

The demography of the lizard *Tropidurus torquatus* (Squamata, Tropiduridae) in a highly seasonal Neotropical savanna

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Abstract

The demography of the lizard *Tropidurus torquatus* (Squamata, Tropiduridae) in a highly seasonal Neotropical savanna. The demography of a population of *Tropidurus torquatus* was studied from March 1996 until December 1998, in the Cerrado biome of central Brazil, using the method of capture and recapture. Population size, number of incoming individuals in the population, and age structure varied seasonally, reflecting the reproductive cycle of the species. The instantaneous rate of population increase did not differ from zero throughout the study. In general, the permanence rates of juveniles and adults were low, indicating a large turnover of individuals in the population, with a maximum life expectancy of three years. The sex-ratio among adults was biased toward females. Since no bias was observed among juveniles and there was no difference in adult permanence between sexes, we suggest that the biased adult sex-ratio resulted from a lower permanence of males during a short ontogenetic period, when secondary sexual characteristics develop. When compared to *T. itambere*, the studied population of *T. torquatus* attained a higher density and a greater female bias in the sex-ratio. In general, the studied population presented characteristics that, according to life history theory, should be associated with early age at maturity and polygyny: short life expectancy, high population turnover, and female biased sex-ratios.

Keywords: Squamata, Tropiduridae, *Tropidurus torquatus*, demography, population structure, sex-ratio, central Brazil.

Introduction

The number of studies on lizard ecology has increased greatly since 1960 (Huey *et al.* 1983), improving our knowledge on the evolution of life history characteristics, one of the most important tools for understanding the diversity

and complexity of life cycles (Stearns 1992). The life history of a species can be summarized by demographic parameters such as birth and death rates, migratory movements, and population structure throughout time, as they deal with the interaction between longevity, reproductive age, growth pattern, and age-specific mortality versus the environment (Zug 1993). Interactions among these parameters throughout life make the demography of

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populations subject to constant variation through time. The demography of lizard populations can be influenced by various factors, such as temperature (Adolph and Porter 1993, Parker 1994), precipitation (Andrews 1988, Bull 1994), food availability (Ballinger 1977, Howland 1992, Smith 1996), and morphological and phylogenetic constraints (Ballinger 1983).

Some patterns can be singled out relating the dynamics and structure of populations to life history characteristics (Tinkle 1969). Lizards with delayed sexual maturity tend to have longer life cycles, along with major energetic investments in maintenance instead of reproduction (Tinkle 1969, Tinkle *et al.* 1970), and lower adult mortality (Hasegawa 1990, Bull 1995). Lizards with early sexual maturity have shorter life cycles and higher mortality rates for young and adults (Ballinger and Congdon 1981, Andrews and Nichols 1990), resulting in a larger population turnover (Ferguson *et al.* 1980, Tinkle *et al.* 1993). This dichotomy represents the extremes of a gradient, but many intermediate combinations exist (Dunham *et al.* 1988). The population structure can also be influenced by the mating system. Populations with higher incidences of polygyny tend to have higher male death rates than populations where polygyny is reduced (Schoener and Schoener 1980, Stamps 1983), generating a female biased sex-ratio. Life history theory, however, was developed mainly from data of temperate lizard species (Ballinger 1983) but, in tropical regions, which harbor the largest lizard diversity, long-term studies of population dynamics are scarce (e.g., Rocha and Bergallo 1992, Van Sluys 1993b, Rocha 1998).

The genus *Tropidurus* ranges from tropical to temperate South America, east of the Andes (Frost 1992). The *torquatus* group consists of abundant diurnal species located in various types of open formations (Rodrigues 1987). The ecology and reproductive cycles of some species have already been studied, including *T. etheridgei* (Cruz 1997), *T. hispidus* (Vitt and Goldberg 1983, Vitt *et al.* 1996), *T. oreadicus*

(Rocha and Bergallo 1990), *T. itambere* (Van Sluys 1993a, b, Van Sluys *et al.* 1994), and *T. torquatus* (Bergallo and Rocha 1993, 1994, Giaretta 1996). However, demographic studies exist only for *T. itambere* (Van Sluys 2000).

Tropidurus torquatus Wied is a seasonal breeder, with reproduction occurring from August to January (Vieira *et al.* 2001, Wiederhecker *et al.* 2002). Sexual maturity is reached in less than six months, and males are territorial and polygynous (Pinto 1999). Therefore, according to life history theory (Ballinger 1983, Dunham *et al.* 1988) it is expected that this species has a life history characterized by a short life cycle and populations with large turnover, high seasonal variation in size, and biased sex-ratios. Herein we identify temporal patterns of variation in population size, age structure, and sex-ratio of *T. torquatus* in the Cerrado of central Brazil, and make comparisons with a congeneric species, to evaluate predictions of current life history theory.

Materials and Methods

We carried out the study in Brasília, Brazil (15°54'05"S, 047°56'18"W). The climate is Aw following Köppen's classification (Haffer 1987). It has a pronounced concentration of rain from October to April and annual mean temperature (21.2° C) is relatively constant year-round.

We studied a population of *T. torquatus* along a transect of 313 m with mean width of 10 m (3130 m²). This transect was isolated from any other area with a high density of the species. It was surrounded by a road on one side and by a gallery forest and a small lake, associated with the Santuário Ecológico do Riacho Fundo, on the other side. Another lizard, *Ameiva ameiva* (Teiidae), and several other potential predators were also recorded in the transect such as coati (*Nasua nasua*), brown capuchin (*Cebus apella*), guira cuckoo (*Guira guira*) and false coral snake (*Oxyrhopus trigeminus*).

We collected lizards weekly with a noose from March 1996 to December 1998, with the exception of September 1996, February 1997 and 1998, and July 1998. We measured, sexed, and marked all captured lizards and released them at the capture site. We measured snout-vent length (SVL) with a ruler to the nearest mm. We made two kinds of marks on each lizard: an individual and permanent mark with digit clipping, avoiding the use of more than one digit per limb, and a temporary mark, a small nail polish spot on the dorsum, at the base of the tail. We used a different color each week to avoid recaptures during the same week. We determined sex only for adult individuals (males: SVL > 70 mm; females: SVL > 65 mm) (Wiederhecker *et al.* 2002), using the ventral coloration typical of adult males (Pinto 1999).

Mark-recapture data were used to estimate monthly population size, permanence rates, and number of incoming individuals, including standard errors, using a model of the Jolly-Seber type implemented by the freeware POPAN 4 (Arnason *et al.* 1995). Jolly-Seber models are widely applied for population analysis and estimate population parameters based on the history of captures and recaptures of individuals from a population (details on Jolly 1965). We used a modified version of the Jolly-Seber full model, developed to estimate parameters of open populations (with births, deaths, and exchange of individuals with other populations), allowing for possible heterogeneity among individuals in the loss rate, implemented by POPAN 4 (Arnason *et al.* 1995). The model assumptions are the following: unequal probability of capture among individuals, no tag loss, and no temporary migration. Since we analyzed data from more than one cohort and mortality tends to be higher among juveniles than among adults, the model well suited our data when considering the heterogeneity of the loss rate (Arnason *et al.* 1995). The model cannot estimate population size in the first and last months, therefore they are equal to zero in the graphs but this is not a valid estimation.

We calculated the instantaneous rate of natural increase (r) for each month as: $r = \ln(N_{t+1}/N_t)$, where N_t is the population size at time t and N_{t+1} is the population size at time $t+1$ (Stearns 1992). To test if the r value for each year and for the whole study period differed from zero, we used the Student's t -test (Zar 1984). We estimated population age structure and recruitment period by the monthly distribution of SVL for captured lizards.

To analyze cohort data for 1996, 1997, and 1998, we used the Jolly-Seber model without incoming individuals (birth and immigration). The model assumptions are the following: absence of new individual entries, maintenance of individual marks, and absence of temporary migration. This simplified model option reduces the number of demographic parameters, increasing the precision of the estimated values (Arnason *et al.* 1995), being appropriate since reproduction of *T. torquatus* is seasonal and recruitment is restricted to a short period.

We compared permanence rates between males and females from the end of one reproductive season to the beginning of next with a Student's t -test (Zar 1984). The estimates were calculated for two population subsets: all adults and cohort from 1996. All lizards captured in one reproductive season and recaptured during or after the next reproductive event were considered as persistent. To compare permanence rate between juveniles and adults we estimated the rate for both groups from the recruitment period to the first month of each year in which no juveniles were registered, using the Student's t -test. We considered as adults individuals with a SVL equal to or greater than the minimum reproductive size.

To obtain the sex-ratio, we compared the population sizes of males and females considering all captured adults using a chi-square test (Zar 1984). We obtained additional data on the juvenile sex-ratio from dissected lizards collected from October 1997 to September 1998 in Brasilia and surroundings (Wiederhecker *et al.* 2002).

To conduct statistical analyses we used Systat v. 5.2 for Macintosh employing a significance level of 5% in all tests. Throughout the text we report means (\bar{x}) followed by \pm one standard deviation, while the estimated population parameters are followed by \pm one standard error.

Results

During the sample period we made 821 captures of 413 individuals: 74 males, 116 females, and 223 juveniles. About 60% of the individuals were captured only once, 65 % of which were juveniles. Population size varied from 18 to 257 individuals during the study period (Figure 1). In each year a population peak occurred from April to June, followed by a steady decline. The smallest population sizes occurred from December 1996 to February 1997, and from November 1997 to March 1998. Mean density was 406.0 ± 60.0 individuals/ha in 1996, 256.0 ± 39.2 individuals/ha in 1997, 276.8 ± 73.7 individuals/ha in 1998, and 307.4 ± 34.7 individuals/ha during the whole study period.

Variation in the number of incoming individuals in the population was associated with variation of population size (Figure 1). In all years, maximum values for entry rate occurred before population size peaks, with minimum values occurring in December. However, the permanence rate oscillated across months (Figure 1), with no evident pattern associated with population size. The instantaneous rate of natural increase of the population varied from -0.9 to 1.8 , with mean values for each year separately, and for the whole study, showing no significant difference from zero (Table 1). Population age structure varied seasonally (Figure 2). Adults were captured in all months, but recently hatched individuals, with $SVL < 40$ mm, occurred only from March to June. After November, most captured individuals were larger than 80 mm during the three years.

The variation in population size for the

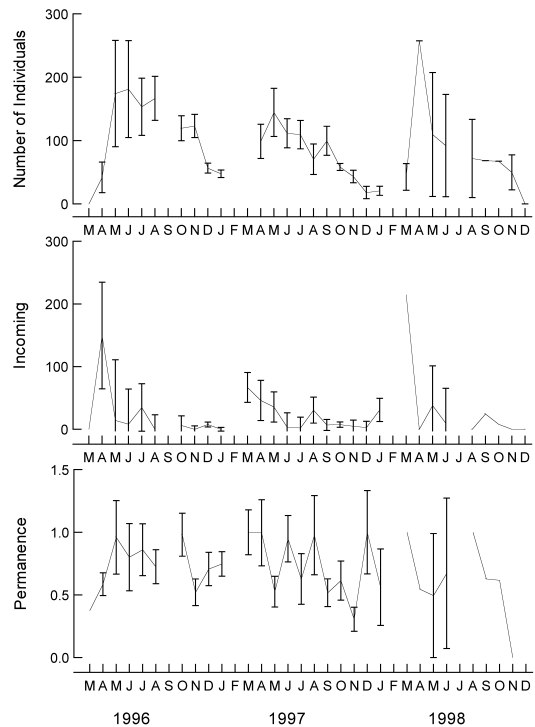


Figure 1 - Monthly distribution of estimates and standard errors of population size (top), rate number of incoming individuals (center), and permanence rate (bottom) of a population of *Tropidurus torquatus* from Brasília, Brazil, between March 1996 and December 1998.

cohorts of 1996, 1997, and 1998 presented similar patterns (Figure 3). The initial estimated size for the cohorts was 191 ± 77 in 1996, 207 ± 63 in 1997, and 146 ± 50 in 1998. A large portion of individuals disappeared from population before the first reproductive season in September (73% in 1996, 88% in 1997, and 90% in 1998), and few remained in the population during two or more years. In total, for 112 captured individuals from 1996 cohort, only two individuals, a female and a male, were recaptured in 1998. The longest life expectancy registered was three years, with no adults captured in 1996 being recaptured after the first

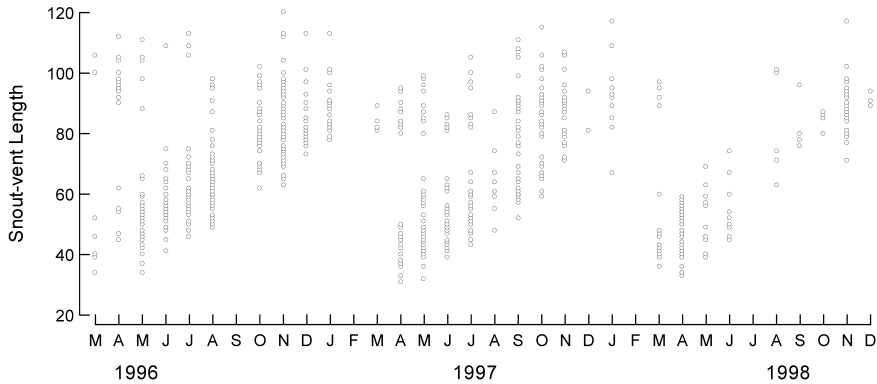


Figure 2 - Monthly distribution of snout-vent length of captured individuals of a population of *Tropidurus torquatus* from Brasília, Brazil, between March 1996 and December 1998.

half of 1998. Permanence rates for juveniles, from recruitment until adulthood, in 1996 and in 1998 were significantly lower than adult rates (Table 2). In 1997, however, there was no significant difference between permanence rates for juveniles and adults.

The sex-ratio, calculated from the total number of captured females (116) and males (74), differed statistically from 1:1 ($\chi^2 = 9.28$, $p = 0.002$), there being a bias toward females. Among the dissected juveniles, however, the sex-ratio was not significantly different from 1:1 (males: 21, females: 29; $\chi^2 = 1.28$, $p = 0.261$). There were no significant difference between permanence rates of adult females and males in all tested intervals (Tables 3 and 4).

Discussion

During the study period, the population size of *Tropidurus torquatus* varied markedly, but the seasonal pattern of abundance was similar among years. The absence of a cyclical pattern in the permanence rate, coupled with the association between population size and recruitment rate, suggest that the variation in population size is a consequence of the seasonal reproductive cycle of this species (Wiederhecker *et al.* 2002). Furthermore, the occurrence of

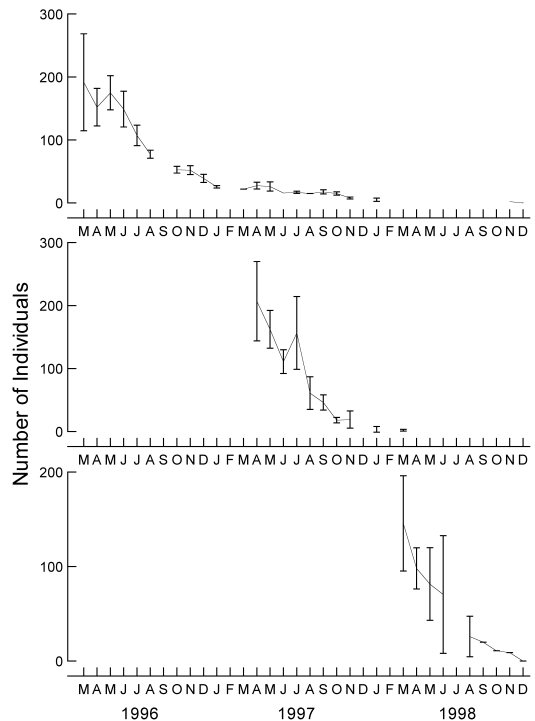


Figure 3 - Monthly distribution of estimates and standard errors of number of individuals in cohorts of 1996 (top), 1997 (center), and 1998 (bottom) of a population of *Tropidurus torquatus* from Brasília, Brazil, between March 1996 and December 1998.

Table 1 - Mean value of instantaneous rate of natural increase (r) and t -test results ($H_0: r = 0$) of a population of *Tropidurus torquatus* from Brasília, Brazil. SE, standard error.

Period	Mean r (SE)/N	t	p
March to December 1996	0.105 (0.295)/6	0.356	0.736
January to December 1997	-0.208 (0.135)/9	-1.549	0.160
January to December 1998	0.161 (0.235)/7	0.495	0.638
March 1996 to December 1998	-0.006 (0.139)/22	-0.040	0.968

Table 2 - Male and juvenile estimates of permanence rates and t -test results (H_0 : juvenile permanence = adult permanence) of a population of *Tropidurus torquatus* from Brasília, Brazil. n, initial number of individuals.

Period	Juveniles rate (n)	Adults rate (n)	t (p)
May to November 1996	0.392 (52.1)	1.000 (24.0)	5.272 (<0.01)
May to November 1997	0.178 (107.0)	0.271 (38.9)	0.943 (0.35)
May to November 1998	0.170 (53.0)	0.563 (10.7)	2.364 (0.02)

Table 3 - Male and female permanence rates from January to November and t -tests (H_0 : male permanence rate = female permanence rate) of a population of *Tropidurus torquatus* from Brasília, Brazil. n, initial number of individuals.

Year	Males rate (n)	Females rate (n)	t (p)
1996	0.217 (22.7)	0.096 (51.6)	1.042 (0.30)
1997	0.111 (19.8)	0.158 (18.3)	-0.050 (0.96)

Table 4 - Male and female permanence rates of the 1996 cohort and t -tests (H_0 : male permanence rate = female permanence rate) of a population of *Tropidurus torquatus* from Brasília, Brazil. n, initial number of individuals.

Period	Males rate (n)	Females rate (n)	t (p)
1996 to 1997	0.3333 (15)	0.5568 (37)	1.15 (0.25)
1997 to 1998	0.6000 (5)	0.1053 (19)	1.80 (0.07)
1996 to 1998	0.2000 (15)	0.0541 (37)	1.10 (0.27)

population peaks and high numbers of incoming individuals in the population during periods with high incidence of hatchlings indicate that the population increase results principally from recruitment. Therefore, births are probably more important than immigration for the increase in population size of *T. torquatus*. A relationship between recruitment and population peaks also occurs in *T. itambere* (Van Sluys 2000) and in various lizard species with seasonal reproductive patterns, such as *Liolaemus darwini* (Viana *et al.* 1994), *Mabuya buettneri* (Barbault 1976), and *Anolis gingivinus* and *A. pogus* (Roughgarden 1995).

Age structure of the population also varied seasonally. During the recruitment period, from March to June, there was a predominance of juveniles that were not recorded from November onward. These results are a consequence of the seasonal reproduction (Wiederhecker *et al.* 2002) and early age of maturity, estimated at five months for this species (Pinto 1999). The estimated initial cohort size is much larger than population size before recruitment in all three years. Therefore, the importance of juvenile recruitment for population size is basically due to the low permanence rates and the population annual reproductive success, as in *Anolis limifrons* (Andrews 1988). The predominance of juveniles, at least in part of the year, is typical of species with short life cycles (Barbault 1976, Ortega and Arriaga 1990, Howland 1992) resulting in a high annual turnover of individuals in the population.

Despite its marked monthly fluctuation, the instantaneous rate of natural increase did not differ from zero during the study period. A compilation of data from 29 species suggests that lizards maintain relatively constant population sizes when compared to other vertebrates (Schoener 1985). However, this statement is weakened because the author considered only species from temperate regions and islands and also species with longer life expectancies, resulting in a biased sample when considering lizards in general (Andrews 1988).

Lizard populations with short life cycles and high annual turnover of individuals should be more susceptible to large variations in population size among years (Andrews and Wright 1994, Bull 1994), directly reflecting the recruitment success during the reproductive period (Andrews 1988). A stable population size was also found in *Tropidurus itambere* (Van Sluys 2000) and *Liolaemus lutzae* (Rocha 1998), demonstrating that even species with short life cycles can maintain constant population sizes. The stability in these cases suggests that environmental fluctuations were not sufficient to affect drastically recruitment, maintaining population size.

Juveniles had a lower permanence rate than adults in 1996 and 1998. A lower juvenile permanence is common among lizards, tending to be higher for long-lived species (Hasegawa 1990). Disappearance of juveniles occurs mostly due to more potential predators of small organisms (Bull 1995) and the permanent emigration of individuals that reach sexual maturity (Stamps 1993, Parker 1994). In 1997, the adult permanence rate was lower in relation to other years and there was no significant difference between juvenile and adult permanence rates. This reveals that the relationship between permanence and age can vary through time. However, this variation did not affect the instantaneous rate of natural increase. The simultaneous occurrence of population size stability and permanence rate variation suggests the existence of density-dependent compensatory mechanisms (Sinclair and Pech 1996). For instance, in 1998, the population size was smaller in the months that preceded recruitment and the number of incoming individuals was larger in relation to 1996 and 1997, indicating that the lower density of adults favors the establishment of juveniles, as observed in *Sceloporus graciosus* (Tinkle *et al.* 1993).

In general, juvenile and adult permanence rates were low, indicating a large turnover of individuals in the population. Despite the

maximum life expectancy estimation of about three years, most individuals did not survive more than a year. These characteristics are expected in species with short life cycles, indicating a low investment in maintenance and a high cost of reproduction (Tinkle 1969, Tinkle *et al.* 1970).

Considering the total number of captured individuals, the sex-ratio differed from 1:1. A female biased sex-ratio is common in polygynous species (Parker and Pianka 1975, Ballinger and Congdon 1981, Rose 1981) and can result from inter-sexual differences in the permanence rate and/or in the birth rate. In *T. torquatus*, the sex determination mechanism is of the XY:XX type, being genetically fixed (Kasahara *et al.* 1996). The expected sex-ratio at birth in species with this sort of mechanism is 1:1 (Smith 1989), in agreement with the sex-ratio found for juveniles, indicating that the asymmetry is caused by differences in the adult permanence rates. However, the adult permanence rate was not significantly larger for females, neither considering all individuals in the population nor only individuals of the 1996 cohort. This suggests that the sex-ratio deviation is a consequence of the lower permanence of males during a very short period, probably at the onset of secondary sexual characters. During this period, young males that reach sexual maturity would be susceptible to aggression by larger males, therefore being expelled to peripheral areas and unfavorable habitats (Stamps 1983).

With the exception of a few months during the reproductive period the sex-ratio in *Tropidurus itambere* did not deviate from 1:1 (Van Sluys 2000). In various lizard species the sex-ratio is related to the degree of polygyny (Schoener and Schoener 1980), being susceptible to variations on a temporal scale (Pianka 1970, Schoener and Schoener 1980) and also being directly correlated with the degree of sexual dimorphism (Stamps 1983). Considering the ratio between male and female size at maturity (male size / female size) as an indicator

of sexual dimorphism (Stamps 1983), *T. torquatus* presents a slightly larger dimorphism than *T. itambere* ($70.0 / 65.0 \text{ mm} = 1.08$ and $57.3 / 56.1 \text{ mm} = 1.02$, respectively). If sexual dimorphism in these species is due to sexual selection, it is expected that *T. torquatus* has a larger degree of polygyny.


The development of polygyny depends on the temporal availability of receptive females and tends to be greater when the reproductive period is long, allowing dominant males to monopolize receptive females (Emlen and Oring 1977). However, females of *T. itambere* and *T. torquatus* have vitellogenic follicles for a similar amount of time (5 months). Therefore, there is no difference on the time availability of receptive females between the two species. Another factor that influences the degree of polygyny is population density. The overlap in home ranges of insectivore female lizards permits their agglomeration in favorable habitats, facilitating their monopoly by dominant males (Emlen and Oring 1977, Stamps 1983). In this manner, the larger the population density, the larger the number of females in relation to males, therefore, the higher the degree of polygyny (Schoener and Schoener 1980). For *T. itambere*, the mean density of individuals per hectare (52.3) (Van Sluys 2000) was lower in relation to *T. torquatus* (307.4), suggesting that differences between the two species can result from higher competition among males in the denser population, generating a female biased sex-ratio.

Another factor that may contribute to a proportional higher number of females in the population of *T. torquatus* is the greater size difference between established males (territory owners) and males at the onset of sexual maturity. The relation between asymptotic size and minimum reproductive size in males of the two species is 1.80 ($126.0 / 70.0 \text{ mm}$) in *T. torquatus* and 1.68 ($96.0 / 57.3 \text{ mm}$) in *T. itambere*. The higher value for *T. torquatus* suggests that males of this species that have just entered adulthood should possess a lower

potential to displace older adults that already own territories.

Differences observed between *T. itambere* and *T. torquatus* can have origin either in proximate or genetic factors and the determination of prevalence for each one depends on long term studies and also on comparative studies involving populations from other localities, including those where the two species are sympatric. The studied population of *T. torquatus* had a short life expectancy, high recruitment rates, high juvenile mortality, high population turnover, and a female-biased sex-ratio. Overall, the observed data and the expectations of current life history theory for an early maturing and territorial species (Ballinger 1983, Dunham *et al.* 1988) are in agreement.

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