Chameleons on the move: survival and movement of the Cape dwarf chameleon, *Bradypodion pumilum*, within a fragmented urban habitat

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Reptiles have an amazing diversity of life-history attributes ranging from the shortest- to longest-lived of vertebrate species. Estimating survival in wild populations is of key importance when understanding population dynamics and life-history evolution. However, data are lacking for a large and charismatic group of lizards, the chameleons. We conducted a Robust Design (RD) capture–mark–recapture (CMR) experiment on the Cape dwarf chameleon, *Bradypodion pumilum,* at two nested sites within the Cape Town Metropolitan Area, South Africa, in order to estimate survival and movement of adults in and around an isolated 3.5 ha patch of suitable habitat. Over a nine-week period, 97 individuals were identified in 379 captures from five primary capture sessions with three secondary events each. Analysis of CMR data provided evidence that smaller chameleons have a substantially lower survival per 10-day period than larger chameleons. RD analysis showed that males were more prone to temporary emigration than females, while open multi-strata analysis revealed that smaller chameleons more readily moved between the sites than larger chameleons. Our findings offer first important insights into chameleon survival and life-history dynamics, which suggest a more vagile subadult population and the possibility of male biased dispersal. Our results have implications for managing the conservation of threatened chameleon populations in highly fragmented urban habitats.

Key words: **capture–mark–recapture, robust design, Chamaeleonidae, survival.**

INTRODUCTION

Estimates of survival are key for understanding population dynamics and life-history evolution (Stearns 1992; Sandercock 2006). They are also important parameters for population viability analyses and other quantitative methods in conservation biology (Caswell 2001; Morris & Doak 2002; Keogh *et al.* 2007). There is a wealth of studies on survival rates under natural conditions for reptiles (see Shine & Charnov 1992), but chameleons are relatively poorly known in this respect. At one extreme, some reptiles (e.g. *Furcifer pardalis, Ichnotropis capensis, I. squamulosa*) are known to have annual life cycles (Branch 1998; Karsten *et al.* 2008). At the other extreme, some (e.g. crocodiles, tortoises, monitors and iguanas) are notable for their longevity and slow reproduction (e.g. Shine & Iverson 1995; Branch 2009). Given the range of possibilities for variation in survival between and within species, species specific estimates of seasonal and annual survival are particularly important, especially in the application of practical management in transformed habitats. Restoration and maintenance of urban fragments often come at great cost and effort, and it would be beneficial to know if these fragments contain viable populations in the long term.

The Cape dwarf chameleon, *Bradypodion pumilum* Daudin (1802), is a small (adult body length *c.* 50–90 mm), viviparous lizard endemic to the southern part of the Western Cape of South Africa (Fig. 1). Its distribution covers a range of habitats including fynbos, renosterveld, thicket,

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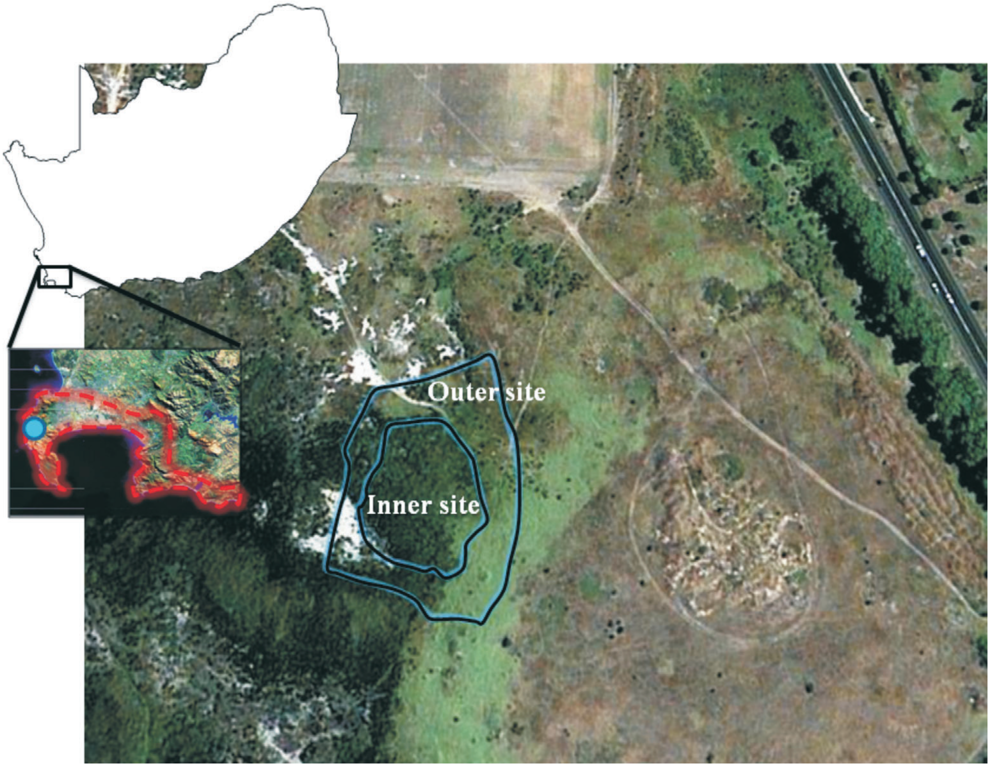

Fig. 1. Location of the Noordhoek Wetlands sampling site (dot shown, inset) and the outlines of the inner and outer sites superimposed over a Google Earth image. Distribution of the Cape dwarf chameleon is outlined in the inset.

exotic and native trees and riparian vegetation (Tolley & Burger 2007). This species is under intense pressure from anthropogenic change, as the majority of its distribution has been urbanized and falls within a 'critically endangered ecosystem' (see Driver *et al.* 2005). Furthermore, it is essentially absent from some large areas of monoculture (Tolley & Measey 2007). The trend for habitat transformation is continuing, with at least 6.5 km^2 per year of undeveloped land lost to urbanization within the Cape Town metropolis region (Rebelo *et al.*, in press), where this species is primarily distributed (Fig. 1). This is especially alarming, as bioclimatic models suggest *B. pumilum* could suffer substantial losses of climatic space in the future, under scenarios predicted by the Intergovernmental Panel on Climate Change (Houniet *et al.* 2009). At present, the Cape dwarf chameleon is mainly distributed in planted garden vegetation (frequently non-indigenous) in urban environments, or isolated patches of highly disturbed plots of land within the metropolitan area. *Bradypodion pumilum* appears to undergo substantial demographic fluctuations in these small remnant populations (K.A.T., G.J.M., pers. obs.), and this might have important implications for its management in the urban setting. Fragments which are not thought to be suitable due to low densities at one point in time, may have quite high densities at another point in time, and therefore be extremely valuable in maintaining population numbers and connectivity between patches.

Despite these substantial pressures, approximately 40% of the distribution of *B. pumilum* lies within relatively pristine montane areas (Tolley & Burger 2007), much of which is under formal protection (Driver *et al.* 2005). However, because of the intense pressure on this species in urban areas, it is currently being evaluated as a candidate for the IUCN Red List (Tolley, unpubl. data). To ensure that such conservation assessments are comprehensive, and to provide information that can be used toward a framework for conservation planning for both provincial and metropolitan authorities, an understanding of survival in these small remnant fragments is essential. Many authorities are charged with making rapid assessments of chameleon populations in apparently isolated, threatened patches of habitat (e.g. Armstrong 2008). To this end, we were interested in whether isolated populations are likely to represent stable populations with little movement, or whether populations are more volatile, and whether this can be determined by rapid assessments.

In this study, we estimated survival and migration of Cape dwarf chameleons in a seasonal wetland in the Cape Town metropolitan area, in a patch that consists of core area of good-quality habitat, and a surrounding area of poor-quality habitat. We hypothesized that daily survival would be high, with no sex or size dependency. We anticipated that net migration would be toward the habitat of higher quality, and that temporary migration into the surrounding area of poor-quality habitat (e.g. lawn, sports fields and dirt parking areas) would be low.

MATERIALS & METHODS

Study area

The study was carried out at Noordhoek Wetlands (34°11′S, 18°38′E), in a patch of transformed habitat, bounded on two sides by an urban residential area and a recreational parkland (Fig. 1). Connections with other vegetated patches were present on the remaining two sides, but these areas were considered unattractive for chameleons due to sparse vegetation, and channels of flowing water. The overall study area was divided into two nested, roughly circular 'sites': an 'inner site' with good habitat of approximately 2170 m^2 and a surrounding 'outer site' with poor habitat of approximately 3450 m^2, forming a ring around the inner site (Fig. 1). The position and size of the sites were subjectively determined, primarily by the state of the vegetation. The inner site was relatively homogenous in terms of vegetation coverage, dominated by dense patches of exotic (planted) restio (Restionaceae) species, exotic bulrushes, plus native shrubs, *Osteospermum* sp. and *Senecio* sp. (Asteraceae). The outer site was far patchier in terms of vegetation cover, with short lawn grasses and patches of sand, sparse restios, and small (young) alien trees (*Acacia saligna*).

Study design and data collection

The capture–mark–recapture (CMR) study followed a multi-strata Robust Design (RD), with the two sites treated as separate strata. In the RD (Kendall *et al.* 1997), each primary capture session consisted of a series of secondary capture occasions during which the system was assumed to be closed to migration, death and recruitment. Between primary sessions, mortality was allowed to occur, with the population open to immigration and emigration. The combination of open and closed captures yielded estimates of survival and temporary emigration.

Secondary capture occasions were conducted on three consecutive nights, whereas the five primary occasions were 9–12 days apart, over a period of nine weeks (16 March to 13 May 2009). Adult chameleons (≥45 mm body length, Jackson 2007) were caught by hand at night (20:00–22:00) using torch light for spotting (Tolley & Burger 2007).

Each individual was marked at initial capture with a number (using indelible ink) on its ventral surface, and a small (<3 mm) clipping was taken from the tip of the tail, which doubled as a batch mark and a tissue sample for DNA analysis (not part of the present study). Photographs were taken at each capture of the right side of the body and head, and the top of the head. These photographs were used to successfully identify all individuals that had lost their ink number after shedding, but who were identified as recaptures through the batch mark. The latitude/longitude of all captures were recorded to the nearest 10th second (±5 m accuracy), and the chameleon was returned to its perch immediately after processing. The sex of every individual was recorded, and snout–vent length was measured on each capture occasion.

Analysis

Capture–mark–recapture (CMR) methods were used to estimate survival and movement (Lebreton *et al.* 1992) using the program MARK 5.1 (White & Burnham 1999). Underlying assumptions of the CMR models are equal probability of survival and recapture for all individuals, marks are not lost or missed, and all samples are instantaneous, relative to the interval between occasions (i) and (i + 1). Models were tested for goodness of fit (GoF), using the program RELEASE and the median-$\hat{c}$ approach in program MARK. Standard procedures in model fitting and notation were used, and model selection was based on Akaike's Information Criterion (Lebreton *et al.* 1992). We started by fitting the most general model including all effects we anticipated to be potentially important (except for body size) and then simplified model parts. Models including body size as an individual covariate are more computationally demanding to fit, and we therefore only entered body size after arriving at a relatively simple, parsimonious model structure.

Our intention was to use multi-state robust-design (RD) models. However, we found that individuals moved between the sites daily, thus violating the closure assumption with regard to movement. We therefore conducted two separate analyses. The first analysis used the RD, without distinguishing between the two sites. In a second analysis, an open multi-strata analysis was used (Brownie *et al.* 1993) with unequal time intervals to examine site-specific survival and recapture, plus movement between the inner and outer sites.

Robust Design

The RD with Huggins closed captures in program MARK was used to estimate survival, capture, and recapture rates for the study area (both sites combined) as a whole (Kendall *et al.* 1997). This approach also estimated the probability of being available for capture (γ), which we interpreted as temporary emigration and immigration from the study area (Kendall *et al.* 1997).

The RD model consisted of five parts: survival (S), emigration (γ'), immigration (γ'') capture probability (p) and recapture probability (c). The emigration and immigration in this analysis refers to movement out of the study area, not to movement between the inner and outer site, which were pooled here. The effects of time, sex and size on all model components were considered. Initial analyses showed that (re)capture probabilities were homogeneous among secondary occasions within primary sessions.

The RD had three underlying assumptions in addition to the ones mentioned above: the population is closed to additions and deletions across secondary sampling occasions within a primary session; temporary emigration is either completely random, Markovian or based on temporary response to first capture; and survival rate is the same for all animals in the population, regardless of availability for capture.

There is no specific goodness of fit analysis for the RD with Huggins closed captures. However, the RD models share assumptions with the Cormack-Jolly-Seber (CJS) approach, and we therefore partly relied on the GoF test results from a CJS model, using pooled secondary occasions. Goodness of fit tests (program RELEASE, tests 2 & 3) showed that the general model allowing for time and sex effects on survival and recapture rates provided a good fit of the data, with little over dispersion ($\chi^2 = 17.63$, d.f. = 13, $P > 0.05$; $\hat{c} = 1.35$). The data therefore did not violate the model assumptions significantly.

In addition, the RD assumes closure across secondary sampling occasions. This assumption may be violated here, especially with respect to emigration. However, as long as emigration is random; the parameter estimates should remain unbiased (Kendall 1999). The random movement model best described movement during primary periods (see below), it is therefore reasonable to assume that movement between secondary sampling occasions was also close to random.

Finally, the RD assumes that all individuals in the population have similar probabilities of being captured initially. Violation of this assumption was explored by fitting models that allowed for some heterogeneity in capture rates (finite mixture models based on two groups, Pledger 2000). These models did not result in a better fit, and we conclude that the assumption of homogeneity in probability of capture was met by our data.

Multi-strata models

The multi-strata model consists of three parts, each then divided into two, representing each stratum (inner site (I) and outer site (O)). The parts represent survival (S_{I} and S_{O}), recapture probability (p_{I} and p_{O}) and movement between the strata (Ψ_{IO} and Ψ_{OI}). The most general model for this analysis included all factors found to be important in the RD analysis, plus differences in survival and recapture between the two sites. This model fitted the data well (Model $S(\mathrm{str})P(\mathrm{str}*\mathrm{time})\Psi_{\mathrm{IO}}(\mathrm{sex})\Psi_{\mathrm{OI}}(\mathrm{sex})$: $\hat{c} = 1.05$, S.E. = 0.01).

RESULTS

Over the nine-week period, 97 individuals (37 females and 60 males) were captured at least once, with 379 captures in total. Average SVL for females was 64.65 mm (range 45.0–77.9, S.D. 7.20) and for males was 62.92 mm (range 45.0–79.02, S.D 9.39). Average mass for females was 6.92 g (range 3.50–13.75, S.D. 2.93) and 5.86 g for males (range 2.50–10.50, S.D. 2.90).

Robust Design analysis

The top models all included an effect of size on survival, showing that larger chameleons survived better than smaller individuals (Table 1, Fig. 2). Model selection slightly favoured Model 1 (in

Table 1. Summary of model selection for Robust Design models, using Huggins Closed Captures for Cape dwarf chameleons, *Bradypodion pumilum.* The models consist of five components: survival (*S*), emigration (γ''), immigration (γ'), capture (*p*), and recapture (*c*) rates. Model selection was based on the sample-size adjusted Akaike's Information Criterion (AICc). *K* is the number of estimated parameters.

Model		ΔAICc	AIC weight	*K*	Deviance
1	*S*(size) $\gamma'' = \gamma'$(sex) *p*(time) *c*(time)	0.000	0.449	14	1180.934
2	*S*(size*sex) $\gamma'' = \gamma'$(sex) *p*(time) *c*(time)	1.670	0.195	16	1178.255
3	*S*(size) $\gamma'' = \gamma'$(sex) *p*(time+size) *c*(time+size)	1.755	0.187	16	1178.339
4	*S*(size) $\gamma'' = \gamma'$(sex+size) *p*(time) *c*(time)	2.093	0.158	15	1180.858
5	S() $\gamma'' = \gamma'$(sex) *p*(time) *c*(time)	9.180	0.005	14	1190.114
6	*S*() γ''(sex) γ'(sex) *p*(time) *c*(time)	10.279	0.003	15	1189.044
7	*S*()γ''(time) γ'(time) *p*(time) *c*(time)	10.884	0.002	18	1183.071
8	*S*()γ''() γ'() *p*(time) *c*(time)	10.999	0.002	13	1194.089
9	*S*(sex) γ''(sex) γ'(sex) *p*(time) *c*(time)	11.998	0.001	16	1188.582
10	*S*(time) γ''() γ'() *p*(time) *c*(time)	13.251	0.001	16	1189.836
11	*S*(sex) γ''(sex) γ'(sex) *p*(sex*time) *c*(sex*time)	28.209	0.000	26	1182.308

which only survival was size-dependent) over Models 2 to 4, which allowed for a sex-specific size effect on survival, a size effect on recapture, or a size effect on movement, respectively (Table 1). All top models suggested that emigration (γ'') was similar to immigration (γ'), but these rates differed between the sexes. The best-supported model estimated immigration and emigration rates ($\gamma' = \gamma''$) of females at 0.05 (95% confidence interval 0.01 to 0.26) and males at 0.20 (0.11–0.34). The (re)capture probabilities ranged from 0.38 (0.28–0.48) to 0.73 (0.55–0.87).

Multi-strata analysis

The best supported multi-strata models included size-dependent survival and movement (Table 2). Smaller chameleons were more likely to move between the inner and outer sites than larger ones (Fig. 2). Model selection also clearly favoured models that constrained movement to be the same in both directions. The top model suggested survival is constant across the two sites. However, there was also considerable support for Model 2, whereby survival was slightly lower in the outer site. This difference could well have been caused by permanent emigration, which would have been higher from the outer site than from the inner.

DISCUSSION

Survival and movement

Contrary to our original hypothesis, survival of *Bradypodion pumilum* was dependent upon body size in this small habitat fragment studied within the Cape Town metropolitan area. In this population, smaller chameleons showed substantially lower survival per 10-day period than larger chameleons, with survival ranging from 0.49 to 0.98 over the range of observed body sizes (Fig. 2). Our two analyses offer insight into two different aspects of movement. While the Robust Design (RD) analysis estimates temporary unavailability to capture (which we interpret as temporary emigration from the study area as a whole), the open multi-strata analysis estimates physical movement between the inner and outer site. The results suggested that males were more likely to be temporarily absent from the study area than females, whereas small chameleons moved more often between the two sites (inner and outer) than large ones (see Fig. 2). Surprisingly, different factors thus appeared to be affecting the two types of movement. This could mean that movement at different spatial scales is governed by different processes. The alternative possibility is that some chameleons could be unavailable to capture for reasons other than movement off the study area. For example, if males were more likely to pursue activities that made them unavailable to capture at night, such as perching low within the vegetation to avoid other males, then this might partly explain the apparent discrepancy in our results. However, if this were the case, we might also expect to capture fewer males in total than females, a result that we did not obtain (60 males, 37 females). This might suggest that the turnover of males in the study area is higher.

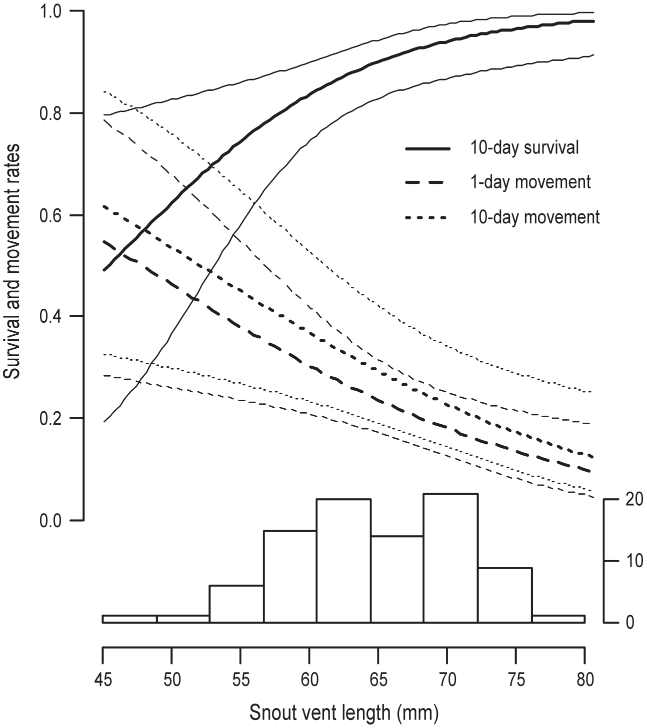

Fig. 2. Survival and movement in relation to snout–vent length of Cape dwarf chameleons, *Bradypodion pumilum.* The heavy solid line shows estimated survival from the Robust Design analysis (Model 1, Table 1), whereas the broken lines show estimated movement rates among the two sites within the study area from the multi-strata analysis (Model 1, Table 2). Thin lines show the respective 95% confidence intervals around the fitted lines. The histogram shows the number of chameleons sampled with a given snout–vent length ('size').

Investigating the cause for sex-dependent differences, either within the site, or movements off the site would be important for rapid assessments of chameleon populations. Sex-dependent dispersal in lizards is well known, as with other animals, and has been previously found to be greater in males (Doughty *et al.* 1994; M'Closkey *et al.* 1998; Clobert *et al.* 2001; Keogh *et al.* 2007). Whether the increase in male movement that we detected relates to dispersal would be revealed by a longer study period over a larger area. Our results further suggest that larger, older chameleons were more

Table 2. Summary of model selection of multi-strata models for Cape dwarf chameleons, *Bradypodion pumilum.* The models consist of four parts: survival (*S*), recapture (*p*), movement from the inner to the outer site (Ψ_{IO}), and movement from the outer to the inner site (Ψ_{OI}). Model selection was based on the sample-size adjusted Akaike's Information Criterion (AICc). *K* is the number of estimated parameters.

Model		ΔAICc	AIC weight	*K*	Deviance
1	S(size) p(time) $\Psi_{IO} = \Psi_{OI}$(size)	0.000	0.575	11	1362.174
2	S(site+size) p(time) $\Psi_{IO} = \Psi_{OI}$(size)	1.389	0.287	12	1361.417
3	S(site+size) p(time) $\Psi_{IO} = \Psi_{OI}$(sex+size)	3.229	0.114	13	1361.099
4	S(site+size) p(time) $\Psi_{IO} = \Psi_{OI}$()	6.870	0.019	11	1369.044
5	S(site) p(time) $\Psi_{IO} = \Psi_{OI}$()	10.555	0.003	10	1374.862
6	S() p(time) $\Psi_{IO} = \Psi_{OI}$()	11.663	0.002	9	1378.09
7	S(sex+site) p(time) Ψ_{IO}() Ψ_{OI}()	15.625	0.000	13	1373.495
8	S(sex+site) p(time*site) Ψ_{IO}(sex) Ψ_{OI}(sex)	24.577	0.000	20	1366.968

sedentary at the local scale than smaller, younger ones, and could indicate that the former have smaller home ranges. We found no bias in movement direction in both analyses, suggesting there is no net movement from unsuitable (outer site) to suitable (inner site) vegetation. Regardless, small chameleons were found to move frequently between areas of what we considered high- and low-quality vegetation, suggesting they have larger home ranges, are more prone to dispersal, and/or can tolerate marginal habitat. Size-dependent dispersal is known from a number of lizards, including chameleons, in which juveniles move into and colonize less favourable habitats (e.g. M'Closkey *et al.* 1998; Keren-Rotem *et al.* 2006; Warner & Shine 2008). Larger movements of juveniles could possibly make them more prone to predation, which would be consistent with lower survival in smaller individuals and in the outer site (considered to be lower quality). Despite the greater chance for predation, smaller individuals may move for a great many reasons, including finding adequate resources (food and cover) that are not already occupied by larger, older individuals (see Clobert *et al.* 2001). The question remains as to whether survival of smaller adults would be enhanced if the quality of vegetation in the outer site were healthier.

Habitat partitioning has been observed in the common chameleon (*Chamaeleo chameleon*), with smaller chameleons inhabiting grasses and larger chameleons found mainly in bushes and trees (Keren-Rotem *et al.* 2006). In that study, avoidance of cannibalism was suggested to be the main driver of habitat partitioning. This is unlikely for *B. pumilum,* as the habitat is not discretely partitioned (restios are interspersed with large bushes in the inner site). In addition, preliminary examination of stomach contents from this species does not provide any evidence of cannibalism (K.A.T. & G.J.M., unpubl. data). Although cannibalism cannot be ruled out entirely, it seems more likely that small chameleons simply cannot adequately grasp the large perches that are available on bushes. In addition, the large bushes are already occupied by larger chameleons, which would aggressively drive off the smaller ones. Although adult/juvenile interactions have not been studied, it is known that female *B. pumilum* aggressively drive away males (Stuart-Fox & Whiting 2005) and many individuals are found with bite marks (Measey *et al.* 2009), suggesting that they are relatively intolerant of conspecifics.

Conservation

Habitat loss and fragmentation has been identified as one of the greatest threats to biodiversity worldwide (Millennium Ecosystem Assessment 2005). As a counter-measure, corridors of quality habitat are thought to greatly increase the connectivity between fragments (Debinski & Holt 2000), promoting gene flow, and reducing founder effects, population bottlenecks and local extinctions. Therefore, it is important to maintain corridors between fragments to ensure that adaptive potential is not lost (Templeton *et al.* 2001). For *B. pumilum,* the utility of corridors has not been investigated, but these results suggest that it would be necessary to provide corridors of high-quality habitat that is relevant for small animals of both sexes, plus larger adult males (the age and sex classes most likely to disperse), in order to facilitate movement. Although a preference in vegetation type (e.g. perch sizes, amount of leafy cover) has not yet been investigated, such information would be vital in any rehabilitation or establishment of corridors for this species.

Habitat alteration has affected a wide range of species, including small mammals, birds, beetles, and lizards (e.g. Robinson *et al.* 1995; Davies & Margules 1998; Templeton *et al.* 2001). For *B. pumilum,* most of its distribution is within a highly fragmented and altered environment, and we are only beginning to understand the effects of this habitat transformation. If the survival of this, and other, species is to be ensured, population level processes must be considered as part of any management actions or rehabilitation efforts.

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