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Effect of toe-clipping on the survival of several lizard species

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Toe-clipping is an extensively used technique for individual identification of amphibians and reptiles. However, this method might result in negative effects including reduced survival. In this study, we used capture-mark-recapture data obtained from ten different lizard species, including more than one population for two species, to examine whether survival rates varied as a function of the number of toes that were clipped. We used likelihood methods and multi-state models to estimate survival probabilities. Specifically, we tested if the number of clipped toes had an effect on annual survival, comparing survival among groups of individuals that shared the same number of toes that were clipped. We found clear reductions in survival associated with the removal of several toes in seven study sites that correspond to five different species. These represent 37% of all the species and populations that we examined. Therefore, we conclude that this marking method potentially causes severe damage and may lead to biased parameter estimates in ecological studies of lizard species. Whenever possible, toe-clipping should be avoided and replaced by less invasive methods for individual identification.

Key words: Dactyloidae, marking methods, Phrynosomatidae, survival, toe-clipping, Xenosauridae.

INTRODUCTION

Many ecological studies of animals have used different marking techniques to identify individuals over long periods of time (Rodda et al., 1988; Hudson, 1996; Boone & Larue, 1999; Ferner, 2007). One of the main assumptions of all these marking techniques is that the survival probability of the marked animals must not be affected by the marking method (Ricker, 1956). However, few studies have formally tested this assumption (e.g., Parris & McCarthy, 2001; McCarthy & Parris, 2004; Waddle et al., 2008).

Toe-clipping is one of the most widely used methods to mark small-sized vertebrates like rodents (Melchior & Iwen, 1965; Kumar, 1979), amphibians, and reptiles (Perry et al., 2011). Nevertheless, the potential effects of removing toes have only been evaluated in a relatively small number of species (Ott & Scott, 1999; Paulissen & Meyer, 2000; Borges-Landáez & Shine, 2003; Bell & Pledger, 2005). The results of these evaluations are contrasting. Some studies have found no negative effects of toe-clipping (Lüddecke & Amézquita, 1999; Paulissen & Meyer, 2000; Kinkead et al., 2006; Jones & Bell, 2007), whereas other studies have demonstrated negative effects such as swelling, infections, necrosis, and changes in behaviour (Golay & Durrer, 1994; Hudson, 1996; Lemckert, 1996; Schmidt & Schwarzkopf, 2010). All these negative consequences may ultimately result in decreased survival probabilities (Waddle et al., 2008). Obviously, estimates of survival rates and other demographic parameters that are obtained from animals whose toes have been removed may be biased and misleading if the marking method itself causes lower survival.

In this study we gathered capture-mark-recapture data on ten lizard species to test the effect of clipping several toes on survival probabilities. All the capture-mark-recapture data that we gathered were obtained from previous or ongoing ecological studies on these species (Table 1). In all these studies, toe-clipping was implemented as the only marking method and thus we could not compare survival rates of lizards whose toes were clipped against survival of

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lizards marked by a different method. However, we were able to test whether clipping more toes, say four or five, resulted in lower survival compared to clipping only one or two toes. Specifically, we predicted a decrease in survival as a function of the number of toes that were clipped, with lowest survival in those lizards with more clipped toes. This study is a quantitative evaluation of a widely used and controversial marking method that at present represents a legitimate concern for both the scientific community and institutions that oversee the ethical use of animals in scientific research (May, 2004; Parris et al., 2010; Perry et al., 2011).

MATERIALS AND METHODS

Study species and number of clipped toes

We gathered capture-mark-recapture data on ten species of lizards that represent three families: Dactyloidae (*Anolis mariarum*, *A. nebulosus*), Phrynosomatidae (*Sceloporus anahuacus*, *S. graciosus*, *S. mucronatus*, *S. grammicus*, *S. variabilis*), and Xenosauridae (*Xenosaurus grandis*, *X. platyceps*, *X. mendozai*). For most species, data were only available for a single population. However, for one species (*S. grammicus*) we obtained data from nine different populations, and for another species (*X. platyceps*) we obtained data from two different populations. In all of the species, individual lizards were marked by toe-clipping, but different marking schemes were implemented for each species. For instance, some studies used the system proposed by Tinkle (1967), whereas other studies used the system proposed by Medica et al. (1971). In all cases, the different combinations of particular toes that were removed resulted in unique marking of each individual lizard. However, different marking schemes resulted in differences among study species in the number of toes that were clipped (Table 1). In addition, the total duration of the study, the particular years when the study was conducted, total sample sizes, and the time intervals that separated consecutive capture occasions also varied among study species (Table 1).

To test whether the number of clipped toes had an effect on survival, we compared survival of groups of individuals that shared the same number of toes that were clipped (as per Waddle et al., 2008). In other words, for each species we grouped individuals according to the number of toes that were removed: lizards with only one clipped toe, lizards with two clipped toes, lizards with three clipped toes, and so on. Table 1 shows the particular groupings that we used for each species.

Estimating survival, recapture, and transition rates

We used maximum likelihood methods implemented in the computer program MARK to estimate survival rates (Lebreton et al., 1992; White and Burnham, 1999). Based on the capture-mark-recapture data and using a multistate framework (Brownie et al., 1993), MARK estimates rates of survival (ϕ), recapture rates of surviving individuals (*p*), and transition rates between stages (ψ). Recapture rates are estimated because accurate estimates of survival depend on accurate measures of the probability of detection (Lebreton et al., 1992). Individuals were classified as either juveniles (J) or adults (A). Thus, transition rates (ψ) represent the probability of juveniles growing to the adult stage. We estimated ϕ for each category of removed toes in an attempt to examine whether juvenile and adult survival varied as a function of the number of toes that were clipped. We separately estimated juvenile and adult survival because the effects of clipping several toes might be stage-dependent, with younger individuals being more affected by toe removal (Byron, 1992; Pike et al., 2008).

Model set and model selection

We built *a priori* models that represented different hypotheses about variation in ϕ, *p*, and ψ. Then, we calculated the strength of evidence for each competing model in our data sets. Regarding ϕ, seven types of models were constructed. (1) Survival unaffected by stage, time, or number of clipped toes (“constant” model). (2) Survival varying between stage classes (juveniles or adults; “stage” model, S). (3) Survival varying among sampling occasions (“time” model, T). (4) Survival decreasing as a linear function of the number of toes that were clipped (“toe-clipping” model, TC). In this model we constrained survival estimates to follow a negative trend, from highest survival in individuals with fewest clipped toes to lowest survival in individuals with the largest number of clipped toes. (5) Survival affected by the interaction between stage and time (S × T). (6) Survival affected by the interaction between stage and number of clipped toes (TC × S). This model represents the possibility that the decrease in survival as a function of the number of clipped toes differs between juveniles and adults, potentially being more drastic in juveniles. (7) Survival affected by the interaction between time and number of clipped toes (TC × T). This model represents the possibility that the decrease in survival as a function of the number of clipped toes changes throughout time (for example, being more drastic in the last months of the study compared to early in the study).

Regarding *p*, two types of models were constructed. (1) Recapture probability remaining constant across sampling occasions (“constant” model). (2) Recapture probability varying among sampling occasions (“time” model, T). In all models, we kept the transition rate between juveniles and adults (ψ) invariant across sampling occasions (“constant” model). The combinations of these types of models for ϕ, *p*, and ψ resulted in a total of 14 models that we fitted to our capture-mark-recapture data sets. Given that the number of capture occasions and the time intervals that separated consecutive capture occasions differed among species and populations, the candidate models were fitted separately for each species and population.

Model selection was based on the Akaike’s Information Criterion (AIC), which is a measure of model likelihood and parsimony (Akaike, 1973). In particular, we used an adjusted version of the AIC for small sample sizes (AIC_c, Burnham & Anderson, 2002; Anderson, 2008). The lowest AIC_c score indicated the best-fitting model. However, models with a difference in their AIC_c scores (ΔAIC_c) smaller than two units were considered as having similar fit to the data. We also calculated model-specific Akaike weights (w_i), which measure the relative support or weight of evidence for

Table 1. Studied species and populations and description of each particular data set. The different categories of removed toes into which we structured each data set are also shown. *n* = total number of marked lizards.

Species	Country	Duration of the study (years)	Years of the study	*n*	Number of capture occasions	Mean interval between capture occasions (days)	Maximum number of clipped toes	Categories of clipped toes	References
Anolis mariarum	Colombia	1	2008-2009	103	6	30	4	2, 3, 4 toes	Rubio-Rocha et al., 2011
Anolis nebulosus	Mexico	2	2010-2012	353	8	90	5	1 toe 2, 3, 4, 5 toes	Siliceo-Cantero, 2015
Xenosaurus grandis	Mexico	4	2000-2004	568	51	32	6	1 toe 2, 3 4, 5, 6 toes	Zúñiga-Vega et al., 2007
Xenosaurus mendozai	Mexico	3	2001-2004	145	25	50	5	1 toe 2, 3, 4, 5 toes	Zamora-Abrego et al., 2010
Xenosaurus platyceps	Mexico								Rojas-González et al., 2008
Site 1		3	2000-2003	260	26	52	5	1 toe 2, 3, 4, 5 toes	
Site 2		4	2000-2004	587	30	46	5	1 toe 2, 3 4, 5, 6 toes	
Sceloporus anahuacus	Mexico	2	2007-2009	598	13	30	6	1 toe 2, 3 4, 5, 6 toes	Maceda-Cruz, unpubl.
Sceloporus graciosus	U.S.A.	9	1976-1985	428	11	428	3	2 toes 3 toes	Cuellar, 1993
Sceloporus mucronatus	Mexico	1	2003-2004	273	15	30	5	2, 3, 4, 5 toes	Ortega-León et al., 2007
Sceloporus variabilis	Mexico	1	2003-2004	214	16	30	5	1 toe 2, 3, 4, 5 toes	Serna-Lagunes, 2005
Sceloporus grammicus	Mexico								Pérez-Mendoza et al., 2013
Site 1		2	2009-2011	98	11	78	4	1 toe 2, 3, 4 toes	
Site 2		2	2009-2011	272	12	65	5	1 toe 2, 3, 4, 5 toes	
Site 3		3	2009-2012	265	17	67	5	1 toe 2, 3, 4, 5 toes	
Site 4		2	2009-2011	168	12	69	5	1 toe 2, 3, 4, 5 toes	
Site 5		2	2009-2012	347	16	70	6	1 toe 2, 3 4, 5, 6 toes	
Site 6		2	2009-2011	233	12	64	5	1 toe 2, 3, 4, 5 toes	
Site 7		2	2009-2011	95	12	64	5	1 toe 2, 3, 4, 5 toes	
Site 8		2	2009-2011	145	13	70	5	1 toe 2, 3, 4, 5 toes	
Site 9		6	1991-1997	585	13	180	5	2, 3, 4, 5 toes	Zúñiga-Vega et al., 2008

each model in the data (Amstrup et al., 2005). Based on these Akaike weights, we calculated weighted averages for survival, recapture, and transition rates across all models as per Burnham & Anderson (2002). These model-averaged estimates of ϕ, *p*, and ψ incorporate the uncertainty inherent in the process of model selection and, thus, are more robust than those derived from any single model alone (Johnson & Omland, 2004). All estimates are given on an annual basis to facilitate biological interpretation.

RESULTS

In *A. nebulosus*, *X. grandis*, two populations of *X. platyceps*, *S. variabilis*, and four populations of *S. grammicus* (sites 1, 5, 6, and 8), at least one of the models with strong support hence, had greater relative support than the model where survival decreased as a linear function of the number of clipped toes (Table 2).

In all other species and in all other populations of *S. grammicus*, the best-fitting model (with respect to survival) was either the constant model (.), the stage model (S), or the time model (T). Models including an effect of the number of clipped toes on survival had weaker support ($\Delta AIC_c > 2$; Table 2). In other words, annual survival was apparently unaffected by increasing the number of clipped toes in these species and populations.

According to model-averaged estimates, the decrease in survival that resulted from removing a relatively large number of toes was quite evident in the seven species and populations where this effect of toe-clipping was included

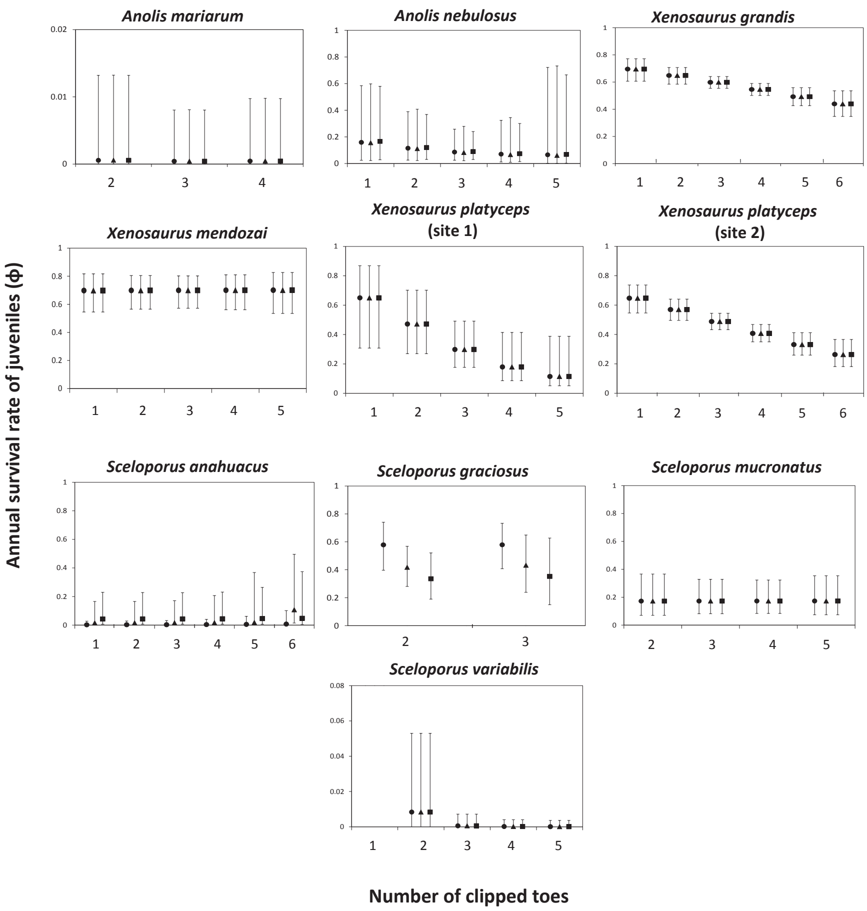

Figure 1. Model-averaged estimates of annual survival rates for juvenile individuals that differ in the number of toes that were clipped. We show survival estimates for nine species of lizards, including two different populations of *X. platyceps*. Different symbols represent three different sampling intervals arranged chronologically, from early (circle), intermediate (triangle) and late (square) phases of the study. Missing values in *S. variabilis* correspond to parameters that were not properly estimated. Error bars indicate 95% confidence intervals.

in the data (models with $\Delta AIC_c < 2$) included an effect of the number of clipped toes (TC) on survival (Table 2). In seven of these nine cases, this effect of clipping toes was included in the best-fitting model. In the other two cases (sites 1 and 5 of *S. grammicus*), the effects of increasing the number of clipped toes were not as evident because the constant model was the best-fitting model and, in the best-fitting model (*A. nebulosus*, *X. grandis*, both populations of *X. platyceps*, *S. variabilis*, and sites 6 and 8 of *S. grammicus*; Figs. 1-4). This decrease in survival probabilities varied between 32% in site 1 of *X. platyceps* (from 0.73 in adult individuals with one removed toe to 0.50 in adult individuals with five removed toes; Fig. 2) to 92% in site 8 of *S. grammicus* (from 0.61 in adult individuals

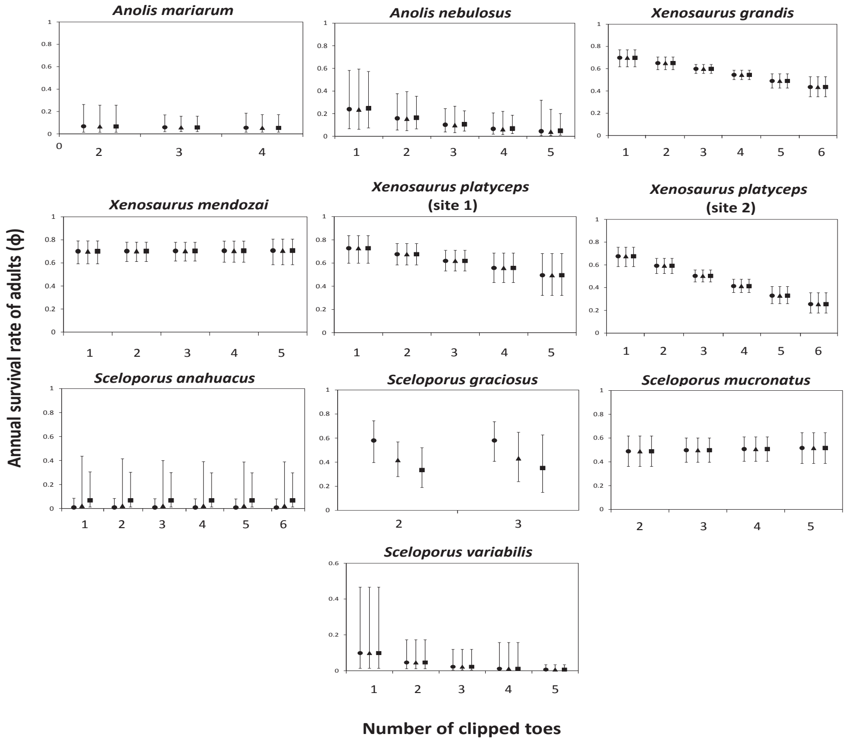

Figure 2. Model-averaged estimates of annual survival rates for adult individuals that differ in the number of toes that were clipped. We show survival estimates for nine species of lizards, including two different populations of *X. platyceps*. Different symbols represent three different sampling intervals arranged chronologically, from early (circle), intermediate (triangle) and late (square) phases of the study. Error bars indicate 95% confidence intervals.

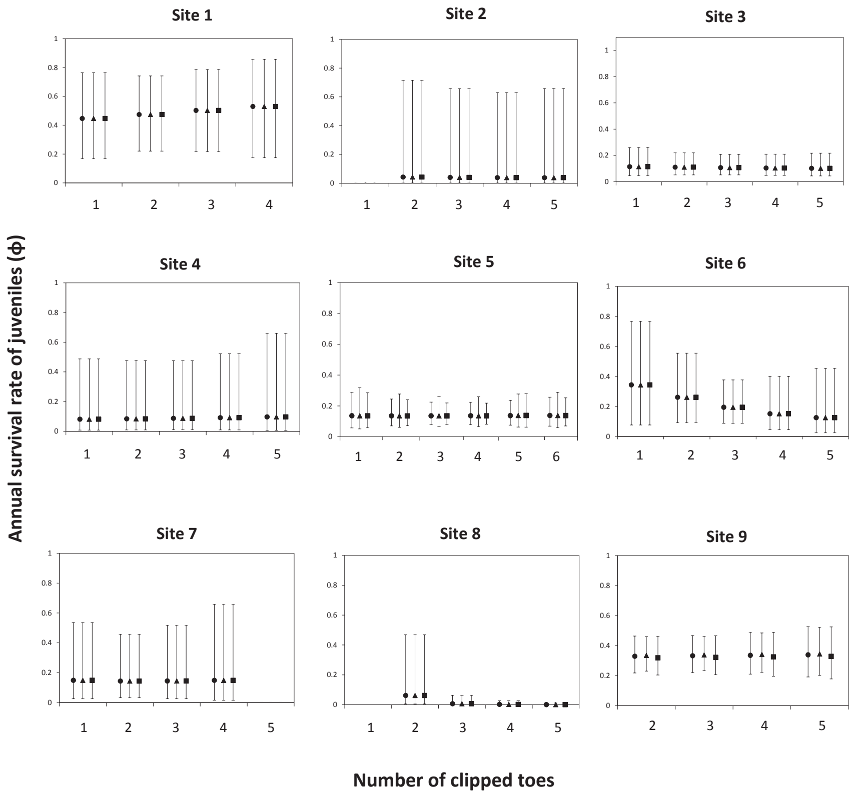

Figure 3. Model-averaged estimates of annual survival rates for juvenile individuals that differ in the number of toes that were clipped. We show survival estimates for nine different populations of the lizard *S. grammicus*. Different symbols represent three different sampling intervals arranged chronologically, from early (circle), intermediate (triangle) and late (square) phases of the study. Missing values in sites 2, 7, and 8 correspond to parameters that were not properly estimated. Error bars indicate 95% confidence intervals.

with one removed toe to 0.05 in adult individuals with five removed toes; Fig. 4). In the two populations of *S. grammicus* where the effect of the number of clipped toes was included in one of the models with strong support ($\Delta AIC_c < 2$), but not in the best-fitting model (sites 1 and 5; Table 2), model-averaged estimates of survival did not show an evident negative trend as a function of the toes that were removed (Figs. 3-4).

In *A. nebulosus*, one population of *X. platyceps* (site 1), *S. variabilis*, and one population of *S. grammicus* (site 8), the interaction between stage and number of clipped toes (TC × S) had strong support in the data ($\Delta AIC_c < 2$; Table 2). In *A. nebulosus*, adult individuals experienced a steeper decrease in survival as more toes were removed compared to juveniles (Figs. 1-2). In contrast, in site 1 of *X. platyceps*, *S. variabilis*, and site 8 of *S. grammicus*, we observed a more drastic decrease in juvenile survival as a function of the number of clipped toes compared to the observed decrease in adult survival (Figs. 1-4). In the three other cases where the best-fitting model indicated a negative effect of the number of clipped toes on survival (*X. grandis*, site 2 of *X. platyceps*, and site 6 of *S. grammicus*; Table 2), no clear difference in this negative trend was observed between juveniles and adults (Figs. 1-4).

According to model-averaged estimates, time variation was evident only in *S. graciosus*: survival decreased through time regardless of the number of toes that were clipped (Figs. 1-2). Model-averaged estimates of recapture probabilities (p) varied widely among species and populations. Table 3 shows the minimum and maximum estimates of p for each species and population, as well as model-averaged estimates of the annual transition rate between juveniles and adults (ψ).

DISCUSSION

We found an evident negative effect of removing several toes on survival in seven study sites corresponding to five species (*A. nebulosus*, *X. grandis*, *X. platyceps*, *S. variabilis*, and *S. grammicus*). The reduction in survival may be as drastic as 92% after removing a relatively large number of toes. These species and populations where a negative effect of clipping several toes was clearly supported by the mark-recapture data, represent 37% of all the species and populations that we considered in this study (seven out of 19). In contrast, no effect of the number of clipped toes was evident in 10 study sites that correspond to six different species (53% of our study species and populations; Table 2). These results suggest that toe-clipping may be a harmful marking technique for particular lizard species and under particular environmental conditions. A decrease in survival associated with removing several toes in such particular species and sites may be associated with infections, necrosis, impaired foraging ability, and changes in behaviour, such as have been observed in other organisms (Clarke, 1972; Golay & Durrer, 1994; Parris & McCarthy, 2001; McCarthy et al., 2009). In consequence, previous demographic estimates that have been reported for these species might be biased and misleading because the marking method itself could have reduced survival (Serna-Lagunes, 2005; Zúñiga-Vega et al., 2007; Rojas-González et al., 2008; Pérez-Mendoza et al., 2013; Siliceo-Cantero, 2015).

To understand the differential effects of the number of clipped toes that we documented among our study species, we must consider the particular habits of each genus. For example, xenosaurid lizards are strict crevice-dwellers with low mobility (Zamora-Abrego et al., 2007; Zúñiga-Vega et

Table 2. Model selection results for the species and populations that we examined. Survival rates (ϕ) were affected by number of clipped toes (TC), ontogenetic stage (adult or juvenile, S), particular sampling period (T), by interactions between factors (TC × T, TC × S, and S × T) or remained constant (.) throughout the duration of the study. Recapture rates (***p***) were affected by sampling occasions (T) or remained constant (.). Transition rate from juveniles to adults (ψ) remained constant (.) across sampling occasions. The fit of each model to the mark-recapture data was evaluated using the Akaike's Information Criterion adjusted for small sample sizes (AIC_c). The model with the lowest AIC_c score best fit the data. Hence, models are listed according to the AIC_c (from lowest to highest, from best to worst). ΔAIC_c represents the difference in AICc scores between each model and the best-fitting model. We only show here models with strong support in the data (i.e. models with $\Delta AIC_c < 2$). Akaike weights (w_i) measure the relative support in the data for each fitted model.

Species	Models	AIC_c	ΔAIC_c	W_i
Anolis mariarum	ϕ(S) *p*(.) ψ(.)	410.42	0.00	0.48
	ϕ(S) *p*(T) ψ(.)	411.06	0.64	0.34
A. nebulosus	ϕ(TC) *p*(T) ψ(.)	867.34	0.00	0.49
	ϕ(TC x S) *p*(T) ψ(.)	868.75	1.41	0.24
Xenosaurus grandis	ϕ(TC) *p*(.) ψ(.)	8758.35	0.00	0.87
X. mendozai	ϕ(.) *p*(T) ψ(.)	3459.57	0.00	0.58
X. platyceps				
Site 1	ϕ(TC x S) *p*(.) ψ(.)	54899.24	0.00	0.58
	ϕ(S) *p*(.) ψ(.)	54899.94	0.69	0.41
Site 2	ϕ(TC) *p*(T) ψ(.)	5378.03	0.00	0.76
Sceloporus anahuacus	ϕ(T) *p*(.) ψ(.)	2135.82	0.00	0.66
	ϕ(S x T) *p*(.) ψ(.)	2137.31	1.49	0.31
S. graciosus	ϕ(T) *p*(T) ψ(.)	970.34	0.00	0.70
S. mucronatus	ϕ(S) *p*(T) ψ(.)	2018.46	0.00	0.82
S. variabilis	ϕ(TC x S) *p*(.) ψ(.)	347.11	0.00	0.88
S. grammicus				
Site 1	ϕ(.) *p*(.) ψ(.)	244.12	0.00	0.50
	ϕ(S) *p*(.) ψ(.)	245.41	1.30	0.26
	ϕ(TC) *p*(.) ψ(.)	245.79	1.68	0.22
Site 2	ϕ(S) *p*(.) ψ(.)	527.78	0.00	0.44
	ϕ(S) *p*(T) ψ(.)	528.65	0.87	0.29
Site 3	ϕ(.) *p*(.) ψ(.)	2278.98	0.00	0.53
	ϕ(S) *p*(.) ψ(.)	2280.51	1.53	0.25
Site 4	ϕ(S) *p*(T) ψ(.)	544.42	0.00	0.81
Site 5	ϕ(.) *p*(.) ψ(.)	1147.32	0.00	0.53
	ϕ(TC) *p*(.) ψ(.)	1149.14	1.81	0.21
	ϕ(S) *p*(.) ψ(.)	1149.22	1.89	0.21
Site 6	ϕ(TC) *p*(.) ψ(.)	606.26	0.00	0.50
	ϕ(.) *p*(.) ψ(.)	607.39	1.13	0.28
Site 7	ϕ(.) *p*(T) ψ(.)	191.54	0.00	0.43
	ϕ(S) *p*(T) ψ(.)	191.95	0.41	0.35
Site 8	ϕ(TC x S) *p*(T) ψ(.)	466.71	0.00	0.78
Site 9	ϕ(S) *p*(T) ψ(.)	2650.68	0.00	0.52
	ϕ(S x T) *p*(.) ψ(.)	2652.39	1.71	0.22

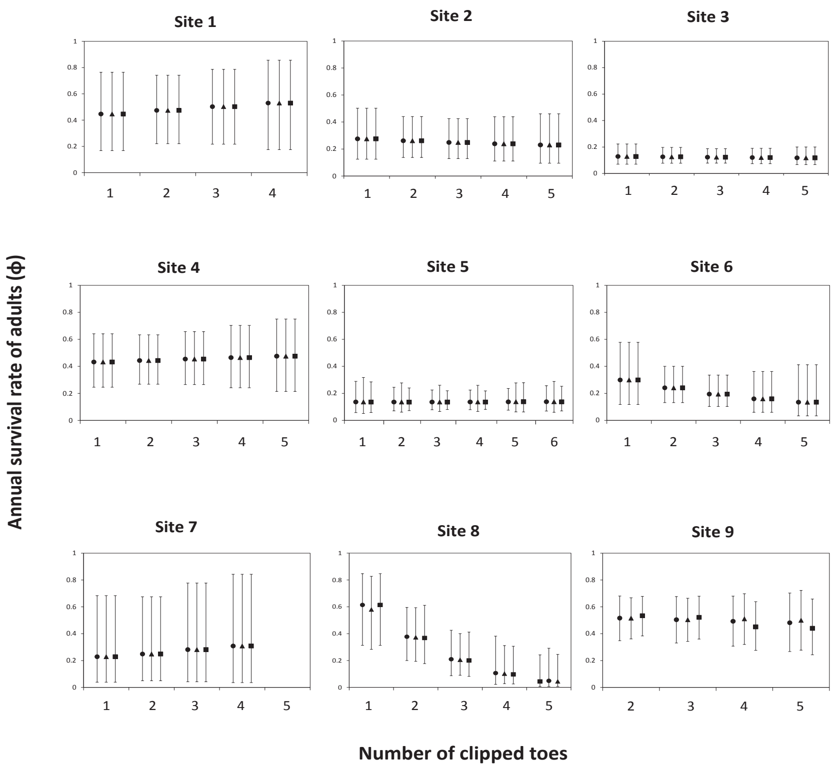

Figure 4. Model-averaged estimates of annual survival rates for adult individuals that differ in the number of toes that were clipped. We show survival estimates for nine different populations of the lizard *S. grammicus*. Different symbols represent three different sampling intervals arranged chronologically, from early (circle), intermediate (triangle) and late (square) phases of the study. Missing values in site 7 correspond to parameters that were not properly estimated. Error bars indicate 95% confidence intervals.

al., 2007). They rarely go out of their rock crevices and do not exhibit active thermoregulation (Ballinger et al., 1995; Lemos-Espinal et al., 2003). Hence, we expected to find the smallest negative effect of removing several toes on xenosaurid lizards compared to other species such as *Anolis* lizards, which are predominantly arboreal with higher rates of mobility (Losos, 2009). For arboreal lizards, toe removal was expected to be more harmful because this marking method might cause severe locomotion impairment (Mahendra, 1941; Schmidt & Schwarzkopf, 2010). In fact, in another *Anolis* species (*A. carolinensis*) toe-clipping reduced clinging performance (Bloch & Irschick, 2004). In addition, in some arboreal amphibians, toe-clipping has been demonstrated to cause increased mortality (Waddle et al., 2008). We found indeed a decrease in the survival of *A. nebulosus* as a function of the number of clipped toes. However, we also detected strong negative effects of clipping many toes on the survival of two xenosaurid species. The causes of the negative effects from removing several toes in these low-mobility crevice-dwellers remain unknown. One hypothesis to be tested is that their poor ability to actively thermoregulate might limit their ability to deal with infections (Kluger et al., 1975).

Another phenomenon observed was that species in the same genus, and populations of the same species, differed in their susceptibility to toe-clipping. In contrast to what we found in *X. grandis* and *X. platyceps*, survival of another congener (*X. mendozai*) appeared to be unaffected by increasing the number of toes that were clipped. Similarly, survival of *A. mariarum*, an arboreal lizard, was unaffected by the number of clipped toes, whereas its congener, *A. nebulosus*, experienced a clear reduction in survival apparently caused by clipping several toes. Three species of the genus *Sceloporus* (*S. anahuacus*, *S. graciosus*, and *S. mucronatus*) were unaffected by the number of clipped toes, whereas *S. variabilis* and at least two populations of *S. grammicus* experienced reductions in survival after clipping several toes. Within *S. grammicus*, the effect of clipping several toes was clear in two populations, uncertain in two other populations, and apparently absent in the remaining five populations. Presumably, differences in local environmental conditions such as habitat quality might explain these intrageneric and intraspecific differences. At some localities lizard endurance, locomotion, and performance might have a stronger dependence on the integrity of their limbs and toes. Depending on conditions such as the type of substrate, the availability of suitable microhabitats, and predation intensity, toe-removal might be more or less critical. For instance, among all the populations of *S. grammicus* that we studied the effect of clipping more toes was stronger in site 8. This is the only site in which these lizards inhabit walls of houses and small buildings (Pérez-Mendoza et al., 2013). Clinging ability on these vertical surfaces may be crucial for survival. Thus, toe removal in this population presumably resulted in an impaired ability to reach refugia and, in turn, in lower survival probabilities.

We must emphasise that in two populations of *S. grammicus* (sites 1 and 5), at least one of the models that indicated an effect of the number of clipped toes on

Table 3. Model-averaged estimates of recapture probabilities (*p*) and rates of transition from juveniles to adults (ψ) for the species and populations that we studied. We report the minimum and maximum estimates of *p*. The parameter ψ could not be accurately estimated for site 1 of *S. grammicus*.

Species	Minimum *p*	Maximum *p*	ψ
Anolis mariarum	0.663	0.773	0.381
A. nebulosus	0.097	0.310	0.781
Xenosaurus grandis	0.160	0.160	0.044
X. mendozai	0.111	0.531	0.090
X. platyceps			
Site 1	0.145	0.145	0.099
Site 2	0.068	0.455	0.030
Sceloporus anahuacus	0.203	0.210	0.271
S. graciosus	0.492	0.931	0.947
S. mucronatus	0.072	0.692	0.175
S. variabilis	0.105	0.105	0.283
S. grammicus			
Site 1	0.109	0.113	-
Site 2	0.085	0.158	0.098
Site 3	0.233	0.234	0.388
Site 4	0.067	0.403	0.317
Site 5	0.232	0.232	0.474
Site 6	0.144	0.144	0.197
Site 7	0.001	0.398	0.155
Site 8	0.104	0.477	0.173
Site 9	0.414	0.712	0.430

survival had similar fit compared to the best model (the constant model in both cases; Table 2). Hence, in these populations, a negative effect of clipping several toes cannot be completely discarded. The lack of a clearer effect of the number of toes that were removed in these populations might be due to relatively small sample sizes or to low recapture rates, both of which resulted in low statistical power and in imprecise survival estimates (Amstrup et al., 2005). In any case, given our current data sets and our model selection results, the scenario in which removal of several toes caused lower survival is also likely for these populations.

We also predicted a stronger negative effect of the number of clipped toes on juveniles. We found support for this hypothesis in one population of *X. platyceps* (site 1), in *S. variabilis*, and in one population of *S. grammicus* (site 8). In these cases, juvenile survival decreased more drastically after removing several toes compared to adult survival. In natural populations, juvenile survival in lizards is usually lower than adult survival presumably because juveniles are more vulnerable to predation and parasitic infections (Civantos & Forsman, 2000; Miles, 2004). Also juveniles are outcompeted by larger (older) individuals when searching for food and potential territories (San-Jose et al., 2016). Therefore, toe removal may have more critical effects in such younger individuals. However, in one case (*A. nebulosus*), we detected a stronger negative effect of the number of clipped toes on adult survival compared to juvenile survival. We do not know the causes of this unexpected pattern but one hypothesis is that in this particular arboreal species, adults engage in intense social interactions (whereas juveniles do not) and, therefore, the integrity of the toes becomes critical for energetic locomotion on tree branches.

In this study we have examined whether clipping a relatively large number of toes resulted in lower survival compared to clipping only one or two toes. We found reductions in survival in seven study sites likely caused by removing several toes (*A. nebulosus*, *X. grandis*, two populations of *X. platyceps*, *S. variabilis*, and two populations of *S. grammicus*). In those cases where toe-clipping is the only option for individual identification, removing fewer toes (between two and three) would have the lowest negative impacts (see for example survival estimates for *X. grandis* in Figs. 1-2). However, we did not compare survival of lizards marked by toe-clipping versus lizards marked by other methods such as paint marks or scale-clipping (Ott & Scott, 1999; Lindner & Fuelling, 2006; Schmidt & Schwarzkopf, 2010). Therefore, we recognise that based on our analyses and results we cannot know whether removing a single toe affects survival or not. Some laboratory studies have tested the effects of toe-clipping by comparing marked animals by this technique with unmarked animals or with animals marked by alternative methods. For instance, Borges-Landáez & Shine (2003) found no difference in running speed between individuals with removed toes and unmarked individuals of the skink *Eulamprus quoyii.* Ott & Scott (1999) compared growth and survival of the salamander *Ambystoma opacum* marked by toe-clipping and passive integrated transponder (PIT) tags, and found no short-term effects of either marking method. However, given that animals in controlled conditions do not have to search for food or to escape from predators, the actual impact of toe-clipping in natural conditions may be greater than what has been observed in captivity. Further tests in natural conditions of the negative effects of toe-clipping on lizard behaviour, locomotion, or survival must compare individuals marked by this technique with individuals marked by a different method (e.g., paint marks, photo-identification, PIT tags; Zaffaroni-Caorsi et al., 2012).

In summary, our results suggest negative effects of the number of clipped toes on lizard survival. Clipping several toes might reduce survival under particular conditions or in particularly vulnerable species. In such cases, this technique violates one of the main assumptions of marking methods in ecological studies, namely, that the survival probability of the marked animals must not be affected by the marking method (Ricker, 1956; Ferner, 2007). Perhaps, the observed negative effects of removing several toes may arise from an inappropriate handling or treatment of the marked animals. However, in most cases only the first (most distal) phalanx of each toe was removed and local antiseptics were applied immediately after removing the toes. In addition, the decrease in survival may arise from overlooking some recommendations for the implementation of toe-clipping as a marking method, such as no more than four clipped toes in total and no more than one toe per limb (Paulissen & Meyer, 2000). As indicated in Table 1 some authors removed up to six toes and, thus, more than one toe per limb.

Given the observed negative effects of removing several toes on lizard survival, we conclude that this marking technique should be avoided. Whenever possible, we recommend the use of less invasive methods for the permanent marking of lizards. For instance, Winne et al. (2006) and Ekner et al. (2011) proposed a marking technique based on heat-branding with pen-like medical cautery units. Visible implant elastomer tags are another alternative (Penney et al., 2001). However, even though these recent techniques for marking vertebrates seem less aggressive, we also recommend studies to evaluate potential negative effects.

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