Behav Ecol Sociobiol (1993) 32:185–189

Behavioral Ecology and Sociobiology

Tail loss reduces mating success in the Iberian rock-lizard, *Lacerta monticola*

Jose Martín and Alfredo Salvador

Departamento de Ecologia Evolutiva, Museo Nacional de Ciencias Naturales, José Gutierrez Abascal 2, E-28006 Madrid, Spain

Received July 2, 1992 / Accepted October 10, 1992

Summary. Many lizards autotomize their tails to escape when grasped by a predator. It is hypothesized that tail loss causes a reduction in social status, thereby potentially lowering their reproductive success. We experimentally induced tail loss in *Lacerta monticola* in a semi-natural enclosure, and show that tail loss reduced social status and mating access in males. Tailless males increased body mass more rapidly than tailed dominant males, probably due to lower aggression costs. Also, tailless females were courted less and copulated less than tailed females, supporting the hypothesis that tail loss decreases reproduction potential.

Introduction

Autotomy of body parts as a predator defense mechanism is a conspicuous feature of many organisms (Edmunds 1974), such as numerous lizards which autotomize their tail to escape when grasped by a predator (Bellairs and Bryant 1985). Autotomy produces an immediate benefit to survival, but associated costs during tail regeneration may reduce individual fitness (Arnold 1988). Among these costs are lack of equilibrium (Ballinger 1973; Arnold 1984), lower running speed (Ballinger et al. 1979; Punzo 1982; Arnold 1984) and microhabitat restrictions (Martín and Salvador 1992). Tailless lizards are also more vulnerable to predation than tailed lizards (Congdon et al. 1974; Dial and Fitzpatrick 1984), although lizards may compensate by modifying their behavior (Formanowicz et al. 1990).

One of the most important consequences of social status is that dominant animals could gain differential access to mating and consequently could leave more offspring than subordinate animals (Dewsbury 1982). Tail loss decreases social status of juvenile and subadult *Uta stansburiana* (Fox and Rotsker 1982; Fox et al. 1990). Therefore, if tail loss decreases social status of adult male lizards it may also reduce their reproductive success.

Regeneration costs in tailless lizards may be met by increased food intake (Dial and Fitzpatrick 1981) or by diversion of energy from other functions, such as somatic growth (Ballinger and Tinkle 1979) or reproductive effort (Dial and Fitzpatrick 1981). Dominant male lizards perform numerous aggressive behaviors toward other males, but aggression may reduce male survival because of a lower energy balance (Marler and Moore 1988, 1991). Therefore, if tailless males have subordinate status, they may have lower aggression levels, save energy for tail regeneration and increase their survival.

Female tail loss reduces egg mass or clutch size (Smyth 1974; Dial and Fitzpatrick 1981). The female tail may be a signal of resource-holding potential that could be important in mate choice (Fox et al. 1990); tailless females may be less attractive to males.

In this experiment we test these hypotheses by manipulating the tail condition of Iberian rock-lizards *Lacerta monticola* in a semi-natural enclosure. We show that tail loss reduces social status and mating success in males. We also show that tailless females are courted less and copulate less than tailed females, supporting the hypothesis that tail loss indicates decreased reproductive potential.

Materials and methods

We captured 20 adult *L. monticola* (ten males: snout-vent length (SVL), $\bar{x} \pm SE = 76.6 \pm 0.2$ mm; mass $= 9.5 \pm 0.1$ g; ten females: SVL $= 75.4 \pm 0.4$ mm; mass $= 7.1 \pm 0.2$ g) near the Puerto de Navacerrada (altitude 1850 m, Madrid, Spain) on 13 May 1991. Lizards were then housed together on the day of capture in a semi-natural outdoor enclosure (20 × 12 m) located at "El Ventorrillo" Field Station (altitude 1500 m, 5 km from capture site). The plastic enclosure wall was supported by wooden sticks. Within the enclosure grass and annual plants supported abundant invertebrate food. Three rows of seven circular habitats (1 m diameter containing rocks, logs, and *Cytisus oromediterraneus* bushes) were placed within the enclosure.

Correspondence to: J. Martín

One week after housing, we removed the tail approximately 17 mm posterior to the cloaca from five randomly chosen males and five randomly chosen females. To avoid differences in stress related to manipulation, controls and experimental lizards were handled in a similar manner. Each lizard was weighed, permanently marked by toe-clipping and temporarily coded with paint. Lizards were captured, repainted and weighed once a week between 20 May and 30 June. We calculated changes in body mass as percent of weight gained or lost with respect to the initial weight after tail removal.

To analyze social and copulatory behavior we monitored simultaneously all lizards between 0800 and 1800 hours from 20 May to 30 June 1991. We considered the reproductive period to be when lizards were more active, with most social interaction, and all the courtships and copulations (20 May to 12 June). After 12 June activity and social interaction virtually ceased, no more courtships were observed, and this was treated as the postreproductive period (13–30 June). We made observations with binoculars from an elevated viewpoint, and recorded fights, chases, displays, courtships and copulations. During the reproductive period a matrix of dominance relationships was constructed based on the results of agonistic encounters between different male lizards (Oliveira and Hölldobler 1990). The probability of linearity with hierarchies was calculated according to Appleby (1983).

To determine if tail regeneration could change the social status of tailless male lizards, we staged paired encounters between all the possible pairs of males at the end of the postreproductive period. We used a neutral arena measuring 2 × 2 m and observed for 30 min between 1200 and 1400 hours. We calculated an unweighted sum of dominance patterns (aggressive display, charge and supplanting behavior) less subordinate patterns ("challenge wave" foreleg display and flight) for each lizard of each pair and defined the lizard with the highest positive sum as the dominant individual (Fox et al. 1981). When males were together and no dominant or subordinate behavior patterns were observed we considered it an unknown relationship.

We followed individual males during 15 min of undisturbed observation. Each male was followed on a regular schedule at least twice per week during the reproductive period ($\bar{x} \pm \mathrm{SE} = 7.3 \pm 1.0$ total number of observations/male) or once per week during the postreproductive period ($\bar{x} \pm \mathrm{SE} = 2.5 \pm 0.3$ total number of observations/male). We recorded on a pocket tape recorder the time spent in each circular habitat, and noted the number of different females found in the same circular habitat that the male during the observation period. Habitat diversity occupied was calculated from the proportion of time spent in each habitat by using Shannon's diversity index. An average for each male was used as a single datum in the statistical analysis. We analysed data using non-parametric tests described in Siegel (1956), and we considered an alpha of 0.05 in a two-tailed test to be significant.

Table 1. Dominance rank constructed from observations of 237 male *Lacerta monticola* interactions during the reproductive period

Dominant	Subordinate										Total
	A1	A2	A3	A4	A5	B6	B7	B8	B9	B10	
A1	–	21	17	9	15	6	5	3	5	13	94
A2		–	9	8	6	8	3	9	3	5	51
A3		2	–	5	6	3	4	4	9	3	36
A4		3	2	–	5	2	3	1	5	3	24
A5		1			–	1	1	2	3	4	12
B6			1		1	–	1	2	1		6
B7					1	1	–		3		5
B8					3			–		1	4
B9					1		1		–	1	3
B10		1			1					–	2
Total	0	28	29	22	39	21	18	21	29	30	

The numbers refer to agonistic interactions between males. Individuals are coded as follows: A, tailed; B, tailless; number = rank as determined by total number of agonistic "wins"

Table 2. Matrix of relationships between male *Lacerta monticola* at the end of the experiment based upon staged encounters

	A2	B8	A3	B6	A4	A5	B9	B10	B7	Total
A2	–	$^{1}/_{2}$	1	1	1	1	1	1	1	7.5
B8	$^{1}/_{2}$	–	$^{1}/_{2}$	1	1	1	1	1	1	7
A3	0	$^{1}/_{2}$	–	1	1	1	1	1	1	6.5
B6	0	0	0	–	1	1	$^{1}/_{2}$	1	1	4.5
A4	0	0	0	0	–	1	$^{1}/_{2}$	1	1	3.5
A5	0	0	0	0	0	–	1	1	1	3
B9	0	0	0	$^{1}/_{2}$	$^{1}/_{2}$	0	–	$^{1}/_{2}$	1	2.5
B10	0	0	0	0	0	0	$^{1}/_{2}$	–	1	1.5
B7	0	0	0	0	0	0	0	0	–	0

A score of 1 = row individual dominant to column individual; 0 = column individual dominant to row individual; $^{1}/_{2}$ = relationship unknown. Individual code as in Table 1; A, tailed, B, tailless

Results

Social interactions

We observed 237 agonistic encounters between males during the reproductive period (Table 1). Tailed males were dominant in 92.3% ($n = 108$) of interactions with tailless males. Males developed a linear dominance hierarchy ($d = 4.75$, $P < 0.0001$, $K = 0.88$), with each tailed male dominant over one to four tailed males, and over all the tailless males. Tailless males had limited agonistic interactions with each other ($n = 11$). Tailed males had more agonistic encounters with other tailed males ($\bar{x} \pm \mathrm{SE} = 42.4 \pm 6.3$, range = 27–62) than with tailless males ($\bar{x} \pm \mathrm{SE} = 23.4 \pm 3.3$, range = 14–32; Wilcoxon's signed ranks test: $Z = 1.93$, $P = 0.04$), and more than tailless males among themselves ($\bar{x} \pm \mathrm{SE} = 4.4 \pm 0.8$, range = 2–6; Mann-Whitney U-test: $U = 2.51$, $P = 0.01$).

The dominant male (A1) died at the end of the reproductive period, when mating had finished. During the postreproductive period we observed a small number of interactions in the enclosure ($n = 36$), but staged paired encounters showed a linear dominance hierarchy ($d = 2.25$, $P < 0.01$, $K = 0.89$) (Table 2) in which two males that were previously tailless increased their social status. These two males had the highest tail regeneration rates (48 and 55 mm of regenerated tail, vs. 7–10 mm in the others).

Copulations

During the reproductive period tailed males tended to move between more diverse rocky habitats (H': $\bar{x} \pm \mathrm{SE} = 0.56 \pm 0.07$) than tailless males ($\bar{x} \pm \mathrm{SE} = 0.37 \pm 0.11$; Mann-Whitney U-test; $U = 1.68$, $P = 0.09$). While during the postreproductive period the average diversity of

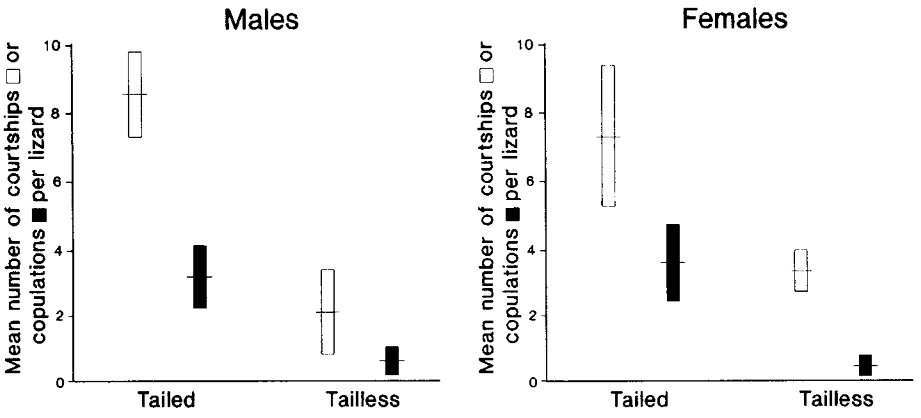

Fig. 1. A comparison of the number of courtships (*open boxes*) and copulations (*black boxes*) between tailed and tailless male and female lizards. Mean (*horizontal bar*) ± SE (*rectangle*)

rocky habitats visited was not significantly different (Mann-Whitney U-test; $U=0$, $P=1$) between tailed ($\bar{x} \pm \mathrm{SE}=0.23 \pm 0.11$) and tailless males ($\bar{x} \pm \mathrm{SE}=0.22 \pm 0.10$).

During the reproductive period the average number of females found in the rocky habitat occupied by one tailed male during an observation period ($\bar{x} \pm \mathrm{SE}=1.1 \pm 0.3$) was significantly higher (Mann-Whitney U-test; $U=2.00$, $P=0.04$) than the number found with tailless males ($\bar{x} \pm \mathrm{SE}=0.4 \pm 0.1$).

Tailed males had a higher number of courtships (Mann-Whitney U-test; $U=2.31$, $P=0.02$) and copulations (Mann-Whitney U-test; $U=2.02$, $P=0.04$) than tailless males (Fig. 1). Tailed males courted significantly more females than tailless males (tailed: $\bar{x} \pm \mathrm{SE}=5.6 \pm 0.7$; tailless: 1.8 ± 0.7; $U=2.33$, $P=0.019$), and showed a tendency to copulate with more females than tailless males (tailed: 2.2 ± 0.5; tailless: 1.0 ± 0.3; $U=1.78$, $P=0.07$). Tailed males copulated more often with tailed females (94.4% of copulations, $n=17$), whereas two of four copulations (50%) of tailless males were with tailless females. The number of copulations was correlated with the rank attained for an individual male (Spearman rank correlation, $r_s=0.73$, $P=0.03$).

Tailed females had no more courtships (Mann-Whitney U-test; $U=1.68$, $P=0.09$) but copulated more ($U=2.36$, $P=0.02$) than tailless females (Fig. 1). Each tailed female was courted by a similar number of males than each tailless female (tailed: $\bar{x} \pm \mathrm{SE}=4.0 \pm 0.8$; tailless: 3.2 ± 0.5; $U=0.33$, $P=0.74$). Each tailed female copulated with one to four males ($\bar{x} \pm \mathrm{SE}=2.4 \pm 0.5$), while three tailless females had no copulations, and the other two only copulated once each.

Body condition

There was no significant difference in initial body mass between tailed and tailless males before tail removal (Mann-Whitney U-test; $U=1.10$, $P=0.33$). Tailed males had a lower weight gain than tailless males during the 3 weeks of the reproductive period (Mann-Whitney U-tests; first week: $U=2.37$, $P=0.018$; second: $U=2.51$, $P=0.012$; third: $U=2.16$, $P=0.03$) (Fig. 2), but there were no differences in weight gain during the postreproductive period (Mann-Whitney U-tests; fourth week: $U=1.67$, $P=0.10$; fifth: $U=0.86$, $P=0.39$; sixth: $U=1.48$, $P=0.14$). The percent of weight gained or lost at the end of the reproductive period was negatively correlated with the number of times each male was observed to chase other males ($r_s=-0.65$, $P<0.05$), and with the total number of interactions ($r_s=-0.70$, $P<0.05$). Tail regeneration of tailless individuals was not observed during the reproductive period. At the end of the postreproductive period tails of males in the tailless treatment had grown between 9 and 55 mm ($\bar{x} \pm \mathrm{SE}=29.6 \pm 9.2$).

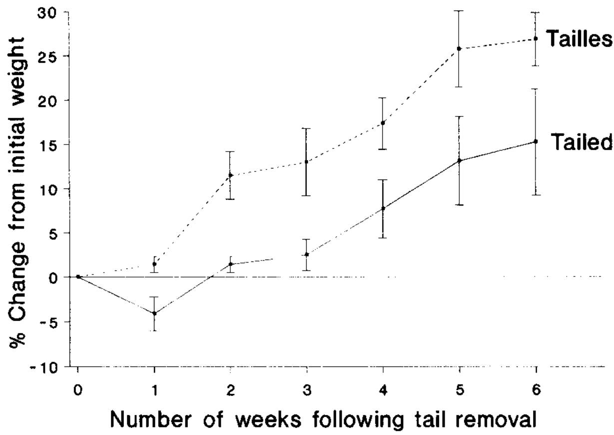

Fig. 2. A comparison of weight changes between males with and without tails over the 6-week experiment. Mean ± SE (*vertical bar*)

Discussion

Most of the literature on reproductive and spacing patterns refers to territorial iguanid lizards. Lacertid spacing patterns are poorly known, although male home-range defense seems to be rare (Stamps 1977, 1983). There are no available data on the spacing patterns and mating systems of *L. monticola* in the field (but see Pérez-Mellado et al. 1987, for the postreproductive period), but we have observed increased male activity and movements during the reproductive period (unpublished data). Also iguanid and teiid males maintain high activity levels during the entire breeding season, because repeated searches of home range establish an encounter rate of males with prospective mates (Rose 1981; McCloskey et al. 1987; Anderson and Karasov 1988).

Lizards that maintain territories in the field commonly develop hierarchies in captivity (Stamps 1977; Deslippe et al. 1990). This may be because of space limitation as hierarchies also form in the field at high population densities (Stamps 1984; Fleishman 1988). We observed a linear dominance hierarchy in the enclosure, although this may not occur in the field.

Tail possession gives dominant status to juvenile (Fox and Rostker 1982) and subadult lizards (Fox et al. 1990). Our results show that tail possession also gives dominant status to adult males and that dominant males courted and copulated more often. In a structurally complex habitat tailless males may, however, gain access to a female by stealth. Tailless subordinate males may be relegated to home ranges of lower overall quality, in which food and female availability would be lower (Fox et al. 1981). As a consequence, tailless males may grow more slowly (Ballinger and Tinkle 1979), and have lower reproductive success and lower survival than tailed males.

Our results suggest that increased weight of tailless males is related to decreased aggression. The energetic cost of increased territorial aggression is reflected in increased energy expenditure, decreased stored energy, and decreased allocation to growth (Congdon 1977; Rose 1981; Marler and Moore 1989). Tailless males seem to avoid agonistic encounters with other males, probably because these encounters are energetically costly (Pough and Andrews 1985). Aggressive males may also suffer lower survivorship which may result from increased predation due to greater conspicuousness (Marler and Moore 1988; Magnhagen 1991; but see Marler and Moore 1991).

Some males were promoted in the social hierarchy when a portion of the tail was regenerated. Artificial restoration of tail to subordinant tailless males of *Uta stansburiana* did not restore social status; however, this could be related to experimental manipulation (Fox et al. 1990). Lizards interact through the regeneration period and may progressively change their social status as the tail grows longer.

Female tail loss reduced the number of copulations. Females investing more energy in tail growth would suffer decreased reproductive output (Smyth 1974; Dial and Fitzpatrick 1984), thus the tail may be important in mate choice, perhaps as an indicator of resource-holding potential (Fox et al. 1990). Males may prefer to mate with tailed females, because copulations with tailless females would produce clutches lower in mass and energy content. Tailless females did, however, copulate as observed in the field, albeit less often than tailed females (unpublished data).

Tailed individuals may indicate to others (males and females) that they have the ability to escape from predators without using autotomy. In this way, the possession of an intact tail may be an "honest" signal of predator avoidance. A regenerated tail may indicate to other individuals a lower ability to escape, because it has been necessary to lose the tail. During courtship females may judge the escape ability of males by tail condition and use this information along with morphology, coloration and behavior in mate choice.

Lizards who lack tails are more vulnerable to predators (Congdon et al. 1974; Dial and Fitzpatrick 1984), and their ability to fight/chase others efficiently may also be lower if they lack a tail. If the risks of locomotion are higher for tailless lizards, then they would be expected to curtail any behavior involving locomotion. *Lacerta monticola* is a relatively long-lived species with short, seasonally restricted breeding, and with high probabilities of future reproduction. After losing their tails males may defer breeding effort, divert their energy to tail growth, and then invest the breeding effort in a subsequent season.

Acknowledgements. We thank Ross Johnston and three anonymous reviewers for comments, and Pilar López for field and logistic assistance. The "El Ventorrillo" Field Station of the Museo Nacional de Ciencias Naturales provided lodging and logistical support. Research was supported by "El Ventorrillo" Field Station to J. Martín.

References

Anderson RA, Karasov WH (1988) Energetics of the lizard *Cnemidophorus tigris* and life history consequences of food-acquisition mode. Ecol Monogr 58:79–110

Appleby MC (1983) The probability of linearity in hierarchies. Anim Behav 31:600–608

Arnold EN (1984) Evolutionary aspects of tail shedding in lizards and their relatives. J Nat Hist 18:127–169

Arnold EN (1988) Caudal autotomy as a defense. In: Gans C, Huey RB (eds) Biology of the Reptilia, vol 16. Alan R. Liss, New York, pp 235–273

Ballinger RE (1973) Experimental evidence of the tail as a balancing organ in the lizard *Anolis carolinensis*. Herpetologica 29:65–66

Ballinger RE, Tinkle DW (1979) On the cost of tail regeneration to body growth in lizards. J Herpetol 13:374–375

Ballinger RE, Nietfeldt JW, Krupa JJ (1979) An experimental analysis of the role of the tail in attaining high running speed in *Cnemidophorus sexlineatus* (Reptilia: Squamata: Lacertilia). Herpetologica 35:114–116

Bellairs A d'A, Bryant SV (1985) Autotomy and regeneration in reptiles. In: Gans C, Billet F (eds) Biology of the Reptilia, vol 15. John Wiley and Sons, New York, pp 301–410

Congdon JD (1977) Energetics of the montane lizard *Sceloporus jarrovi*: a measurement of reproductive effort. Dissertation. Arizona State University, Tempe, Arizona

Congdon JD, Vitt LJ, King WW (1974) Geckos: adaptive significance and energetics of tail autotomy. Science 184:1379–1380

Deslippe RJ, McCloskey RT, Dajczak SP, Szpak CP (1990) A quantitative study of the social behavior of tree lizards, *Urosaurus ornatus*. J Herpetol 24:337–341

Dewsbury DA (1982) Dominance rank, copulatory behavior, and differential reproduction. Q Rev Biol 57:135–159

Dial BE, Fitzpatrick LC (1981) The energetic costs of tail autotomy to reproduction in the lizard *Coleonyx brevis* (Sauria: Gekkonidae). Oecologia 51:310–317

Dial BE, Fitzpatrick LC (1984) Predator escape success in tailed versus tailless *Scincella lateralis* (Sauria: Scincidae). Anim Behav 32:301–302

Edmunds M (1974) Defense in animals: A survey of anti-predator defenses. Longman, New York

Fleishman LJ (1988) The social behavior of *Anolis auratus*, a grass anole from Panama. J Herpetol 22:13–23

Formanowicz DR, Brodie ED, Bradley PJ (1990) Behavioural compensation for tail loss in the ground skink, *Scincella lateralis*. Anim Behav 40:782–784

Fox SF, Rotsker MA (1982) Social cost of tail loss in *Uta stansburiana*. Science 218:692–693

Fox SF, Rose E, Myers R (1981) Dominance and the acquisition of superior home ranges in the lizard *Uta stansburiana*. Ecology 62:888–893

Fox SF, Heger NA, Delay LS (1990) Social cost of tail loss in *Uta stansburiana*: lizard tails as status-signalling badges. Anim Behav 39:549–554

Magnhagen C (1991) Predation risk as a cost of reproduction. Trends Ecol Evol 6:183–186

Marler CA, Moore MC (1988) Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. Behav Ecol Sociobiol 23:21–26

Marler CA, Moore MC (1989) Time and energy costs of aggression in testosterone-implanted free-living male mountain spiny lizards (*Sceloporus jarrovi*). Physiol Zool 62:1334–1350

Marler CA, Moore MC (1991) Supplementary feeding compensates for testosterone-induced costs of aggression in male mountain spiny lizards, *Sceloporus jarrovi*. Anim Behav 42:209–219

Martín J, Salvador A (1992) Tail loss consequences on habitat use by the Iberian rock-lizard, *Lacerta monticola*. Oikos 65:328–333

McCloskey RT, Baia KA, Russell RW (1987) Defense of mates: a territory departure rule for male tree lizards following sex-ratio manipulation. Oecologia 73:28–31

Oliveira PS, Hölldobler B (1990) Dominance orders in the pomarine ant *Pachycondyla apicalis* (Hymenoptera, Formicidae). Behav Ecol Sociobiol 27:385–393

Pérez-Mellado V, Gil MJ, Guerrero F, Pollo C, Rodríguez-Merino E, Marco A, Lizana M (1987) Uso del espacio y el tiempo en *Lacerta monticola* de la Sierra de Gredos. Graellsia 44:65–80

Pough FH, Andrews RM (1985) Use of anaerobic metabolism by free-ranging lizards. Physiol Zool 58:205–213

Punzo CM (1982) Tail autotomy and running speed in the lizards *Cophosaurus texanus* and *Uma notata*. J Herpetol 16:331–332

Rose B (1981) Factors affecting activity in *Sceloporus virgatus*. Ecology 62:706–716

Siegel S (1956) Nonparametric methods for the behavioral sciences. McGraw-Hill, New York

Smyth M (1974) Changes in the fat stores of the skinks *Mabuya boulengeri* and *Hemiergis peronii* (Lacertilia). Aust J Zool 22:135–145

Stamps JA (1977) Social behavior and spacing patterns in lizards. In: Gans C, Tinkle DW (eds) Biology of the Reptilia, vol 7. Academic Press, London, pp 265–334

Stamps JA (1983) Sexual Selection, Sexual Dimorphism and Territoriality. Huey RB, Pianka ER, Schoener TW (eds) Lizard ecology. Studies of a model organism. Harvard University Press, Cambridge, Massachusetts, pp 169–204

Stamps JA (1984) Rank-dependent compromises between growth and predator protection in lizard dominance hierarchies. Anim Behav 32:1101–1107