Journal of Herpetology, Vol. 40, No. 1, pp. 1–6, 2006

Male Reproductive Success and Intrasexual Selection in the Common Lizard Determined by DNA-microsatellites

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ABSTRACT.—**The common lizard (*Lacerta vivipara*) is a small, nonterritorial, live-bearing lacertid that is sexually dimorphic in several morphological traits (e.g., tail length, snout–vent length, head size). Using microsatellites, we examined paternity in a wild population and investigated whether sexual dimorphism could be the result of intra- or intersexual selection. We found multiple paternity in 65.4% of 26 clutches. There was no evidence of assortative mating. Successfully reproducing males were larger and heavier and had longer tail regenerates or intact tails compared to those that did not reproduce. Tail length and body condition of males were related to the number of offspring sired. However, we found no evidence that head width was related to male reproductive success. We conclude that (1) males with higher body condition index might be more successful in male-male interactions or might be able to search more effectively for females, (2) sex divergence in relative tail length in common lizards reflects the action of sexual selection for male reproductive success, and (3) intersexual dietary divergence could be an alternative hypothesis for head size difference between sexes rather than intrasexual selection.**

Mating systems of lizards show considerable variation, from monogamy (Gardner et al., 2001; O'Connor and Shine, 2003) to polygyny (Ferguson, 1970; Jenssen et al., 2000) and promiscuity (Olsson and Madsen, 2001). Despite this variation, most lizards are polygynous (Bull, 2000). The intersexual competition that results from polygyny is thought to have driven the evolution of sexual dimorphism (Andersson, 1994). In lizards, as in many other reptiles, the sexes differ in body shape as well as overall body size; these sexual differences are generally attributed to ways in which morphology affects reproductive fitness. For example, compared to conspecific females of the same relative body length, male lizards tend to have larger heads and shorter snout–vent length (SVL; reviewed in Olsson and Madsen, 1998). Longer trunks of females have been associated with fecundity, presumably because reproductive investment is limited by the size of the abdominal cavity (Olsson and Shine, 1997); thus, these traits are attributed to selection for increased space to hold developing eggs or embryos (reviewed in Andersson, 1994). A relatively larger head in males is believed to enhance male success in intrasexual rivalry (fighting ability; Olsson et al., 2002).

The nonterritorial common lizard, *Lacerta vivipara*, exhibits sexual dimorphism in body size, head width, tail length, and coloration, and individuals of either sex have multiple mates (Bauwens and Verheyen, 1985; Heulin, 1988). This presents an excellent opportunity for studies of factors related to male reproductive success. In the common lizard rivalries between sexually mature males occur less frequently than in the sister species *Lacerta agilis* (Heulin, 1988). Males do not exhibit mate guarding, and, until now, there has been no evidence of varying male mating strategies.

We used microsatellite DNA loci to assign parentage of offspring to quantify male reproductive success and examined several questions related to sexual selection. First, we determined the degree of multiple paternity in 26 clutches of a wild population. Moreover, we genotyped all adults and offspring captured in the population over two years to identify sires. Second, we quantified potential attributes that might influence male reproductive success in *L. vivipara* including male body size and mass, head width, tail length, and body condition as well as phenotypic similarity between successful mates.

MATERIALS AND METHODS

Field Methods.—This study was conducted at the floodplain of the rivers Elster and Luppe, a nature reserve 11 km northwest of Leipzig, Germany (51°22′N, 12°14′E). A population of common lizards was studied throughout the breeding seasons in 2001 and 2002 from mating to the end of hatching (April through September).

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All lizards on the 7000-m^2 area were caught by hand. A blood sample (10 µl) was taken from each individual for DNA extraction. For juveniles with a SVL < 35 mm and a body mass < 1 g, a tissue sample from the tail tip (2–3 mm) was collected and stored in the same way as the blood samples.

Lizards were classified by age class (adult, subadult, or juvenile) and sex, according to body size, body coloration, and sexual characteristics (e.g., basal thickness of tail, state of the occipital-band; Glandt, 2001). The following variables were measured at each capture: head width (HW, across the middle of the tympanum; ± 0.5 mm), SVL (± 1 mm), tail length (TL; ± 1 mm), regenerated tail sector (RT; ± 1 mm), body mass (BM; adults were weighed with a Pesola spring, accuracy ± 0.5 g; juveniles with a Pesola spring, accuracy ± 0.1 g). As a relative index of body condition (BCI), we used residuals of the regression of BM on SVL (Henle, 1990; Jakob et al., 1996).

Body mass and BCI of almost all females had to be excluded from the evaluation because most females were already gravid when captured and measured in the field and because they could not be recaptured after they gave birth. Only the body mass and BCI of 26 temporary caged females were included. Those 26 gravid adults were captured in early July 2001 and 2002 to quantify the extent of multiple paternity in their offspring. Lizards were transported to enclosures where they were maintained in individual cages until they gave birth. After giving birth, each female was weighed and a blood sample was collected. Hatchlings were measured and the tail tip was dissected from each offspring. All females and their viable young were released at the place where the female was captured within two days after birth.

Genotyping Methods and Parentage Assignment.—Genomic DNA isolation from blood or fresh tissue followed a standard protocol supplied with the E.Z.N.A. Tissue DNA Kit II system (Peqlab Biotechnologie). We used five microsatellite markers developed for the common lizard (Boudjemadi et al., 1999) to assign parentage to all offspring. Primers for each locus (one labeled with a fluorescent dye HEX, TET, or FAM on the 5′-end) were used to amplify sample DNA using the polymerase chain reaction (PCR) at optimized annealing temperatures (Boudjemadi et al., 1999). PCR products were resolved on 5% PAA gels and detected with a Sequencer (ABI 377 Applied Biosystems GmbH). Allelic size was determined using GENESCAN software version 2.1 by reference to the GENESCAN ROX 500HD size standard and by comparison to previously scored samples.

We assigned parentage using the likelihood-based approach implemented in program Cervus (Marshall et al., 1998), which allows for inclusion of the identity of the mother if maternity was unambiguous (e.g., in case of the 26 caged clutches). If both parents were unknown, parentage was assigned in a stepwise manner. Offspring maternity was determined first; then paternity was assigned with offspring having a known parent. We used three different conditions: 80% confidence level, 95% confidence level, and based on exclusion. Under exclusion, females or males that had any mismatches in microsatellite alleles with a juvenile, were excluded from parentage. The exclusion power of the five microsatellite loci combined was 99.9% for maternity and 99.7% for paternity.

Simulations required for parentage assignment were run for each year with the following parameters: 10,000 cycles, 55 and 90 potential mothers, 56 and 60 potential fathers (number of females and males caught in 2001 and 2002), 0.99 of loci typed, 0.05 as the proportion of loci mistyped. We estimated the proportion of individuals sampled from capture-mark-recapture data using program MARK (www.cnr.colostate.edu/~gwhite/software.html).

Data Analyses.—Subadults were excluded from all current analyses; only adults were considered. Absolute values of SVL were compared between the sexes using t-test for independent data and relative values of HW and TL using analysis of covariance (ANCOVA) with SVL as covariate (tail-autotomized individuals were not included). To assess the effect of male traits on reproductive success, we first sorted all genotyped adult males ($N = 59$) present in the main research area in 2001–2002 in two groups: "sires" and "potential (but unsuccessful) sires." We classified a male as a sire if it was the father of at least one of the juveniles present in the field or in the clutch of a female in captivity. The group of potential sires included all males that were not been identified as fathers. We compared measured traits of sires and potential sires by multivariate analysis of variance (MANOVA). If a male was captured twice or more during a mating period (April through June), the average value of measurements was used. At the next step, we compared traits among sires grouped by the number of clutches (1, 2, and >2) they fathered.

We calculated the standardized partial regression coefficients of the measured male traits and the body size of the mated female from a multiple regression of the number of offspring a male sired. Therefore, we considered only the adult sires of the 26 caged clutches because the exact number of young a male sired in a clutch was known only for these clutches. To clarify collinearity problems between male traits and to reduce the number of variables, we used a principal components analysis. The components

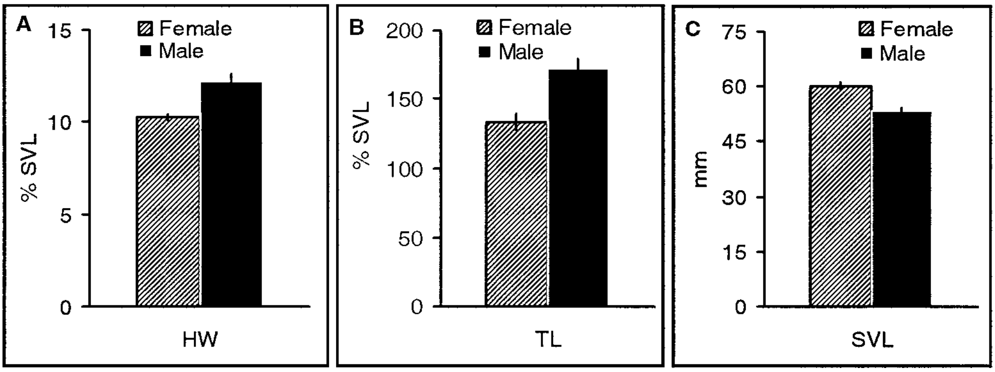

FIG. 1. Means (± SE) of relative head width (HW; A), relative tail length (TL; B), and snout–vent length (SVL) of adult females ($N = 31$) and males ($N = 39$). Tail-autotomized individuals are not included in these figures.

were rotated using the Viramax method with Kaiser's normalization using SPSS (vers. 11.5.1, Cary, NC, 2002).

Finally, we analysed the relationship between body dimensions of the 26 caged females and their identified adult mates by correlating SVL, BM, and BCI to determine whether assortative mating occurred. We grouped those females by the number of mates who had sired their clutches (one, two, or three males) and tested for differences in female body size by ANOVA.

RESULTS

Parentage Assignment.—The sire could be identified for more than 84% of the offspring ($N = 252$) of the temporarily caged females. Paternity remained doubtful or unknown in only 30 cases. Multiple paternity was found in 65% of clutches (17 of 26); in 38% (10 of 26 clutches) females produced offspring sired by two males, and 27% were sired by more than two males. For juveniles captured in the field during 2001 and 2002, parentage of both parents was assigned to 53% of juveniles (109 of 205 individuals). The remaining juveniles could not be assigned reliably to any male or female surveyed as part of the study.

A total of 43 adults were identified as sires. Twenty-one individuals sired only one clutch; 15 sired two and seven males sired more than two clutches.

Sexual Dimorphism and Reproductive Success of Males.—Females had longer trunks than males (Fig. 1; t-test; $t = –5.788$; $F = 8.897$; $P < 0.01$). However, males had larger head widths and longer tails than females relative to SVL (Fig. 1; ANCOVA; df = 2; $F_{[HW]2,64} = 31.324$; $P < 0.001$; $F_{[TL]2,64} = 7.483$; $P < 0.01$).

Sires and nonsires differed in overall traits measured (Table 1; MANOVA; df = 6; Wilks' $\lambda = 0.699$; $F_{6,49} = 3.513$; $P < 0.01$). Sires had larger body size (ANOVA; df = 1; $F_{1,54} = 5.503$; $P < 0.05$), higher body mass (ANOVA, df = 1; $F_{1,54} = 5.396$; $P < 0.05$), and a longer regenerate tail sector (ANOVA; df = 1; $F_{1,54} = 5.533$; $P < 0.05$) compared to nonsires. All other characteristics showed no statistically significant differences between successful and unsuccessful males.

Among sires with different numbers of clutches, no statistically significant difference was found when testing all traits simultaneously (MANOVA; df = 6; Wilks' $\lambda = 0.736$; $F_{12,64} = 0.882$; $P = 0.569$). When testing traits individually, only SVL was related to clutch number (ANOVA; df = 1; $F_{2,37} = 4.454$; $P < 0.05$).

Stepwise multiple regression indicated that the number of offspring an adult sired depended on its body condition index and tail length (Table 2). Principle components analysis reduced the six traits to three principal components (PC), which explained 83.24% of the variance (Table 3). The first principal component was determined mainly by mass (body condition and body mass), the second by size (tail length and SVL), and the third by the length of the regenerated tail sector (PC3, Table 3).

Assortative Mating.—As expected, clutch size depended on female body size (Spearman rank correlation $r = 0.496$, $P < 0.01$). Consequently,

TABLE 1. Characteristics of adult sires and nonsires. HW: head width, SVL: snout–vent length, TL: tail length, BM: body mass, BCI: body condition index, RT: regenerated tail sector.

	Sires		Nonsires	
	N	mean ± SE	N	mean ± SE
HW	42	6.64 ± 0.04	16	6.81 ± 0.12
SVL	42	54.00 ± 0.43	15	52.87 ± 0.85
TL	42	79.93 ± 3.05	15	64.47 ± 7.47
BM	43	4.56 ± 0.09	14	4.25 ± 0.17
BCI	42	0.056 ± 0.08	14	−0.140 ± 0.16
RT	42	24.77 ± 3.87	15	11.63 ± 4.46

TABLE 2. Stepwise multiple regression between the number of sired offspring and the morphological characteristics of adult sires ($N = 22$). Only the sires of the hatchlings of the 26 caged clutches are included. TL: tail length, BCI: body condition index, HW: head width, SVL: snout–vent length, RT: regenerated tail sector, BM: body mass. B: indicates the unstandardized and β the standardized coefficient of the estimated regression model. SE: standard error. $P < 0.05$.

Coefficient[a]	B	SE	β	T	*P*
(constant)	3.219	3.298		0.976	0.341
BCI	5.066	2.226	0.424	2.276	0.035
TL	0.090	0.041	0.411	2.210	0.040

Excluded variables[b]	β	T	*P*	Partial correlation	Colinearity (tolerance)
HW	0.005[c]	0.028	0.978	0.007	0.781
SVL	0.027[c]	0.164	0.872	0.039	0.915
RT	−0.236[c]	−1.506	0.149	−0.335	0.925
BM	−0.046[c]	−0.212	0.835	−0.050	0.534
SVL female	−0.053[c]	−0.317	0.755	−0.075	0.896

[a] Depended variable: number of offspring.
[b] Depended variable: number of offspring.
[c] Influent variable in the model (constant: TL and BCI).

TABLE 3. Principal component factor loadings of male traits. Traits that contribute most strongly to the factor are given in **bold**. Varimax rotation method with Kaiser normalization.

Trait	PC1	PC2	PC3
Head width	0.475	−0.210	−0.466
Snout–vent length	0.278	−0.530	−0.163
Tail length	0.237	**0.538**	0.325
Regenerated tail sector	0.089	−0.470	**0.792**
Body mass	0.500	−0.063	0.143
Body condition index	**0.619**	0.396	0.061
% cumulative variance explained	38.28	70.26	83.24

the number of offspring, which a male fathered in a clutch, depended on the body size of the mother and its clutch size (SVL mother: $r = 0.382$, $P = 0.019$; clutch size: $r = 0.403$, $P < 0.05$, $N = 31$). The larger a female and its clutch size, the higher was the number of young sired by a male. Despite the positive relations, no evidence was found that mating was nonrandom with regard to female body size. Coefficients of variation revealed low variation in SVL and body mass of either sex. A higher variation was only found in body condition index of males. There was no significant relationship in the analysed body measurements between mates (Table 4). Females whose clutches were fertilized by one, two, or three males showed no differences in body size (ANOVA, $F = 0.700$, $P = 0.510$).

DISCUSSION

Consistent with previous studies (Barbadillo and Bauwens 1997; Šmajda and Majláth 1999; Herrel et al., 2001), we found clear sexual dimorphism in body size, relative tail lengths, and head width. Successfully reproducing males were larger, heavier, and had long tail regenerates or intact tails compared to unsuccessful males. Moreover, a sire's quantitative reproductive outcome was correlated with its tail length and body condition index. The high level of multiple paternity is consistant with a mating system in which both, male and female common lizards mate with multiple partners.

The proportion of clutches with mixed paternity (65%) was similar to that documented in a previous study (Laloi et al., 2004). In lizards, multiple paternity often reflects conflicting reproductive strategies. Most cases refer to species with resource-defence polygamy where dominant males sire most of the offspring, whereas floaters achieve a lower number of matings, leading to multiple sired clutches (Gullberg et al., 1997; LeBas, 2001; Morrison et al., 2002). Male common lizards are nonterritorial (Avery, 1975), and mate guarding as in sand lizards (*L. agilis*) (Olsson, 1993) have not been observed. Thus, the number of offspring a male produces depends mainly on the number of clutches it sires, and males should maximize their reproductive success by seeking and mating with many females (Trivers, 1972). Although, as expected, male reproductive success was correlated with female clutch size, we did not find evidence for positive assortative mating. Moreover, our data indicated that clutches of larger females are no more frequently sired by multiple males than clutches of smaller females. Thus, in common lizards, it seems likely that males mate as many females as possible rather than being choosy.

Sires had larger body size and body mass than reproductively unsuccessful males. Body size can indicate survival in species where this trait is positively correlated with age (Halliday and Verrell, 1988; Halliday, 1992), and a higher paternity success for larger males can be the result of their success in dominance interactions with other males and/or female preference for these males (Schuett 1997; Lewis et al., 2000). In common lizards, larger (and consequently heavier) males are dominant over smaller individuals (Heulin, 1988) and, therefore, should be more successful than smaller males, as observed in our study. Surprisingly, we found no difference overall between sires related to the number of clutches they sired. This may be related to the low number of individuals in proportion to the relative high number of variables (6 × 22 cases) included in the multivariate analysis. Notwith-

TABLE 4. Coefficients of variation (CV) and mean ± standard error (SE) of morphological traits of mates ($N_{\mathrm{male}} = 31$; $N_{\mathrm{female}} = 26$). SVL: snout–vent length, BM: body mass, BCI: body condition index. r: Correlation coefficient. $P < 0.05$.

	Mean ± SE		Mean ± SE				
Trait	Male	CV_{male}	Female	CV_{female}	r	df	P
SVL	53.65 ± 3.23	0.06	62.8 ± 5.06	0.08	0.26	31	0.08
BM	4.38 ± 0.46	0.11	5.03 ± 0.56	0.11	0.07	31	0.13
BCI	−0.06 ± 0.42	−6.79	−1.04 ± 0.55	−0.53	−0.16	31	0.22

standing, in univariate analyses SVL showed a significant relationship to clutch number.

The reproductive disadvantage to males with shorter tails and lower body condition indices warrants closer examination. A high body condition may enable males to be more active and search intensively for receptive females. Madsen et al. (1993) found that the distance traveled by male adders during the mating season was a significant predictor of the number of females mated. A similar result was found in northern water snakes (Weatherhead et al., 2002). Likewise, in other taxa where males compete for females (e.g., voles: Gaulin and Fitzgerald, 1986, 1989; Spritzer, 2003; ground squirrels: Schwagmeyer, 1988) searching ability of males contributes to male reproductive success (Andersson, 1994). We suggest that male lizards in better condition spend more energy for movement and search activities during the mating season relative to slighter males and, thus, achieve a reproductive advantage.

A longer tail in males of this species may be the result of morphological constraints imposed by the male copulatory organs on tail autotomy, or it may be the result of improved escape abilities in the sex more likely subjected to heavier predation pressure (Barbadillo et al., 1995; Barbadillo and Bauwens, 1997). In general, tail loss can interrupt different steps in the reproductive process from access to mating to reproductive output. In turn, this may be linked to social status (e.g., Vitt et al., 1977; Fox and Rostker, 1982; Fox et al., 1990) and possibly even habitat use (e.g., Salvador et al., 1996; Martin and Salvador, 1997). Because mating in common lizards is characterised by flank-biting and tail-twisting, it may be that males with long (nonautotomized) or fully regenerated tails may have longer mating times. Hence, they deliver more sperm and a higher number of offspring. An alternative possibility is that females select male partners based on relative tail length. Although it is tempting to speculate, the question whether sexual dimorphism in tail length is a result of intrasexual competition between males or is caused by intersexual selection by female choice, or is the result of natural selection caused by a higher predation pressure on males, can only be resolved by a broad comparative study of the relation between mating patterns, effective reproductive output, and sexual dimorphism in tail length.

Acknowledgments.—This work was supported by the Deutsche Bundesstiftung Umwelt (DBU) and the Centre for Environmental Research Leipzig-Halle. The authors would like to thank C. Jayne and two anonymous reviewers for their help in improving this manuscript. We are grateful to W.-R. Grosse for his encouragement and K. Neumann for advice and assistance in the laboratory.

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Accepted: 11 October 2005.