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Sex and size affect annual survival in a threatened sand lizard

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The sand-dune lizard *Liolaemus multimaculatus* is a threatened species endemic to the coastal ecosystems of Argentina. We assessed annual survival in one of largest known populations, using a mark recapture approach to estimate survival rates between 2006 and 2008. We found effects of size class, sex and year on survival rates. Average survival was 0.474 in adult males, 0.672 in adult females, 0.415 in juvenile males and 0.470 in juvenile females. The observed differences could be related to higher predation of juvenile and male lizards.

Key words: annual survival, ecology, sand-dune lizard, sex, size

Knowledge about annual survival of wild animals is of key importance in ecological studies (Reed et al., 2003). Together with reproductive patterns and growth rates, survival is a main feature of individual life histories (Stearns, 1992). Such population parameters are also of importance to model the demography and, consequently, to assess the conservation status of threatened species (Mills & Lindberg, 2002). However, due to difficulties to obtain demographic information (Pike et al., 2008), studies on annual survival are scarce in neotropical vertebrates (Galindo-Leal, 2000).

Among reptiles, annual survival widely varies between 10% and 97% (see Wright et al., 1984; Wilson, 1991; Sven-Ake, 2005; Bock et al., 2010). Annual survival can also vary between sexes and ages of conspecific individuals (Schoener & Schoener, 1982; Sven-Ake, 2005). For this reason, studies of survival must account for the existence of different classes of individuals.

The sand-dune lizard *Liolaemus multimaculatus* is a sand-dwelling, oviparous lizard endemic to the Pampean

coasts of Buenos Aires and Río Negro Provinces of Argentina (Ceí, 1993). It is a microhabitat specialist (Kacoliris et al., 2009a) with a generalist diet (Vega, 1999). Sexual size dimorphism (Ceí, 1993), *sit-and-wait* foraging behaviour (Vega, 1999) and the possible larger home range of males with respect to females (Kacoliris et al., 2009b) suggest the existence of male territoriality. The low population size (Kacoliris et al., 2009c) and high anthropogenic pressure affecting its habitat are the main arguments to catalogue the sand-dune lizard as a vulnerable species (Avila et al., 2000). Although there are numerous ecological studies, its annual survival rates, a key parameter to understand population dynamics and viability of this species, remains unknown.

Our goal was to estimate the annual survival of one of largest populations of *L. multimaculatus* inhabiting a protected dune area in Argentina. We tested the following hypotheses: i) Selection pressures are different for adult and juvenile lizards: we predict that annual survival will be lower in juveniles than in adults, assuming that predation will be higher at this stage. ii) Selection pressures on adult lizards are different for males and females: we predict that survival will be higher in adult females, assuming that territorial behaviour increases the exposure of males to predators.

We worked at Mar Chiquita Reserve, Buenos Aires, Argentina (30 km², 37°37'S, 57°16'W). This natural reserve represents one of the largest and least altered dunes area of the coast of Argentina (Bilenca & Miñarro, 2004). Coastal dunes in Argentina are considered a particular type of Pampa grassland (Cabrera, 1941). For a detailed description of vegetation communities at the study site see Kacoliris et al. (2009a).

We performed surveys during January and February of three consecutive years (2006 to 2008). We searched for lizards on a daily basis, with a team of 5 people (on average), on an 80 ha area over a period of four to five weeks. We worked from 1000 to 1600 hours, coinciding with the main daily activity pattern (Vega et al., 2000). We individually marked lizards using toe-clipping, and released lizards at the capture site. For each captured individual we recorded snout-vent length (SVL, dial calipers, accuracy: 0.2 mm) and gender (male or female). We compared observed SVL with reported SVL for the species (Vega, 1999), and classified captured individuals into adults (>48 mm) and juveniles (<48 mm). We used ventral colouration (Ceí, 1993) to distinguish males (spotted) from females (not spotted).

We used a multistate robust design approach to estimate annual survival rates (ϕ) in the program MARK. The multistate model allows inclusion of covariates that

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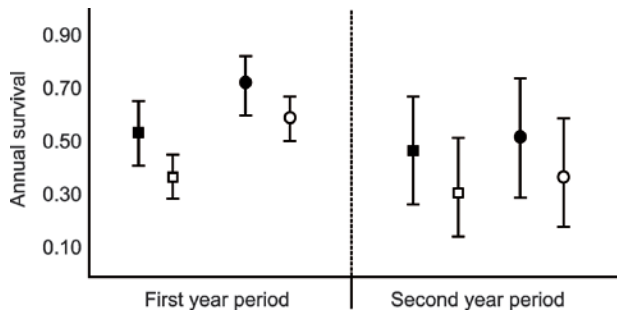


Fig. 1. Average and 95% confidence intervals for survival estimations in sand-dune lizards. Squares: males; circles: females; black: adults; white: juveniles.

vary through time (i.e. size class, White & Burnham, 1999). We built encounter histories of three primary sampling periods of one year each (2006, 2007 and 2008) and secondary sampling periods of 28, 35 and 28 days, respectively. We included two groups (males and females) and two states (adults and juveniles).

We performed models for survival rate by combining group, state, and time (years). For all models, we assumed a recapture probability (p) only varying through years, and an abundance (N) constant over time, groups and states. The probability of moves between states (ψ) was set as constant from juvenile to adult state, and as null from adult to juvenile state. We selected the best models based on Akaike's Information Criterion (AIC), by considering ΔAIC and AIC weights following recommendations of Burnham & Anderson (2002). We also follow these authors to consider the relative support of each model in the set, for survival estimates, by using the weighted averages method.

Between 2006 and 2008 we captured and released 601 lizards: 219 adult males, 279 adult females and 103 juveniles (38 males and 47 females). The best survival model included size class, sex, year and an interaction between size class and sex (Table 1). The four most

parsimonious models showed size class, sex and year affecting survival. The sum of their respective normalized AIC weights was 0.896, indicating 90% support in the data for models that include these three covariates.

Averaged estimated annual survival \pm standard error for both year periods were 0.474 ± 0.049 in adult males, 0.672 ± 0.042 in adult females, 0.415 ± 0.080 in juvenile males and 0.470 ± 0.081 in juvenile females. Annual survival was lower in the second year period (Fig. 1).

Our work provides the first annual survival rates for a sand-dune lizard population, and is one of few studies providing survival information for a *Liolaemus* species. We found that females have a higher annual survival rate than males, and that adults have a higher annual survival rate than juveniles.

Information about survival is scarce for most *Liolaemus* species. Estimates of survival in the Brazilian sand lizards (*L. lutzae*) showed high differences between years and seasons differing from sand-dune lizards which could be related to geographical and temporal habitat variation (Rocha, 1998; Bello-Soares, 2010). Lizards in arid areas, characterized by temporal fluctuations in rainfall and consequently food resources, show temporal variation in population parameters (Martin, 1973; 1977; Dunham, 1978; Andrews & Nichols, 1990), which could also be the reason for the annual survival differences in sand-dune lizard.

Survival rates were higher for females than for males. This pattern was previously observed in European sand lizards (*Lacerta agilis*; Sven-Ake, 2005), although other species such as *L. lutzae* and *Uta stansburiana* showed similar survival values between sexes (Wilson, 1991; Bello-Soares, 2010).

Sometimes low survival rates are linked to high predation pressure (Tinkle, 1969; Pianka, 1970). In our study area, several species could be considered as predators on sand-dune lizards: raptors (*Caracara plancus* and *Milvago chimango*), gulls (*Larus dominicanus*,

Table 1. List of the 12 models analyzed. Note in parenthesis defines each model in terms of the effect of three variables: size class (age), sex and year on annual survival rate (ϕ). The sign (+) indicates summed effect, but not interaction, of variables; the sign (*) indicates sum and interaction between variables; and a dot (.) indicate constant model (no covariables). AIC_c =Akaike's Information Criterion; Num. Par.=number of parameters of the model; $-2\log(L)$ = $-2\log$ likelihood or model deviance.

Model	ΔAIC_c	AIC_c Weights	Num. Par.	$-2\log(L)$
$\phi(\text{age}*\text{sex}+\text{year})$	0.000	0.555	10	-649.562
$\phi(\text{age}+\text{sex}+\text{year})$	2.128	0.192	9	-645.407
$\phi(\text{sex}*\text{year}+\text{age})$	3.922	0.078	10	-645.640
$\phi(\text{age}*\text{year}+\text{sex})$	4.124	0.071	10	-645.438
$\phi(\text{sex}+\text{year})$	4.662	0.054	8	-640.849
$\phi(\text{age}*\text{sex})$	5.368	0.038	9	-642.167
$\phi(\text{age}+\text{sex})$	8.384	0.008	8	-637.128
$\phi(\text{sex})$	10.220	0.003	7	-633.271
$\phi(\text{age}+\text{year})$	14.854	0.000	8	-630.657
$\phi(\text{year})$	17.730	0.000	7	-625.761
$\phi(\text{age})$	19.229	0.000	7	-624.262
$\phi(.)$	21.495	0.000	6	-619.977

Chroicocephalus maculipennis), foxes (*Pseudalopex gymnocercus*), wild cats (*Oncifelis geoffroyi*) and snakes (*Philodryas patagoniensis* and *Clelia rustica*). As shown for other lizard species (Tinkle & Ballinger, 1972; Parker & Pianka, 1973; Iverson et al., 2006), the low survival values observed in male sand-dune lizards could be caused by high exposure to predation during territorial defence. Although female reproductive traits can also increase exposure to predators (Bock et al., 2010), the cost of egg production for female sand-dune lizards seems lower than the cost of territorial displays in males.

We also found differences between adult and juvenile survival. A recent study on 20 lizard species (Pike et al., 2008) showed that survival rates of juveniles are only slightly lower than those of adult conspecifics. Our results confirm a small difference in annual survival between juveniles and adults. Low survival of juvenile lizards can be a consequence of higher predation rates on small individuals (Turner, 1977; Bradshaw, 1986; Bull, 1987). In our case, a high predation rate of juveniles could be linked to poor escaping abilities compared with adults. The main escape behaviour in sand-dune lizard, to bury into the sand, is used less frequently by small individuals (Kacolis, unpublished data), which could decrease their survival rate.

The sand-dune lizard is a threatened species inhabiting dune habitat relicts. Our results contribute to understanding the causes of annual variation in survival, information which allows for a more accurate evaluation of population viability.

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