaz, J. A. 1993. Breeding coloration, mating opportunities, activity, and survival in the lacertid lizard *Psammodromus algirus*. Can. J. Zool. **71**: 1104–1110.

I studied the activity, spacing patterns, courtship behavior, and survival of males (classified into two groups according to the development of the sexual coloration of the head) and females from a population of the lacertid lizard *Psammodromus algirus*. Brightly colored (C+) males were significantly larger (and probably older) than dull-colored (C−) males, but aspects of behavior differed between study years. In 1989, C+ males had larger home ranges, were more active, overlapped with more females, and courted females more frequently than C− males. In 1990, none of these traits differed between the two categories of males. The variables associated with survival were different in the two sexes. Larger and more active males survived less well than smaller and less active ones, whereas survival of females was related to the fact that the times when they were observed were later in the day. Higher mortality rates could have been due to a higher predation risk affecting animals that were active on more days or under less favorable conditions. I postulate that the increased activity of males (mainly category C+ in years favoring stronger selection) would increase their short-term reproductive success but negatively affect their survival.

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J'ai étudié l'activité, l'espacement, le comportement de cour et la survie chez les mâles (divisés en deux groupes selon l'importance de la coloration sexuelle de la tête) et les femelles d'une population du lézard lacertidé *Psammodromus algirus*. Les mâles très colorés (C+) étaient significativement plus gros (et probablement plus âgés) que les mâles de coloration terne (C−), mais les résultats reliés aux divers aspects du comportement ont varié au cours des années de l'étude. En 1989, les mâles C+ avaient des domaines plus grands, ils étaient plus actifs, leurs territoires chevauchaient ceux d'un plus grand nombre de femelles et ils courtisaient plus fréquemment les femelles que les mâles C−. En 1990, toutes ces variables étaient semblables chez tous les mâles des deux catégories. Les variables associées à la survie différaient chez les mâles et les femelles. Les mâles plus gros et plus actifs survivaient moins bien que les mâles plus petits et moins actifs, alors que, chez les femelles, la survie était plus grande chez celles qui étaient actives plus tard dans la journée. La mortalité pourrait s'expliquer par les risques de prédation plus élevés chez les animaux qui sont actifs pendant un plus grand nombre de jours ou qui le sont dans des conditions moins favorables. Je crois que l'activité accrue chez les mâles (surtout chez ceux de la catégorie C+ au cours des années où s'opère une forte sélection) peut augmenter à court terme leurs chances de succès reproducteur, mais avoir un effet négatif sur leur survie.

[Traduit par la rédaction]

Introduction

Although many studies concerned with demography (e.g., Tinkle 1967a, 1967b; review by Turner et al. 1970), territoriality, and mating systems (reviews by Samps 1977, 1983) have focused on lizards, the available information is unequally distributed among families. Whereas the social behavior of agamids and iguanids has been described and investigated extensively (Harris 1964; Stamps 1977, 1983; Ruby 1981, 1984; M'Closkey et al. 1987a, 1987b, 1990a), little is known about the activity and spacing patterns associated with reproduction in lacertid lizards. Stamps (1977) hypothesized that active foraging, relatively large home ranges, and poor visibility in the habitats occupied by most lacertid species tend to yield nonterritorial males. However, lack of territoriality does not preclude individual differences in mate access by males and, hence, in reproductive output. Thus, in nonterritorial lizard species a few males could hold exclusive access to females (Carpenter 1977; Anderson and Vitt 1990) and (or) they could enlarge their home ranges in order to overlap with as many females as possible (Barbault 1974; Fitch and Von Achen 1977). If males competed for access to females, some of their behavioral traits could still be subject to sexual selection pressure (Emlen and Oring 1977).

During the breeding season, males of several species show

head coloration that is nonlabile over the short term (in contrast to *Agama*, or the dewlaps of *Anolis*, for example) and whose functional significance remains largely unexplored (Stamps 1977; but see Kitzler 1941). For example, male *Psammodromus algirus* (L.) develop a reddish coloration of the head during the breeding season (Mellado and Martínez 1974) that is highly variable among individuals. This variation suggests that it would be of interest to search for color-related interindividual differences in body size, activity, spacing patterns, and other characteristics potentially correlated with access to females.

Psammodromus algirus is a ground-dwelling, shuttling heliotherm (Carrascal and Díaz 1989; Díaz 1991), commonest in Mediterranean forests of broad-leaved trees with a well-developed shrub undergrowth (Díaz and Carrascal 1991). For most populations, habitat visibility is rather poor and active home-range defense is unlikely to occur (see above). In this study I explored the differences in activity, spacing patterns, and survival between the sexes and between breeding males divided into two categories on the basis of head coloration. Previous field observations supported the impression that the color could confer an advantage in mating behavior or male–male competition. Thus, the goal of this observational study was to establish the context of head color, body size, courtship

TABLE 1. Physical structure of the study plot

Cover	Percentage
Leaf litter	64.9±24.8
Plants at ground level	25.6±26.5
10 cm above ground level	31.2±20.3
20 cm above ground level	38.0±21.1
30 cm above ground level	34.5±19.1
50 cm above ground level	30.4±20.0
Quercus rotundifolia	
Trees	17.8±21.4
Shrubs	54.5±26.5
Cistus shrubs	4.1±11.2
Halimium shrubs	6.9±11.0
Thymus/Lavandula shrubs	5.4±8.5
Herbs	40.6±28.7

NOTE: Percent cover of vegetation (mean ± standard deviation) at different heights and for various plant types was estimated with the aid of a scored stick that was held vertically at 10 random spots (Díaz and Carrascal 1991) within each of the 5 × 5 m grid cells into which the census plot was divided (n = 324 in all cases).

behavior, and mortality in relation to patterns of sexual selection. I will emphasize the annual variation in the results because of its biological implications (variability of selection pressures) and the significant methodological consequences (the need for temporal replication in behavioral studies).

Methods

Study area

Field sampling was carried out in the center of the Iberian Peninsula, in Soto de Viñuelas, Madrid (40°35′N, 03°34′W). The vegetation of the area consists of a typical holm oak (*Quercus rotundifolia*) forest in which holm oaks, interspersed with *Cistus ladanifer* and *Halimium viscosum*, are also the major components of the shrub layer. Leaf litter is the main type of substrate, although areas of bare ground are common on some slopes. The undergrowth of the holm oaks forms well-defined patches, with an average cover of two-thirds of the total surface. The census plot (90 × 90 m) was located between two parallel valleys running in an east–west direction, with most of its surface area on the south-facing slope. A description of the physical attributes of the census plot can be found in Table 1. It is important to note that previous analyses showed no differences in microhabitat structure between the home ranges of lizards belonging to the different categories; if such differences had existed, they could have obscured the results by influencing the detectability or frequency of sighting.

Field sampling

Observations were carried out, weather permitting, two or three times weekly during the breeding seasons of 1989 (20 sampling days between 19 April and 29 June) and 1990 (18 sampling days between 3 May and 27 June). Sampling dates were chosen according to the reproductive cycle of this species. In *P. algirus*, copulations take place between April and June and the testes begin to decrease in volume after mid-June (unpublished data). I continued monitoring the population during the postbreeding season of 1989, with occasional visits to the study plot.

Adult lizards were noosed, sexed, weighed, measured (snout–vent length, SVL) and marked by toe-clipping and painting a color-coded symbol on their back; I repainted all animals that shed their skin and thus lost their painted symbol. On sampling dates, the study area was carefully searched for lizards and each lizard's location was recorded relative to reference stakes placed in a 5 × 5 m grid throughout the census plot. Within the 5 × 5 m cells, observations were assigned, according to the nearest stake, to one of four possible subcells (quad-
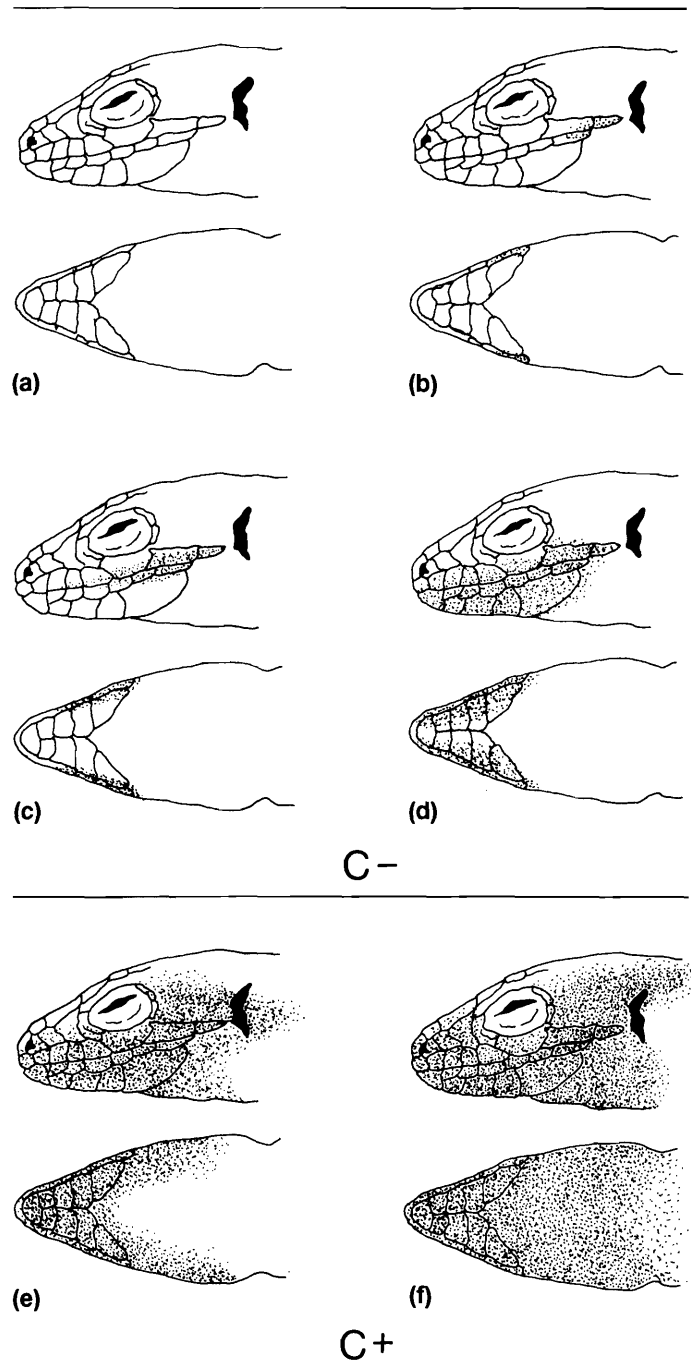

(a) (b)

(c) (d)

C−

(e) (f)

C+

FIG. 1. Classification of adult males as dull-colored (C−) or brightly colored (C+) according to the development of the breeding coloration of the head: absent (a), restricted to the supralabial or infralabial scales (b, c), or covering part of the mental scutes (d) in C− males; affecting the sides of head, entire mental scutes, and throat (e, f) in C+ males.

rants). This provided a final grid size of 1296 possible locations in 0.81 ha. Once all these data had been recorded, the lizards were released at the place of capture.

Males were classified into two groups according to the development of the breeding coloration of the head (Fig. 1): (*i*) brightly colored (hereafter referred to as C+) males with a brilliant red–orange patch on the sides of head, mental scutes, and throat; and (*ii*) dull-colored (C−) males with no color patch or with a less conspicuous red–orange coloration, usually restricted to the supralabial

TABLE 2. Body sizes (snout−vent length, mm) of focal lizards (females, brightly colored (C+) males, and dull-colored (C−) males) in 1989 and 1990

	1989			1990		
	Mean ± SE	Range	n	Mean ± SE	Range	n
C+ males	74.5±1.25	70.2−77.1	5	75.6±1.02	73.4−78.8	5
C− males	70.6±0.74	68.6−76.0	10	71.1±0.86	68.7−73.5	6
Females	71.4±0.85	67.3−75.8	9	73.8±1.37	69.7−78.5	7

or infralabial scales, that could partially involve the mental scutes but without covering the throat (Fig. 1). Because *P. algirus* clearly belongs to the group of single-clutch-laying, large-bodied, late-maturing lizards (Dunham et al. 1988), juveniles (first-year young) and subadults (second-year young) were outside the scope of this study; they were not sufficiently grown to be included as reproductive C− males or females.

Activity and home-range estimates

As an inverse index of the activity of individual lizards during the breeding season, I employed the mean number of days between consecutive observations (MDBO; see Fox 1978) rather than the number of days on which a lizard was seen. This was done to avoid underestimating the activity of animals that were observed frequently but only for a few weeks.

Despite the fact that only three copulations were observed (one in 1989 and two in 1990), I found males involved in what I shall refer to as "courtship observations" (all-day accompaniment that could be pair formation or postcopulatory mate guarding), with a relatively higher frequency of 19 observations of marked males in each study year. These observations allow indirect, correlative estimation of the probability of mate access corresponding to each male lizard, following the approaches adopted by Ruby (1984) and M'Closkey et al. (1990a).

The analyses of activity and spacing patterns were restricted to lizards sighted at least four times during one of the study years. Home-range areas were estimated by means of the minimum convex polygon containing all the positions observed. This simple method, however, has two disadvantages: its assumption of convexity, probably not very important in my rather homogeneous study plot (Table 1; see John Anderson 1982), and its sample-size bias (Jennrich and Turner 1969), with estimated areas increasing as the sample size increases. However, the association between home-range area and activity (and hence number of observations) may be ecologically meaningful; the more active the lizard, the larger its home range may be, and vice versa, so that activity and home range may not be separable (Ruibal 1983). In any case, I repeated all comparisons between population segments, using the residuals of the linear regression relating home-range size to the number of sightings ($r = 0.63, n = 42, P < 0.001$), so that I could assess the effect of activity on estimates of home-range size. Spatial overlap between adjacent home ranges, examined visually on maps of the study area, was considered to be ecologically significant (i.e., a potential source of behavioral interaction) when at least 20% of the smaller area was contained within the larger one. Casual observations of courtship and displacement behavior supported the use of the 20% limit as a useful demarcation.

Survival estimates

In the spring of 1990 I again censused the study plot and classified the 1989 residents either as still present or as absent. Survival estimates were thus based on the repeated sampling of marked animals (Turner 1977); in 1990 my sampling effort was thorough enough that I could be sure that undetected lizards had actually disappeared from the study plot as a result of either mortality or emigration. With respect to the latter possibility, I found that marginal individuals (those for which more than 75% of sightings were in the 20 m wide peripheral strip) did not show higher rates of disappearance. In addition, it is unlikely that the C+ males that were dominant in 1989 and

TABLE 3. Spatial overlaps within and between the sexes, i.e., the number of females overlapped by brightly colored (C+) and dull-colored (C−) males and the number of intrasexual overlaps for both males and females in 1989 and 1990

	1989			1990		
	Mean	SE	n	Mean	SE	n
C+ males × females	2.40	0.51	5	1.20	0.45	5
C− males × females	0.70	0.67	10	1.17	0.17	6
Males × males	1.60	0.32	15	1.45	0.25	11
Females × females	0.22	0.15	9	0.00	0.00	7

disappeared in 1990 (see Results) had simply changed their home ranges from one breeding season to the next.

To maximize sample sizes, I included in the survival analysis the data collected in the postbreeding season (July−September) in 1989. The traits examined for their effect on survival were body size (SVL), intensity of annual activity (number of days on which a lizard was seen in the case of individuals with at least 1 month between the first and last observation dates; this is a better activity index than the MDBO for the sporadic and unevenly distributed censuses carried out in the postbreeding season), and daily distribution of activity (mean time of observation during the day for lizards that were observed at least three times).

Satistical analyses

All statistical analyses were nonparametric (owing to small sample sizes, heterogeneity of variances, and significant deviation from normality) and, unless otherwise specified, the significance level for two-tailed tests was set at $\alpha = 0.05$.

Results

Stability of color development, age, and body size

Focal lizards (those sighted at least four times in the corresponding study year) numbered 24 in 1989 and 18 in 1990, distributed between sexes and between categories of males as shown in Tables 2−5. The breeding color of C+ males reached a peak in April−June and the contrast became less in July−August, but there were no changes in coloration category (see Fig. 1) during the breeding season in either year. Between-years color variation was nevertheless much greater. Two of the 1989 C− males became focal C+ in 1990, and two others changed from pattern *a* (Fig. 1) to pattern *d*. Thus, either the C+ and C− phenotypes were stable over the course of my study or their variation provided at least some evidence that in this species, breeding color is related to age.

In addition, males classified as C+ were larger than males classified as C− in both study years (Mann−Whitney tests on data in Table 2: 1989: $Z = 2.15, P < 0.05$; 1990: $Z = 2.38$, $P < 0.02$), meaning that development of the breeding coloration reached a maximum only in the larger (and presumably

TABLE 4. Estimates of home range size (m²) for females, brightly colored (C+) males, and dull-colored (C−) males in 1989 and 1990

	1989			1990		
	Mean ± SE	Range	n	Mean ± SE	Range	n
C+ males	561±115	328−887	5	335±84	22−328	5
C− males	219±83	16−850	10	128±53	47−678	6
Females	141±40	9−387	9	49±14	6−97	7

NOTE: Minimum convex polygon estimates were based on 6.9 ± 0.9 and 6.4 ± 0.6 (mean ± SE) points in 1989 and 1990, respectively.

TABLE 5. Activity, measured as the mean number of days between consecutive observations (MDBO, an inverse index of activity; see Methods) corresponding to females, brightly colored (C+) males, and dull-colored (C−) males in 1989 and 1990

	1989			1990		
	Mean ± SE	Range	n	Mean ± SE	Range	n
C+ males	0.76±0.24	0.42−1.71	5	1.05±0.15	0.60−1.33	5
C− males	1.73±0.30	0.00−3.00	10	1.56±0.31	0.50+2.67	6
Females	1.68±0.28	0.33−3.00	9	1.48±0.29	0.50−2.50	7

older) males. In fact, only C+ males were significantly larger than females ($Z = 2.00$, $P < 0.05$; for C− males: $Z = 1.51$; $P > 0.10$).

Home-range overlaps and courtship behavior

Males overlapped their home ranges significantly more than did females (Mann−Whitney tests using the data shown in Table 3: 1989: $Z = 2.97$; 1990: $Z = 3.10$; $P < 0.005$ in both cases). Females had nearly exclusive home ranges, whereas nearly all males shared part of their home range with at least one conspecific of their own sex (Table 3). C+ males overlapped with more females than C− males in 1989 (Table 3: $Z = 2.56$, $P = 0.01$) but not in 1990 ($Z = 0$, $P = 1$). This was consistent with field observations of courtship behavior. Considering the combined sample of 2 years, C+ males were seen courting females more frequently than C− males (Fig. 2: Mann−Whitney test: $Z = 2.62$, $P < 0.01$), but the difference was significant only in 1989 ($Z = 1.96$, $P = 0.05$). The fact that C+ males increased their activity significantly exceeding C− males only in 1989 (see below) could explain these divergent patterns of courtship intensity. Among C+ males, the number of courtship observations was negatively correlated with the MDBO index (Spearman correlation: $r_s = −0.705$, $P < 0.05$; $n = 10$) and, hence, positively correlated with activity level. During the 1989 breeding season, C+ males (5 out of 15) did most of the courting (14 of 19 courtship observations; two-tailed Fisher's exact test: $P = 0.036$). Moreover, 53% of the courtship observations (10 out of 19) concerned the two C+ males that were more active, whereas six C− males (40% of all males) were never observed courting females.

Home-range size and activity patterns

Given the clear asymmetry in mating opportunities between the two groups of males, I explored the ecological correlates of the difference observed. Considering the combined sample from 2 years, males had larger home ranges than females (Table 4: $Z = 2.81$, $P = 0.005$), the difference being significant for both categories of males (C+: $Z = 2.32$, $P = 0.02$; C−: $Z = 2.41$, $P < 0.02$). However, there was considerable

interannual variation in the mean estimated home-range sizes (Table 4). Though C+ males had larger home ranges than C− males ($Z = 2.14$, $P < 0.05$) or females ($Z = 2.67$; $P = 0.008$) in 1989, the home ranges of both categories of males did not differ significantly ($Z = 1.55$, $P > 0.1$) in 1990. The home ranges of C+ males were larger in 1989 than in 1990 ($Z = 2.41$, $P < 0.02$). Thus, the larger C+ males apparently expanded their home ranges in 1989 but not in 1990, perhaps because of a decreased density of potential competitors: the population density was 30 adults/ha in 1989 and 22.5 adults/ha in 1990, according to estimates based on home-range maps (see Discussion).

Since the differences in home-range size could be due to the effect of activity (see Methods), I also analyzed the residuals of the linear regression relating home-range size to the number of sightings. Males had larger residuals than females ($Z = 2.02$, $P < 0.05$), mainly because the home ranges of C− males were larger than expected on the basis of their low activity levels (Tables 4 and 5). All other significant differences in home-range size were associated with a larger number of sightings in one of the population segments being compared ($P > 0.1$ in all tests with home-range residuals). For example, the number of sightings per individual in 1989 was larger for C+ males than for C− males. Therefore, I examined the MDBO estimates as an indicator of a behavioral factor (activity) that conditions the spacing patterns of $P.$ $algirus$ during the breeding season. C+ males were more active than C− males (Table 5: $Z = 2.16$, $P = 0.03$) or females ($Z = 2.24$, $P = 0.025$), the difference being most pronounced in 1989 (Table 5) but still out of the range of statistical significance, probably as a result of small sample sizes (C− males: $Z = 1.90$, $P = 0.057$; females: $Z = 1.60$, $P = 0.109$). It seems that the extent to which C+ males were more active than C− males and females also varied between years.

Survival estimates

The proportion of 1989 residents that were seen again in the spring of 1990 was similar for the two sexes (Fisher's exact
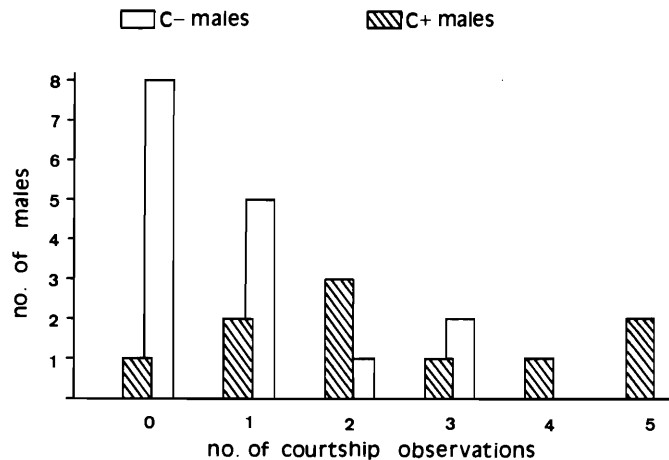
□ C− males   ▨ C+ males

FIG. 2. Distribution of estimated mating opportunities between two categories of adult male lizards (see Methods), i.e., the numbers of males, classified as brightly colored (C+) or dull-colored (C−), that were observed courting females a given number of times. Males with more than two courtship observations usually courted the same female; only four males (three of which were C+) were seen courting two different females.
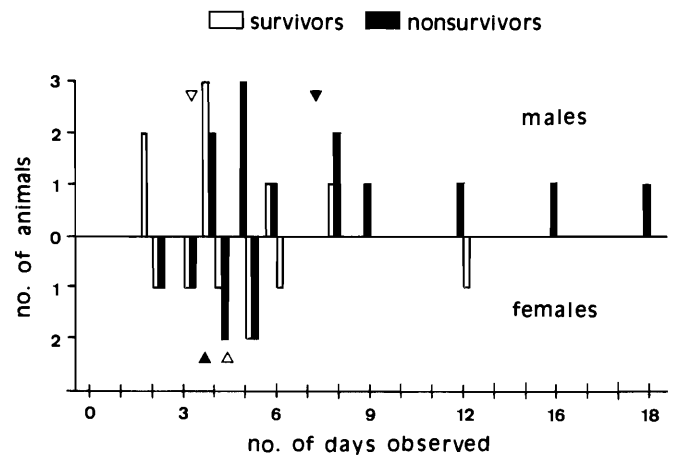
□ survivors   ■ nonsurvivors

FIG. 3. Activity levels (number of days observed) of marked males and females classified as 1989 residents (at least 1 month between first and last sightings) that were seen again in 1990 (open bars) or that had disappeared in 1990 (solid bars). The mean values for the two categories are represented by open and solid arrowheads, respectively.

TABLE 6. Mean observation times during the day in 1989, according to sex and survival categories (1989 residents resighted vs. disappeared in 1990)

	Status in 1990	Time of day	SE (min)	n	Range
Males	Present	10:26	43	5	08:06−12:12
	Absent	10:34	13	16	09:12−12:24
Females	Present	12:40	36	7	11:24−15:54
	Absent	10:54	23	8	09:24−12:18

TABLE 7. Body size (SVL) in 1989 according to sex and survival categories (1989 residents resighted vs. disappeared in 1990)

	Status in 1990	SVL (mm)	n	Range
Males	Present	67.5±1.18	12	59.7−72.8
	Absent	71.5±0.71	22	64.7−76.7
Females	Present	68.7±1.26	8	64.4−74.4
	Absent	69.1±0.74	15	64.1−73.3

test: $P = 1$, two-tailed): 12 out of 34 (35.3%) males vs. 8 out of 23 (34.8%) females. Nevertheless, the variables discriminating survivors and missing animals were different for males and females. On average, males were active earlier in the day than females (Table 6: Mann−Whitney test: $Z = 2.36$, $P < 0.02$). Observations of the females that survived the entire 1989 activity season occurred later in the day than observations of those that emigrated or died (Table 6: $Z = 2.15$, $P = 0.03$), whereas no survival-related difference in mean times of observation was found in the case of males ($Z = 0.04$, $P < 0.95$). Body size (SVL; Table 7) and activity (number of days on which an animal was sighted throughout the 1989 study period; Fig. 3) of males were greater for nonsurvivors − emigrants than for survivors (SVL: $Z = 2.15$, $P < 0.02$; activity: $Z = 2.27$, $P < 0.05$), whereas these variables had no apparent effect on the survival of females (Table 7 and Fig. 4; SVL: $Z = 0.19$, $P > 0.8$; activity: $Z = 0.22$, $P > 0.8$).

Since C+ males were more active than C− males in 1989, one could expect the survival rates to be unequally distributed between the two categories of males. Though significance was marginal, probably because of small sample sizes (one-tailed Fisher's exact test: $P = 0.055$), none of 6 C+ males was found again in 1990 (and only 1 was sighted after mid-July in 1989), whereas 12 of 28 C− males (42.9%) were still present on the study plot in 1990.

With respect to the 1990 focal lizards, all females (seven out of seven) were survivors from 1989. Five of six C− males

(83%) were survivors and two of five C+ males (40%) were (formerly C−) survivors. The remaining males were 1990 immigrants.

Discussion

The results obtained in 1989 suggest that C+ males would increase their probability of siring offspring by exclusively courting one or two overlapping females (personal observation; Stamps 1977), while expanding their home range in order to gain access to as many additional mates as possible (Stamps 1983). These rewards, however, could be counterbalanced by the increased predation risk associated with activity (Rose 1981; Huey 1982). Similarly, Marler and Moore (1988), in experiments with testosterone implants, found that testosterone-treated male Sceloporus jarrovi were more active than controls, and more successful in reproductive competition (Moore and Marler 1987), but experienced greater mortality to an extent that was positively correlated with their activity.

It should be stressed that my data show differences in behavior between brightly and dull-colored males, but without assigning causality to the relationships observed. Thus, the greater conspicuousness of C+ males relative to C− males could function as a signal in the context of male−male competition (in all aggressive interactions observed, C− males were rapidly displaced) or it could provide a stimulus for females' male choice. On the other hand, it is clear that the more brightly colored males were also the larger ones, which implies either that they were older (and hence more experienced and (or) more able to survive) or that they had an advantage in

resource exploitation (Stamps 1988). If C− and C+ males differed simply in age, which was at least partially supported by the data, then the coloration might be a marker by which females could identify the oldest males available in the population for breeding. But if a smaller conspecific was sufficiently imtimidated by large body size only, the intensity and extent of the red−orange patch could have had no direct influence (i.e., as a signal) on the outcome of sexual competition. In this case, the bright coloration of adult males (present though less developed in most C− males; see Fig. 1) could still be useful as a signal in sex recognition (Kitzler 1941; Bauwens et al. 1987; Vitt and Cooper 1985).

A remarkable aspect of the results obtained is the divergence between the 2 study years in nearly all of the traits examined. It should be noted that, according to estimates based on home ranges (mapping method), adult lizards were apparently more numerous on the study plot in 1989 than in 1990, so that in 1989, stronger sexual selection could have been favored. In the breeding season in 1989, when the estimated density was 30 adults/ha and the male:female ratio was 1.67:1, C+ males enlarged their home ranges with respect to those of C− males and females, were more active than C− males, overlapped with more females than their less conspicuous conspecifics did, and courted females more frequently. In the breeding season of 1990, when the sex ratio was similar, 1.57:1, but the density was lower, 22.5 adults/ha, I could not detect any of the previously reported differences. Therefore, in 1989, increased population densities could have produced an increase not only in the number of potential mates (receptive females) but also in the number of competing males. In other words, I suggest that density could have a role in determining activity, range size, and mating opportunities. My indirect estimates of mating opportunities point to a higher reproductive success of C+ males in 1989; Fox's (1978 and 1983) analyses of the survival of juvenile *Uta stansburiana* showed behavioral differences between survivors and nonsurvivors only in the year when selection pressures were greater (Ferguson and Fox 1984). In any case, the between-years variation in activity and home-range size demonstrates the need for long-term studies to assess the temporal constancy of the extant selection pressures shaping the behavior and distribution of lizard populations.

Concerning my survival estimates, the distribution and residence time of adult male lizards have been shown to depend on opportunities to reproduce (Stamps 1983; M'Closkey et al. 1987a, 1987b; Deslippe and M'Closkey 1991), and this makes it unlikely that C+ males had simply abandoned their previous home ranges. On the other hand, adult females are usually more sedentary than males, and in some cases it has been hypothesized that they develop an early site attachment (Stamps 1983; M'Closkey et al. 1987a, 1990b). In fact, all my 1990 focal females had already been marked in 1989. All this evidence supports the conclusion that disappearance of adult animals from the study plot can reasonably be associated with mortality. In addition, the behavioral traits that differed between survivors and missing animals (activity and mean observation time) are consistent with the hypothesis that the population was exposed to heavy predation pressure. Thus, all C+ males, which were more active than C− males in 1989, had disappeared in 1990. In several lacertid species, breeding males have been shown to spend more time moving than females (Bauwens and Thoen 1981; Díaz 1991). Frequent and (or) sudden movements associated with courtship and intraspecific aggression (personal observation; Marler and Moore

1988) would increase the probability of predation by attracting the attention of visually guided predators (Jones and Ferguson 1980; Simon and Bissinger 1983) such as the snake *Malpolon monspessulanus* or birds (*Buteo buteo*, *Lanius excubitor*, and *L. senator*), which are known predators of *P. algirus* (Martín and López 1990) and were frequently observed in the study area. On the other hand, the later daily observation times for surviving females were probably associated with increased heating rates (Díaz 1991) leading to body temperatures that would enhance escape performance (Bennett 1980) and predator detection by means of auditory or chemoreceptive cues (Werner 1972; Van Damme et al. 1990). Later emergence would shorten the time required for basking (Díaz 1991) and shorten the time during which the animal is cool and physiologically impaired. That predator avoidance is important for this lizard population was also suggested by their choice of compass directions that allowed basking lizards to remain within easy reach of the security of shrubs (Díaz 1992).

In summary, the scenario presented seems to reflect a trade-off between two selective forces. Sexual competition would lead males (mainly large C+ ones in years favoring stronger sexual selection) to increase their activity in order to increase their short-term reproductive success (Emlen and Oring 1977). On the other hand, a higher predation risk would counterbalance the benefits of activity by negatively affecting the males' long-term survival. In addition, if, as previously suggested, the color pattern was simply a consequence of age and size, then the C− males would eventually breed as they aged, and their lifetime reproductive success could be equivalent to that of C+ males. Of course, there are several possible explanations for the results obtained (Anderson and Vitt 1990). For example, activity could be high in order to maximize present reproductive effort because of a low probability of surviving to reproduce again. This hypothesis, however, is contradicted by the fact that *P. algirus* belongs to the group of single-clutch-laying, late-maturing, relatively long-lived lizard species (Dunham et al. 1988), so that mortality not due to predation is not expected to differ between the two categories of adult males (Turner 1977).

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