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Correlates of reproductive success in male lizards of the alpine species *Iberolacerta cyreni*

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We followed a field population of the alpine lizard *Iberolacerta cyreni* over 2 consecutive breeding seasons and assigned paternity to the offpring using 8 microsatellite markers. Paternity data, combined with observations of the behavior, morphology, and spacing patterns of lizards, allowed us to document the extent of polygamy, the phenotypic correlates of the number of offspring sired, and the correlation between male reproductive success (RS) and probability of recapture the second year of our study. Multiple paternity was observed in nearly 50% of clutches, and the mating system was highly polygynandrous. In the first year of our study, male RS increased with body size, activity, tail length, and color saturation of the dorsum. In the second year, male RS increased with activity and body condition. Overall, increased male activity, a trait that is expected to decrease survivorship, was the explanatory variable that had the greatest effect on RS. However, the residents of our first study year that were recaptured in the second year had longer tails, were more active, and sired more offspring than their conspecifics that were not recaptured. Thus, contrary to expectations, no negative correlation between present reproduction and future survival was found, which suggests that male investment in reproduction is condition dependent and positively correlated with the ability to pay the underlying costs of increased activity. *Key words:* activity, lizard, microsatellites, polygamy, reproductive costs, reproductive success, survivorship. *[Behav Ecol 19:169–176 (2008)]*

Phenotypic correlates of male mating success have been studied in a large number of terrestrial animals (e.g., Gibson and Bradbury 1985; Weigensberg and Fairbairn 1996; Rasa et al. 1998). Among lizards, mating success is determined by body size, head size, sexual coloration, territory/home range quality, and behavioral traits such as activity, aggressiveness, and alternative mating tactics (Olsson and Madsen 1998). However, estimates of male reproductive performance based on genetic parentage assignment do appear to differ from behavioral estimates of mating success (Olsson et al. 1994; Gullberg et al. 1997; Lebas 2001). New studies that combine the use of molecular markers to assign offspring, with detailed field observations of male behavior and morphology are therefore needed to reassess the relative importance of traits that influence variation in reproductive success (hereafter RS). Genotyping of offspring has revealed that male success increases with body size (Abell 1997; Gullberg et al. 1997; Lewis et al. 2000; Lebas 2001; Hofmann and Henle 2006), but it has produced less clear results concerning the correlation between RS and spacing patterns (e.g., home range size or home range overlap; Abell 1997; Haenel et al. 2003). A remarkable exception is the system studied by Sinervo et al. 2006 who have combined territory data and paternity inference based on microsatellites to document the evolution and mechanisms of alternative male mating strategies (Zamudio and Sinervo 2000), the effects of female preference for experimentally improved territories and/or high-quality sires (Calsbeek and Sinervo 2002), and the complex relationships between spatial proximity, genetic similarity, relatedness, dispersal, and recognition behavior that promote high RS (Sinervo and Clobert 2003; Zamudio and Sinervo 2003; Sinervo et al. 2006). Obviously, overlapping a female's home range does not guarantee successful reproduction, especially in systems with alternative mating strategies and/or female choice. Activity may be more important than home range size per se as a determinant of the behavioral interactions that lead to increased male success, especially in widely foraging lizards that move frequently across their home ranges. Activity is currently regarded as having both costs and benefits, and therefore, activity levels should be optimized by natural selection (Rose 1981). However, there is a paucity of previous studies that have considered the effects of activity on RS through long-term fieldwork and paternity testing of offspring. The genetic assignment of paternity is a better approach to testing for activity effects than the behavioral estimates of mating success, because the variables are unlikely to show a relationship arising from methodological bias, unlike activity and behavioral indicators of RS, which may show partial interdependence (because observations of courting, guarding, or mating behaviors are more likely for the more active males).

Increased activity and movement (but also bright coloration, decreased wariness, reduced escape abilities, or decreased inmunocompetence) may decrease the probability of survival (Marler and Moore 1989; Salvador et al. 1996), that is, they can represent a clear example of reproductive cost (review by Schwarzkopf 1994). In fact, selective constraints on life-history adaptation arise from allocation trade-offs between number versus size of offspring (Sinervo 1990; Sinervo et al. 1992) and current versus future RS (Williams 1966); an increase in current reproduction can decrease the probability of survival and future RS due to ecologically and physiologically mediated costs of reproduction (Sinervo and DeNardo 1996). The general impression that male lizards suffer high survival costs of reproduction (Schwarzkopf 1994; but see Abell 2000) is in contrast with previous reports of positive

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correlations between reproduction and survival in other taxonomic groups (Jennions et al. 2001). In fact, the assessment of reproductive costs requires minor variation among individuals in the amount of resources available; when some individuals perform better and/or have more resources than others, positive correlations between reproduction and survival can be found (van Noordwijk and de Jong 1986). This reinforces the importance of conducting studies that examine the relationship between male RS and survivorship in wild lizard populations. Such studies could also shed light on the ecological factors that shape the sign and intensity of the correlation, if any, between activity, current male reproduction, and probability of recapture the next breeding season. Alpine lizards, for instance, face very different selective pressures than lowland, tropical, or desert species because they experience reduced opportunities for thermoregulation and activity but can reach high population densities as a result of seasonal peaks in productivity and/or a scarcity of competitors or predators. It is therefore difficult to predict whether the costs of reproduction for males should increase or decrease in such environments.

In this study, we followed a field population of *Iberolacerta cyreni* over 2 consecutive breeding seasons and assigned paternity to the offpring using microsatellite markers. *Iberolacerta cyreni* is a lacertid lizard that occupies rocky areas at high elevations (>1700 m) in the mountains of central Spain. Previous studies have suggested a trade-off between current reproduction and survivorship, mediated by a decrease in escape speed suffered by dominant males (López and Martín 2002). Thus, we combined our paternity data with observations of male behavior and morphology to accomplish the following objectives: 1) to document the extent of polygyny and polyandry, 2) to examine the phenotypic correlates of male RS, 3) to analyze the association between male–female spatial proximity and RS, and 4) to study the correlation of male RS and associated traits with survivorship in order to document the survival cost of reproduction. We predict that the number of offspring sired will be positively correlated with traits that are indicative of high male quality, such as body size, tail length, or activity levels. Because these traits may be costly, RS may be traded off against survivorship to the next breeding season. Alternatively, if higher quality (and presumably older) males have more resources to invest in both maintenance and reproduction, then a positive correlation between survival and RS will arise.

MATERIALS AND METHODS

Study species

Iberolacerta cyreni is a small (65–78 mm adult snout-vent length [SVL]) ground-dwelling lizard, abundant (220–328 lizards/ha) in montane areas of central Spain (1700–2350 m.a.s.l.) at sites with rocks, shrubs (*Cytisus oromediterraneus* and *Juniperus communis*), and meadows. It is active from late April to early October, mating in May–June and producing a single clutch in July. Tail autotomy is common in this species (60% of individuals with regenerated tail; Martín and Salvador 1993b). Males form dominance hierarchies in which large individuals are older, more active, and dominant over smaller ones (Aragón et al. 2004), and tail loss reduces male status and access to potential mates (Martín and Salvador 1993a). The mating system is polygynous, and there is extensive overlapping among male home ranges (Aragón et al. 2004). In the closely related species *Iberolacerta monticola*, adults can reach 10 years, most individuals are 3 years or older, and average annual survivorship between 1 and 4 years is about 0.6–0.7 (Moreira et al. 1998).

Field methods

This study was conducted during the reproductive seasons of 2002 and 2003 at the western slope of La Bola del Mundo, at an altitude of 1900 m, near Puerto de Navacerrada (Sierra de Guadarrama, Madrid, Spain). We selected a 50 × 40 m study plot that encompassed a grid that we marked at 10-m intervals. Fieldwork took place from the first day of emergence after hibernation until cessation of all reproductive activities. We visited the study plot 4 days per week, weather permitting, between 22 April and 29 May in 2002 and between 5 and 30 May in 2003.

All adult lizards seen were captured (43 males and 34 females in 2002 and 33 males and 30 females in 2003), and the following variables were recorded: SVL, tail length, head width (across the middle of the temporal region), head length, and body mass. Digital (2003) or 35-mm diapositive photographs (2002) were taken of each lizard's ventral and dorsal sides and color saturation subsequently measured using Adobe Photoshop at 6 random pixels for both the dorsum background (i.e., the coloration outside the black reticulated pattern) and the outer ventral blue spots; means were used in analyses. Body condition was estimated using the residuals of the regression of log-body mass on log-SVL. Lizards were toe clipped for permanent identification and samples stored in 95% ethanol for DNA analysis.

Each lizard was paint marked with a unique combination of 4 dorsal color spots to allow identification at a distance using 8 × 30 binoculars. Grid positions were recorded and home range size estimated for lizards with at least 3 observations on different days using the minimum convex polygon method (Jennrich and Turner 1969). Because our numbers of sightings were low, we reanalyzed our home range data using the residuals of the linear regressions relating home range size to the number of sightings, so that we could assess the effects of home range size on RS independent of activity. To calculate distances between lizards (i.e., between males and females or between the same individual in consecutive years), we used the baricenter of the home range, the midpoint between 2 locations, or the single observation site.

We employed the number of different observations of each lizard as an index of its activity. To ensure independence of data, the time interval between observations was at least 1 h. However, in most cases different observations of the same individual took place on different days. It might be argued that the fact that a lizard is not observed does not mean it is inactive because it could be active somewhere else. However, we believe that we have controlled for this possibility because 1) lizards often remain inactive and out of sight (Rose 1981; see Discussion); 2) we only used data from males with more than half of their locations within the 600 m^2 core area of the study plot (see Data analyses below); and 3) we may expect lizards on larger territories to be active on a different part of their home range and therefore not be observed as often as a lizard with a restricted home range, but the results of this study showed the opposite pattern: lizards with larger home ranges were observed more often.

Between 3 and 21 June 2002 and between 9 and 19 June 2003, we captured all gravid females found at the study plot ($n = 30$ in 2002 and $n = 21$ in 2003) and transported them to "El Ventorrillo" Field Station (5 km from the study area; altitude 1500 m). Females were kept in individual outdoor terraria (60 × 40 cm and 40 cm high), with unrestricted opportunities for thermoregulation and food and water ad libitum, until they laid their eggs. Mean clutch sizes (±1 standard error [SE]) were 5.6 ± 0.24 in 2002 and 5.7 ± 0.33 in 2003. Eggs were incubated at a constant temperature of 28 °C in individual 150-mL plastic containers filled with moistened vermiculite at a proportion of 8 g of water per 10 g of vermiculite, which is approximately equivalent to −200 kPa. Mean hatching success (±1 SE) was 41 ± 4.0% in 2002 and 36 ± 3.4% in 2003. After hatching, tail tips were removed from all individuals for DNA analysis. All females and their hatchlings were released at their respective sites of capture. Release occurred the day after laying for females and the day after hatching for neonates.

Data analyses

For the analyses of male RS, we only used lizards with more than 50% of their observations within the 600 m^2 core area defined after excluding the outer 10-m wide belt of the study plot. This was done to avoid underestimating the RS of peripheral males that might sire offspring outside the study plot. Similarly, only males that were observed after 14 May were included in the analyses to avoid the bias in the relationship between activity and RS that could be caused by males that had disappeared from the study plot at the onset of the reproductive season.

Data were analyzed separately for the 2 study years using general linear models. When necessary, variables were log transformed to meet the requirements of parametric tests. To decide what variables best predict the RS of males, we used a best-subsets approach in conjunction with stepwise methods (Neter et al. 1985). To do so, we chose the most parsimonious model as having the lowest Akaike information criterion (AIC), and we checked its coincidence with the equivalent stepwise solution. Fourteen males that were nonperipheral residents in both years were used to perform within-subject tests of yearly variation. The effects of behavioral and morphological variables on subsequent survivorship of males captured in 2002 were examined using logistic regressions (Generalized Linear Models) with presence and absence data in 2003 as the dependent binomial variables. For these analyses, we only considered those males that were observed after 14 May 2002 and for which the minimum time interval between the first and the last observation was 1 week (mean ± 1 SE = 27.0 ± 2.2 days). This was done to ensure that lizards that were not recaptured in 2003 had actually died or emigrated. Descriptive statistics are given as mean ± 1 SE.

A preliminary principal components analysis (not shown) was able to condense body dimensions into structural body size (SVL, body mass, head length, and head width) and tail length components, for both years. However, results of multiple regressions with RS as the dependent variable and either the original variables or the principal components as the independent variables were very similar. Thus, we maintained the original variables for the sake of clarity, though we did not consider body mass, head length, or head width in the analyses to avoid problems of multicollinearity due to their strong correlation with SVL. Coloration, especially saturation of the dorsum, was not correlated with body size variables. All variables tested in the models explaining male RS had tolerance values higher than 0.85 (2002) or 0.94 (2003) to avoid inconsistent results generated by stepwise regressions when explanatory variables are highly collinear. Normality of regression residuals was examined using normal probability plots.

Microsatellite genotyping

Genomic DNA was isolated from tissue samples using standard proteinase K digestion, phenol–chloroform–isoamyl alcohol extraction, and ethanol precipitation protocols (Hillis et al. 1996). All individuals were typed at 8 *I. cyreni*–specific microsatellite loci (Icy1, 2, 3, 4, 5, 6, 7, and 8) as described in Bloor (2006); no evidence of null alleles or linkage ($P > 0.05$) were found (Bloor 2006). One primer from each pair was fluorescently labeled (with FAM, NED, PET, or VIC) so that the corresponding polymerase chain reaction products could be distinguished from one another by size difference or by different fluorescent dyes (Bloor 2006). Fluorescently labeled polymerase chain reaction products from all 8 loci were pooled and run on an ABI 3700 DNA Sequencer (Applied Biosystems, Foster City, CA) with the GeneScan-500 (LIZ) internal size standard. Allele sizes were assigned using the program Genotyper version 3.7 (Applied Biosystems).

Parentage assignment

Parentage was assigned using the program CERVUS (Marshall et al. 1998). The ratio of the likelihood of paternity corresponding to a specific male relative to the corresponding likelihood of an arbitrary male is known as the LOD score. CERVUS calculates LOD scores for all typed males, with the significance of the score determined by simulation. For the latter, 10 000 cycles were run, with an estimated 95% of male parents sampled. Because of extensive fieldwork in and around the study plot, we are certain that this is a realistic estimate of the true proportion, allowing for a very low probability of paternity corresponding to an unsampled male. Typing errors also appeared particularly low in our study, with no female–offspring mismatches, so an arbitrary low 0.005 value was entered (similar studies have used values around 0.01, e.g., Stow and Sunnucks 2004). The simulations indicated 89% success rate at the strict confidence level (i.e., $\geq$0.95) for offspring from dams with known genotypes and 100% success rate at the relaxed confidence level ($\geq$0.80). Paternity was subsequently assigned to the males with highest LOD scores providing they at least met the relaxed criterion.

RESULTS

Paternity testing

None of the 8 loci deviated significantly from Hardy–Weinberg equilibrium after applying a standard Bonferroni correction to the results of the 8 goodness-of-fit tests (i.e., $P > 0.00625$ in all cases; only 1 locus was significant at the unadjusted significance level [locus 4; $P = 0.018$]).

Of 111 offspring, 96 were assigned at the strict 0.95 confidence level, with 14 being assigned at the relaxed level. One individual for which the maternal genotype was not known (of only 4 similar individuals) had a LOD score corresponding to a confidence in paternity of less than 0.80 but was assigned to the most likely male because it differed by just 1 repeat at a single locus.

Trait relations of males and females

A description of the morphological variables and spacing patterns of males and females can be found in Table 1. Males showed variable levels of activity, as estimated by the number of observations per individual (2002: 4.6 ± 0.6 observations, $n = 28$; 2003: 6.5 ± 1.2 observations, $n = 21$). Females showed lower activity levels (2002: 2.6 ± 0.4 observations, $n = 30$; 2003: 1.8 ± 0.3 observations, $n = 20$) and had smaller home ranges than males (Table 1, all $P < 0.03$). Neither SVL nor tail length was significantly correlated with number of observations or home range size in any of the 2 sexes or years (Pearson's correlations, all $P > 0.10$).

A repeated-measures analysis of variance (ANOVA) using the fourteen 2002 and 2003 males showed a change in SVL between years, as expected (2002: mean SVL = 71.7 ± 1.31; 2003: mean SVL = 73.6 ± 0.84; $F_{1,13} = 5.8$, $P = 0.032$). Similar analyses on the remaining variables (tail length, number of

Table 1

Morphological and spacing variables (mean ± 1 SE, sample size in parentheses) of lizards of both sexes in 2002 and 2003

	Males		Females	
	2002	2003	2002	2003
Mass (g)	7.3 ± 0.3 (27)	7.4 ± 0.3 (21)	7.5 ± 0.2 (30)	7.5 ± 0.3 (21)
SVL (mm)	71.9 ± 1.1 (27)	71.7 ± 0.9 (21)	74.5 ± 0.8 (30)	75.0 ± 1.1 (21)
Tail length (mm)	93.9 ± 6.8 (27)	93.2 ± 7.2 (21)	98.0 ± 3.3 (30)	75.4 ± 8.3 (21)
Home range area (m^2)	75.1 ± 13.4 (20)	97.5 ± 23.5 (16)	50.6 ± 12.8 (9)	25.6 ± 12.9 (4)
Females overlapped	2.6 ± 0.5 (20)	3.3 ± 0.6 (16)	1.0 ± 0.4 (9)	0.0 ± 0.0 (4)
Males overlapped	3.9 ± 0.4 (20)	4.3 ± 0.7 (16)	3.4 ± 0.6 (9)	4.0 ± 1.0 (4)

observations, home range size, number of overlapped males and females, number of offspring sired, or number of fertilized females) revealed no significant between-year variation ($P > 0.15$ in all cases). Between-years repeatability was low for all variables except SVL (intraclass correlation coefficient = 0.657; $F_{13,14} = 4.8$, $P = 0.003$). The repeatability of RS (number of sired offspring) was 0.229 ($F_{13,14} = 1.6$, $P = 0.198$).

Both males and females that were recaptured in 2003 showed high fidelity to their former home ranges, as deduced from the short distances between their locations in consecutive years (males: 7.8 ± 0.8 m, $n = 14$; females: 5.9 ± 1.1 m, $n = 17$).

Parentage assignment

Over the 2 years, there were 16 clutches of 2 viable hatchlings (7 showed dual paternity) and 17 clutches of at least 3 viable offspring (5 showed dual paternity and 4 had triple paternity). The high degree of multiple paternity (55.0% and 38.5% in 2002 and 2003, respectively) is particularly noteworthy in *I. cyreni* given the high proportion of clutches containing only 2 offspring (as a consequence of low hatching success). After controlling for the effects of original clutch size, clutches with multiple paternity produced more viable hatchlings than clutches sired by only 1 male, both in 2002 ($F_{1,27} = 4.2$, $P = 0.049$) and 2003 ($F_{1,18} = 6.9$, $P = 0.017$).

The mating system of males was highly polygynous in our population (Figure 1), with about half of the individuals not siring any offspring and with a few males siring the offspring of several females (26% of the males obtained 81% of the successful matings in 2002, and 24% of the males obtained 65% of the successful matings in 2003; see Figure 1).

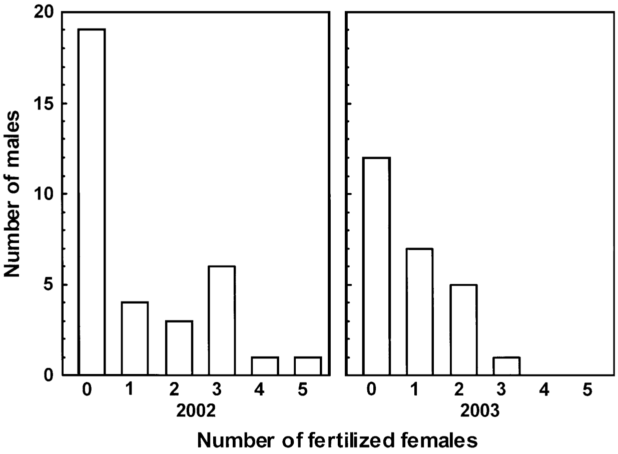

Figure 1
Polygyny in males of *Iberolacerta cyreni*: number of males that sired the offspring of no female, a single female, or more (2–5) females.

Correlates of RS

Within years, the number of offspring sired by males was correlated with the number of fertilized females (Pearson's correlations with males that sired at least 1 viable offspring; 2002: $r = 0.950$, $n = 14$, $P < 0.001$; 2003: $r = 0.505$, $n = 10$, $P = 0.137$), indicating that males increased RS by mating with several females, at least in our first study year. Although analyses using the number of fertilized females as the dependent variable produced very similar results, we shall only present the analyses that use the number of offspring sired as a direct measure of male RS.

Some males could have been transients because they were observed only 1 or 2 (consecutive) days. Some of these males managed to obtain some paternity. In 2002, 3 of 9 "transients" sired 5 of 70 offspring; of these, 2 were observed after 14 May 2002 and were thus included in our analyses of RS. In 2003, 3 of 9 transients sired 6 of 41 offspring but they were excluded from our analyses of RS because we did not observe them after 14 May 2003.

Because home range size could only be estimated for males with at least 3 observations on different days, we firstly assessed the relationships between activity, home range size, and RS. In 2002, the correlation between activity and home range size was positive but not significant ($r = 0.356$, $n = 20$, $P = 0.123$) and RS increased with activity ($r = 0.472$, $n = 28$, $P = 0.011$) but not with home range size ($r = -0.214$, $n = 20$, $P = 0.364$). In 2003, activity and home range size were positively correlated ($r = 0.888$, $n = 16$, $P < 0.001$) and RS increased with activity ($r = 0.521$, $n = 21$, $P = 0.015$) but not with home range size ($r = 0.112$, $n = 16$, $P = 0.681$). There was no correlation between RS and residual home range size, independent of activity, either in 2002 ($r = -0.331$, $n = 20$, $P = 0.153$) or 2003 ($r = -0.145$, $n = 16$, $P = 0.593$). These results suggest that activity is a better predictor of RS than home range size. Therefore, and to retain acceptably high sample sizes, we decided to exclude home range size from the remaining analyses of RS.

In 2002, RS was positively correlated with activity (see above), SVL ($r = 0.483$, $n = 27$, $P = 0.011$), and tail length ($r = 0.424$, $n = 27$, $P = 0.027$). Males with complete tails had a higher RS (5.3 ± 2.1 offspring, $n = 6$) than males with autotomized tails (1.3 ± 0.4 offspring, $n = 21$; $F_{1,25} = 6.7$, $P = 0.016$). The best model based on AIC included SVL, tail length, activity, and dorsal saturation of the dorsum as explanatory variables. A stepwise multiple regression analysis ($R^2 = 0.70$, $F_{4,19} = 11.3$, $P < 0.001$) confirmed that male RS increased with SVL ($\beta = 0.280$, $P = 0.051$), tail length ($\beta = 0.401$, $P = 0.005$), activity ($\beta = 0.510$, $P = 0.001$), and color saturation of the dorsum ($\beta = 0.332$, $P = 0.021$).

In 2003, RS was positively correlated with activity (see above) and body condition ($r = 0.532$, $n = 21$, $P = 0.013$). The RS of males with complete and autotomized tails did not differ significantly ($F_{1,19} = 2.0$, $P = 0.175$). The best model based on AIC included activity and body condition (residuals of body mass on SVL) as explanatory variables. A stepwise multiple regression analysis confirmed that male RS increased with activity ($R^2 = 0.28$, $F_{1,17} = 6.5$, $P = 0.020$) and left body condition close to statistical significance ($P = 0.078$). In fact, both variables had a significant effect on RS when 2 additional males for which there were no color data were included in the model (activity: $\beta = 0.414$, $P = 0.035$; body condition: $\beta = 0.428$, $P = 0.030$; whole model ANOVA: $F_{2,18} = 7.15$, $R^2 = 0.443$, and $P = 0.005$).

Spatial relationships between sires and dams

The mean distance of each sire to its associated dam or dams was 9.5 ± 1.5 m ($n = 14$) in 2002 and 11.3 ± 2.4 m ($n = 10$) in 2003. The mean distance of each female to her offspring's father or fathers (Figure 2; 2002: 12.8 ± 1.9 m, $n = 29$; 2003: 11.6 ± 2.6 m, $n = 18$) was significantly larger than the distance to her nearest male (Figure 2; 2002: 3.0 ± 0.3 m; 2003: 4.5 ± 0.7 m; repeated-measures ANOVAs; 2002: $F_{1,28} = 26.1$, $P < 0.001$; 2003: $F_{1,17} = 10.1$, $P = 0.006$). The same results were obtained when considering only the distance to the nearest sire in cases of multiple paternity (results not shown). In 2003, the relative fecundity of females (estimated using the residuals of the regression of clutch size on SVL) was positively correlated with the mean distance to her offspring's father or fathers ($r = 0.545$, $n = 18$, $P = 0.019$).

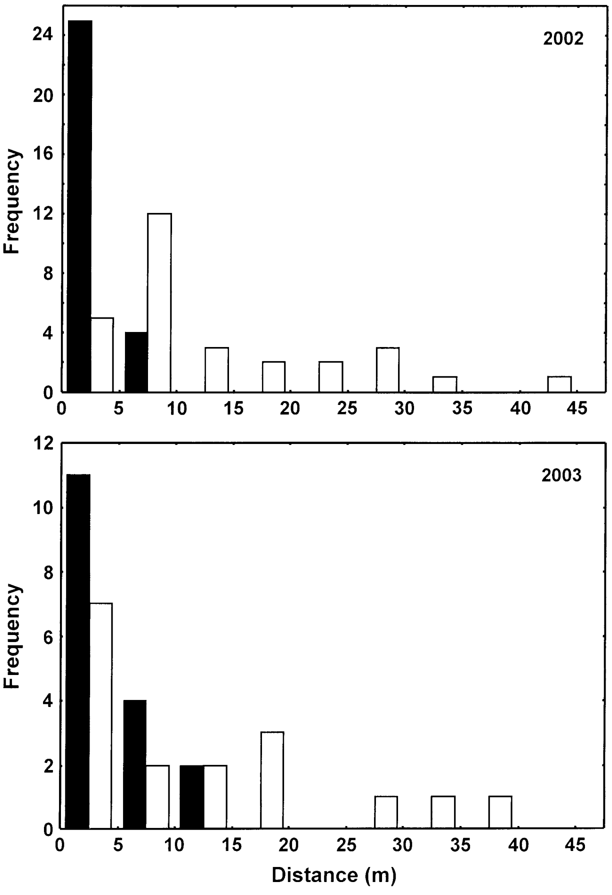

Figure 2
Distances between male and female *Iberolacerta cyreni*. Filled bars show the distance of each female to her nearest male, and open bars show the distance of each female to her offspring's father or the mean distance to her offspring's fathers.

Recapture probability of males

The 2002 males that were recaptured in 2003 were slightly larger, had longer tails, had been observed on more days, and had sired more offspring in 2002 than their conspecifics that were not recaptured (Table 2). RS was the single variable with the highest effect on recapture probability, correctly classifying 81% of individuals as recaptured (10 of 13) or not recaptured in 2003 (7 of 8), and it was the only one selected in a stepwise logistic regression with SVL, activity, tail length, and number of offspring sired as the explanatory variables (results not shown).

DISCUSSION

Our results show 3 main findings. First, the mating system was clearly polygynandrous: there was a high frequency of multiply sired clutches, about half of the males sired no offspring, and a few males obtained most of the successful matings, siring the offspring of several females. Second, the mean distance of females to their offspring's sires was significantly larger than the distance to their nearest males, which suggests a role for mate choice. Third, the high variance in male RS was explained by a few male traits, most noticeably activity levels, that may be costly and indicative of dominance and/or high quality. These traits, which may change over the lifetime of individuals, were associated with a higher recapture probability the next year, so that the males with higher RS were more likely to be recaptured. These findings are discussed within the context of the ecological pressures imposed by the alpine environment to long-lived lizard species with a short breeding season.

Multiple-partner matings

Multiple matings are common in many species of reptiles (Olsson and Madsen 1998), as they are clearly advantageous for males, which increase their RS by mating as often and with as many different partners as possible. Multiple partners may also have benefits for females, which may obtain larger clutches (Fitze et al. 2005), reduced number of stillbirths, increased hatching success, decreased malformations, or increased survival subsequent to birth (Madsen et al. 1992; Olsson et al. 1994; Calsbeek and Sinervo 2002). Among lacertids, multiple paternity has been reported for females of *Lacerta agilis* (4 out of 5 clutches sired by more than 1 male; Gullberg et al. 1997) and *Lacerta vivipara* (between 50% and

Table 2
Traits of 2002 males that were or were not recaptured the following activity season (mean ± 1 SE, sample size in parentheses) and results of the corresponding logistic regressions

	Survivors	Not recaptured	Wald statistic	P
SVL (mm)	73.9 ± 1.4 (13)	68.1 ± 3.1 (7)	2.97	0.085
Tail length (mm)	110.8 ± 8.3 (13)	66.3 ± 15.2 (7)	4.41	0.036
Dorsal saturation	16.8 ± 2.2 (12)	19.6 ± 2.4 (5)	0.57	0.452
Observations (No.)	6.6 ± 0.7 (13)	3.6 ± 0.7 (8)	5.09	0.024
RS (No. of offspring)	4.2 ± 1.1 (13)	0.3 ± 0.3 (8)	5.25	0.022

70% multiply sired clutches; Laloi et al. 2004; Fitze et al. 2005). We reveal a similarly high proportion of multiply sired clutches in *I. cyreni* (38.5–55%), which is quite notable given the much smaller clutch sizes we used (only 2 juveniles in almost half the clutches). In fact, our low hatching success might bias our conclusions, in particular if it generated nonrandom variation in paternity. However, several lines of evidence suggest that this is not the case. Firstly, all clutches received exactly the same treatment, and as a consequence mortality was evenly distributed among clutches rather than due to whole-clutch failure. Secondly, low hatching success might explain why some males with high numbers of observations reached low RS, thus making our analyses conservative. In spite of this, we obtained a large number of significant relationships, which make it unlikely that undetected sources of variation related to low hatching success, but different from the hypotheses being tested, could be biasing our conclusions.

Thus, multiple paternity could be much higher than our estimate, and polygynandry might be the rule within this family of actively foraging, chemically oriented lizards. In the case of *I. cyreni*, several ecological factors could further promote promiscuity: high local population densities, extensive home range overlap, and a short breeding season typical of the alpine environment. This mating system would allow the coexistence of alternative mating strategies, as suggested by the successful matings obtained by putative "transients" and by the fact that large males did not monopolize females; males as small as 68 (2003) or 60 (2002) mm in SVL, that could be young and/or subordinate, also managed to sire some offspring. Given the high adult survivorship rate and associated long life span of *I. cyreni*, it is likely that the explosive nature of the breeding season in montane environments (only 2–3 weeks) translates into alternative despotic and satellite strategies that may have a strong ontogenetic component (young males transform from satellite to dominant as they grow up), thus reflecting phenotypic plasticity rather than genetic differentiation (Zamudio and Sinervo 2003).

Spatial proximity between sires and dams

The average distance between sires and dams was short enough to confirm that matings revealed by DNA genotyping were consistent with the distribution of lizard home ranges within the study plot. However, females did not mate with the nearest male available. This suggests that either male mate choice or, more likely, that females were selecting mates from outside their home range (Zamudio and Sinervo 2003), which may be adaptive if hatchling dispersal is low and mating with unrelated males is selected to favor inbreeding avoidance (Sinervo and Clobert 2003; Hoffman et al. 2007). In fact, the possible existence of overdispersion with respect to genetic similarity due to kinship should provide a fertile area for future studies in *I. cyreni*.

Correlates of male RS

Despite small sample sizes, our results indicate that several morphological (body size, body condition, tail length, and color saturation of the dorsum) and behavioral factors are important for explaining interindividual variation in the number of offspring sired by *I. cyreni* males and that the relevance of such factors may vary between years (Oring et al. 1991; Sinervo and Lively 1996). However, the number of different days on which a male was observed, as an index of its activity level, was the single explanatory variable that had a more consistent effect on RS between years. It is widely acknowledged that lizards, as typical ectotherms, can modulate their activity levels on a seasonal basis as a function of the costs and benefits of activity and inactivity and that inactivity may be adaptive per se not merely as a response to unfavorable weather conditions. Thus, the activity of male lizards tends to be low outside the breeding season, because inactivity reduces risk of predation and conserves energy, thereby increasing the opportunities of survival and future reproduction (Rose 1981). On the other hand, during the breeding season males increase their activity to enhance their RS. Ruby (1981) observed that mated males of *Sceloporus jarrovi* displayed higher activity than unmated ones, and more active males of the lacertid *Psammodromus algirus* courted females more frequently than less active ones (Díaz 1993; Salvador and Veiga 2001). In *I. cyreni*, activity of individual males was correlated with their social rank (Martín and López 2000). More active males gained access to more females by overlapping not only home ranges of a larger number of females but also those of a larger number of male competitors, which increased the cost of agonistic interactions (Aragón et al. 2001). Moreover, higher activity may also decrease survivorship by increasing energy expenditure and risk of predation (Marler and Moore 1989; Díaz 1993).

Tail length was a successful predictor of male RS in *I. cyreni* during 2002. It is known that tail loss reduces access to potential mates in this relatively long-lived species (Martín and Salvador 1993a) and that tailless males may defer breeding effort, divert energy to tail growth, and then reassume breeding effort in a subsequent season. Tailless males may also show a suite of behavioral adjustments in their use of space and time, such as basking at closer distances from refuges (Martín and Salvador 1993b). As a result, average home range size was smaller in tailless males (Martín and Salvador 1997). It has also been reported that activity decreased after autotomy in males of *I. cyreni*, allowing tailless lizards to reduce costs of agonistic encounters and predation risk while simultaneously saving energy that could be devoted to tail regeneration (Martín and Salvador 1997). All these strategies may compromise the RS of tailless individuals. Moreover, the compensatory behaviors described above may fail to prevent mortality, as suggested by our result that probability of survivorship increases with tail length and by previous reports that tailless lizards are more vulnerable to predation than tailed ones (Dial and Fitzpatrick 1984; Fox and McCoy 2000).

In 2003, the physical condition of males, which may enable them to be more active and search more intensively for receptive females (Hofmann and Henle 2006), was a significant predictor of RS. It should be noted that the second year late snowfalls delayed the emergence of lizards from their winter refuges for almost 2 weeks. This may have prevented males in poor condition to gain mass before engaging in breeding activities, thus reducing their ability to maintain high activity levels and reach high RS. The later emergence in 2003 could also explain why in that year activity and body condition were the only significant predictors of RS. This could be due to the longer time available in the first year to establish social bonds with other individuals, allowing females to be more selective in their mate choice and hence more sensitive to male sexual signals.

Activity and color saturation (another trait that increased male RS during 2002) seem to be subject to hormonal regulation, probably mediated by testosterone. Thus, our results may be consistent with previous findings that the increased testosterone levels at the beginning of the reproductive season promote the development of breeding coloration (Díaz et al. 1994; Salvador et al. 1996), activate courtship (Tokarz et al. 2002), and produce higher activity levels (DeNardo and Sinervo 1994). However, high testosterone levels may raise energy expenditure associated with territorial defense (Marler et al. 1995), reduce immunocompetence (Veiga et al. 1998), and increase susceptibility to infestation by ectoparasites (Salvador et al. 1996).

Male RS and recapture probability

The males that sired more offspring in 2002 were more active and had a more intense dorsal coloration, presumably as a result of higher testosterone levels, than their less successful conspecifics. In principle, these features are expected to decrease survivorship, and a trade-off has previously been inferred for *I. cyreni* on the basis of a negative correlation between traits that promote social dominance and those that favor locomotor performance (López and Martín 2002). However, our data showed that the probability of recapture the next breeding season was higher for the males that achieved higher RS. Thus, "high-quality" males, despite affording the costs of high activity, were able to combine the benefits of both higher RS and higher survivorship (Abell 2000), indicating that male investment in reproduction varies in relation to the ability to pay the underlying costs of sexually selected traits (review by Jennions et al. 2001). Our results are thus consistent with the expectation that when some individuals have more resources and perform better than others, positive correlations between reproduction and survival should arise (van Noordwijk and de Jong 1986). Interestingly, this is in contrast with the data available for other lacertids from lower altitudes, such as *P. algirus,* a species with a shorter life span (Salvador A, Díaz JA, Veiga JP, Bloor P, Brown RP, unpublished data) in which brightly colored males were larger, more active, and courted females more frequently than dully colored ones, but at the cost of decreased survivorship (Díaz 1993; Salvador et al. 1996).

Thus, our results yield 2 main conclusions. Firstly, the phenotypic correlates of male RS are indicative of dominance and/or good physical condition, either directly (e.g., SVL, tail length, residuals of the regression of body mass on SVL) or because they are costly to maintain (e.g., high activity levels). These male characteristics may reflect a plastic set of alternative male mating strategies that transform from satellite early in life to dominant in the oldest males; young males would be forced to emigrate (which could facilitate inbreeding avoidance), die, or behave as transients. Secondly, and more important, these same traits (and, first of all, RS itself) were associated with a higher probability of recapture the next breeding season, suggesting that male success in reproduction varied in relation to the ability to pay the underlying costs and that current investment in reproduction did not decrease future RS. This is the expected result when there is large variation among individuals in the amount of resources available, in such way that some of them (those older, with larger SVL, longer tails, more saturated dorsal coloration, and/or better condition) can spend more in reproduction and maintenance than others (van Noordwijk and de Jong 1986). To our knowledge, this is the first time that a positive correlation between male RS and survivorship, perhaps related to the characteristics of the alpine environment that induce low annual reproductive output (e.g., short mating season), has been described for a wild population of lizards. This result is in contrast with previous reports of high survival costs of reproduction in male lizards (review by Schwarzkopf 1994), and it supports the pattern found in natural populations of other taxa in which a few high-quality males enjoy both high mating success and high survival (Pelletier et al. 2006, Townsend and Anderson 2007).

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