Survival and abundance of Cape dwarf chameleons, *Bradypodion pumilum*, inhabiting a transformed, semi-urban wetland

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The Cape dwarf chameleon, *Bradypodion pumilum*, inhabits urban areas within a critically endangered ecosystem. In this study, temporal dynamics of local demographic parameters were investigated for a population of *B. pumilum* inhabiting a 0.56 hectare patch of transformed habitat bordering an urban area in Noordhoek, South Africa. Robust Design (RD) capture-mark-recapture (CMR) models were used to estimate population demographics because of their ability to distinguish and account for temporary unavailability of individuals versus being captured. RD models were fit to one year of CMR data to examine adult survival and local abundance. Additionally, multi-strata (MS) models were used to analyze chameleon growth rate and size-specific survival. The results indicate the site supports a fluctuating abundance of individuals, ranging from ca. 25–91 adult chameleons. Larger chameleons showed higher 30-day and annual survival rates than smaller individuals regardless of sex (30-day range: 0.56–0.84; annual range: 9.51x10^−5–0.12). Chameleons that survived to the beginning of each age class spent on average 1.1 months at 40–50 mm; 1.7 months at 50–60 mm; 2.5 months at 60–70 mm; and 6.3 months at >70 mm. Despite seasonality in the environment, there was no significant seasonal variation in chameleon survival. These findings indicate chameleon population dynamics characterized by local population fluctuations despite predominately constant, low survival; our findings suggest reproduction drives population fluctuations. *Bradypodion pumilum*’s high fecundity and low survival should allow for their persistence in disturbed habitats assuming they are able to take advantage of suitable conditions. Alternatively, these biological traits may make *B. pumilum* prone to large demographic fluctuations, yielding a high risk of local extinction. This study provides temporal data on local population dynamics and survival for a potentially threatened reptile species inhabiting altered habitats.

**Key words:** capture-mark-recapture, Chamaeleonidae, demographic modelling, habitat alteration, robust design, temporal population dynamics

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**INTRODUCTION**

Habitat alteration is a major cause of biodiversity loss (Rosenzweig, 1995; Shochat et al., 2010) that can increase risk of population decline or local extinction for inhabiting species (Bender et al., 1998; Holsinger, 2000; Driscoll, 2004; Fischer & Lindenmayer, 2007). To assess the impact that habitat alteration has on species or local populations, estimates of demographic parameters for species in these altered habitats are particularly valuable (Harper et al., 2008) as they allow us to identify changes in local population dynamics. Demographic parameters are also useful for assessing the threat status of potentially imperiled species (Sandercock, 2006).

Among terrestrial vertebrates, reptiles are documented to experience population declines, and these result in an increase in threat status (Gardner et al., 2007; Böhm et al., 2013). The Cape dwarf chameleon, *Bradypodion pumilum* (Gmelin, 1789), is a reptile species under intense pressure from habitat alteration (Tolley et al., 2010), as the majority of its distribution has been urbanized and falls within a critically endangered ecosystem (Driver et al., 2012). These chameleons are endemic to the Western Cape Province (South Africa), from Cape Town to Cape Agulhas and are found in fynbos, renosterveld, thicket, trees and riparian vegetation, but also occasionally on planted garden vegetation within urban environments (Tolley & Burger, 2007; Tolley et al., 2010). Habitat loss proceeds at a rate of approximately 6.5 km² annually within the Cape Town metropolis region (Rebelo et al., 2011) and presumably amplifies habitat alteration among the remnant patches of chameleon habitat.

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A short-term demographic study on *B. pumilum* found that 10-day survival (range: 0.49–0.98) was positively correlated with body size, although not significantly different between males and females (Tolley et al., 2010). Additional studies monitoring survival in small-bodied lizards generally find adult annual survival rates below 0.30 (Schoener & Schoener, 1982; Wright et al., 1984; Andrews & Nichols, 1990). Here, we report the results of a comprehensive demographic study aimed at estimating and understanding local dynamics for a population of *B. pumilum*. We collected demographic data from capture-mark-recapture (CMR) surveys conducted over one year at a disturbed, semi-urban wetland within the Cape Town metropolis. We then analyzed data to i) quantify *B. pumilum* annual and monthly survival, ii) examine potential differences between male and female chameleon survival, and iii) assess the effect of body size and/or season on survival rate. Though no previous

![Satellite image of the study site at the Noordhoek Wetlands Nature Reserve, Western Cape Province, South Africa (Source: Google Earth). The solid line shows the study site and the dotted line delimits the larger adjacent fragment of vegetation.](image)

**Fig. 1.** Satellite image of the study site at the Noordhoek Wetlands Nature Reserve, Western Cape Province, South Africa (Source: Google Earth). The solid line shows the study site and the dotted line delimits the larger adjacent fragment of vegetation.

**Table 1.** Summary of Robust Design model selection, using Huggins closed captures, for *Bradypodion pumilum*. The models consist of five sets of parameters: $S$ (survival), $y^\prime$ (emigration), $y^\prime$ (immigration), $P$ (capture), and $C$ (recapture) rates. Model selection was based on the sample-size adjusted Akaike’s Information Criterion (AICc). $K$ is the number of estimated parameters.

<table>
<thead>
<tr>
<th>Model</th>
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<th>AICc Weight</th>
<th>$K$</th>
<th>Deviance</th>
</tr>
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<td>44</td>
<td>3061.366</td>
</tr>
<tr>
<td>2</td>
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<td>0.158</td>
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<td>12</td>
<td>4.871</td>
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<table>
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<th>$\Delta$AICc</th>
<th>AICc Weight</th>
<th>$K$</th>
<th>Deviance</th>
</tr>
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<tbody>
<tr>
<td>$S$ (sex<em>time) $y^\prime$ (sex</em>time) $y^\prime$ (sex<em>time) $P$ (sex</em>time) $C$ (sex*time)</td>
<td>329.570</td>
<td>0.000</td>
<td>198</td>
<td>2902.640</td>
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</table>
work investigates seasonal variation in *B. pumilum* survival, other studies indicate seasonal abiotic factors (temperature) often exert proximate influences on lizard life histories, including survival (Dunham, 1981; Jones et al., 1987). We hypothesized that 30-day and annual survival would be similar to other small-bodied lizards, with similar survival rates between males and females, and that survival would be size dependent and vary among seasons.

**METHODS**

**Study Area**

This study is a comprehensive follow-up to Tolley et al. (2010), and we used their original study site; a patch of transformed habitat, bordering an urban area, at the Noordhoek Wetlands Nature Reserve (34°06’S, 18°22’E), Cape Town, South Africa (Fig. 1). Local anthropogenic impacts include the transformation of natural habitat into real-estate, roads and recreational parkland. Human impact on the study area includes pedestrian use as a thoroughfare and recreational trail use for walking and horseback riding. At its interior, the site supports a dense, heterogeneous mix of vegetation, including native shrubs (*Osteospernum sp.* & *Senecio sp.*), exotic restios (*Restionaceae*), reeds (*Typhaceae*), Port Jackson acacia (*Acacia saligna*) and papyrus (*Cyperaceae*). At its exterior the site supports a patchier distribution of *Acacia saligna* and papyrus (*Cyperaceae*). At the northernmost and southernmost points of the study site. Movement through the site progressed in a circular fashion, switching nightly between clockwise and counter-clockwise directions.

When encountered, chameleons that were first-time captures were removed from their roost and given a unique identification number written on the ventral surface (using indelible ink), and a small (<3 mm) tail clipping was collected to serve as a batch mark (Tolley et al., 2010). All encountered chameleons were photographed (right body-side, gular region and top of the head – *B. pumilum* exhibit unique patterning at these areas; Fig. 2). Photos were later used to identify individuals that had lost their ink number after shedding, but who were identified as recaptures through the batch mark (Tolley et al., 2010). Sex was distinguished by the presence (males) or absence (females) of a hemipenal bulge or by evertion of the hemipenes in males. Snout-vent length (SVL), tail length (TL) (nearest 0.1 mm, ±0.1 mm accuracy) and mass (nearest 0.25 g) were also recorded for all chameleons. Chameleons were handled for fewer than five minutes (usually ca. two minutes) during capture to minimize disturbance to the animal. After processing, chameleons were returned to the exact perch where they were found.

**Surveys**

Capture-mark-recapture (CMR) surveys followed a Robust Design (RD) where primary sessions consisted of multiple secondary sampling occasions during which the system was assumed closed to migration, death and recruitment (Kendall et al., 1997). Closure was not assumed between primary sessions creating a combination of open and closed designs that enabled estimation of survival and abundance.

Primary sessions (n=11) were conducted 24–33 days apart, over a one year period (30 November 2009–4 November 2010). Within each primary session, secondary sampling occasions were conducted over five consecutive nights, for two hours, after dark. During surveys, a team of two field workers located and captured adult chameleons (>40 mm snout–vent length, Jackson, 2007) with the aid of torch light. Nocturnal surveys were conducted because *B. pumilum* is readily visible at night when asleep, as they tend to perch higher up in the vegetation (Tolley & Burger, 2007). Secondary sampling occasions were initiated alternating between the northernmost and southernmost points of the study site. Movement through the site progressed in a circular fashion, switching nightly between clockwise and counter-clockwise directions.

**Robust Design Models**

Standard CMR models implemented in MARK v.5.1 (White & Burnham, 1999) were used to estimate survival and recapture (Lebreton et al., 1992). 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 (i) and (i+1).

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**Table 2.** Summary of multi-strata size-survival models for *Bradypodion pumilum*. The models consist of three sets of parameters: $\Phi$ (survival rate), $P$ (capture probability), $\psi$ (transitions among size categories). Model selection was based on the sample-size adjusted Akaike’s Information Criterion (AICc). $K$ is the number of estimated parameters.

<table>
<thead>
<tr>
<th>Model</th>
<th>$\Delta$AICc</th>
<th>AICc Weight</th>
<th>$K$</th>
<th>Deviance</th>
</tr>
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<td>0.724</td>
<td>20</td>
<td>662.356</td>
</tr>
<tr>
<td>2</td>
<td>3.184</td>
<td>0.147</td>
<td>24</td>
<td>656.453</td>
</tr>
<tr>
<td>3</td>
<td>4.610</td>
<td>0.072</td>
<td>17</td>
<td>673.644</td>
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<tr>
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<td>0.029</td>
<td>26</td>
<td>655.078</td>
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<tr>
<td>5</td>
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<td>0.025</td>
<td>18</td>
<td>673.580</td>
</tr>
<tr>
<td>6</td>
<td>10.818</td>
<td>0.003</td>
<td>23</td>
<td>666.379</td>
</tr>
<tr>
<td>7 (GoF)</td>
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<td>0.000</td>
<td>42</td>
<td>648.819</td>
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<td>General</td>
<td>292.163</td>
<td>0.000</td>
<td>140</td>
<td>540.711</td>
</tr>
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</table>
The Robust Design (RD) with Huggins closed captures approach was used for estimating survival, abundance, and the existence of temporary unavailability of individuals to being captured (Kendall et al., 1997; Cooch & White, 2009). The RD takes the view that there is a super-population that consists of individuals that are available for capture and a part that is unavailable for capture. Individuals can emigrate from the first to the second part of the population and immigrate back into the first part. Permanent emigration from the super-population cannot be distinguished from death. Immigration from outside the super-population, e.g., through birth, is not directly estimated under this design but could be estimated as a derived parameter. Traditionally, RD models are composed of five sets of parameters: $S$ (survival rate), $\gamma^e$ (emigration rate), $\nu^i$ (immigration rate), $P$ (capture probability) and $C$ (recapture probability), with the size of the super-population (abundance) estimated as a derived parameter (Kendall et al., 1997). The RD approach has additional underlying assumptions to those previously mentioned: the population is closed to additions and losses across secondary sampling occasions within each primary session; temporary emigration is either completely random, Markovian or non-existent; and survival rate is the same for all animals in the population, regardless of availability for capture (Kendall et al., 1997). The assumption of closure across secondary sampling occasions may be violated here, especially with respect to movement (Tolley et al., 2010); however, as long as movement is either random or non-existent the parameter estimates should remain unbiased (Kendall, 1999). Goodness of Fit (GoF) tests, standardized time intervals, and model fitting, notation and selection followed Tolley et al. (2010). An additional covariate was used to estimate the effect of season on survival (December–March; April–May; June–August; September–November). Annual survival rate ($\Phi_A$) was derived from the 30-day survival estimates ($\Phi_{30}$).

### Multi-Strata Models

In a separate analysis, we used multi-strata (MS) capture-mark-recapture models to estimate chameleon growth rate and the effect of body-size on survival (Cooch & White, 2009; Tolley et al., 2010) by defining the strata as four size classes based on SVL. Incorporating individual covariates that stay constant for the duration of the study is straight-forward in the CMR modelling framework; however, because notable growth of individual chameleons was observed during the study, body-size could not be treated as a constant. To examine the effect of size on survival while allowing for growth, secondary occasions were pooled, and because chameleons do not shrink, transition rates to smaller size classes were set to zero. A transition into a larger size class represents growth whereas the stratum-specific survival estimates are size-specific survival rates. GoF analysis relied on the median-ć approach in the program MARK v.5.1 (White & Burnham, 1999). Based on the estimated survival and stage transition probabilities, we calculated the expected

### Table 3

Upper triangular symmetric matrix summarizing the probability of chameleon size-class transition(s) per 30-day period (growth rates) for *Bradypodion pumilum* within the most parsimonious multi-strata capture-mark-recapture model (Table 2). Diagonal entries correspond to the probability of staying in the same size class, whereas off-diagonal elements are the probabilities of growing into the larger size class.

<table>
<thead>
<tr>
<th>Size Classes (mm)</th>
<th>&lt;50</th>
<th>50–60</th>
<th>60–70</th>
<th>&gt;70</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;50</td>
<td>0.177</td>
<td>0.737</td>
<td>0.086</td>
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</tr>
<tr>
<td>50–60</td>
<td>---</td>
<td>0.510</td>
<td>0.490</td>
<td>0.00</td>
</tr>
<tr>
<td>60–70</td>
<td>---</td>
<td>---</td>
<td>0.788</td>
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<td>&gt;70</td>
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<td>---</td>
<td>---</td>
<td>1.00</td>
</tr>
</tbody>
</table>

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**Fig. 2.** Typical photographs of the right body-side (upper-left), gular region (upper-right), and top of the head (bottom) taken during capture-mark-recapture study.

**Fig. 3.** Male and female abundance estimates (separate) obtained from the most parsimonious Robust Design model (Table 1) for *Bradypodion pumilum* in a habitat patch near Noordhoek, South Africa during 2009/2010. The solid lines represent Robust Design abundance estimates with accompanying dotted lines representing 95% confidence intervals.
time an individual spends in each age class using methods developed for stage-based matrix population models (Caswell, 2001).

**RESULTS**

We made 737 total captures of 119 males and 99 females during our CMR surveys. Mean values for unique males and females respectively (calculated using data collected from final captures for each individual) include: SVL (mm): 61.51 (SD=10.74) and 64.02 (11.84); TL (mm): 66.81 (14.24) and 59.47 (10.03); mass (g): 5.24 (2.60) and 6.24 (3.63). We found no significant difference in mass between the sexes. Significantly greater masses were found for females (t=-2.32, df=200.16, p=0.0106), however significantly greater masses were found for females (t=-2.32, df=210.00, p=0.021), and TL (t=4.42, df=216, p<0.0001) for males.

**Robust Design Models**

Goodness of fit tests applied to Cormack-Jolly-Seber models showed that the general model provided a good fit to the data, with slight under dispersion ($\chi^2=23.59$, df=38, $p=0.968$; $\hat{c}=0.62$, RELEASE, tests 2 and 3; $\hat{c}=0.99$, SE=0.020 [median $\hat{c}$]). The data did not therefore violate the model assumptions significantly. ‘No-emigration’ and random movement models combined to accumulate approximately 76% of the overall model support during primary periods (Table 1), it is therefore reasonable to assume that movement between secondary occasions was also either close to random or non-existent (Tolley et al., 2010).

The most parsimonious RD models estimated 30-day survival rates of 0.78–0.79 (95% CI 0.73–0.83) independent of both time and sex, accumulating approximately 47% of the model support (sum of AICc weights over Models 1–3, Table 1). Model 4 allowed for sex dependent survival independent of time, but its deviance was almost identical with Model 1; this shows that adding a parameter for the sex effect did not improve the fit of the model (Table 1). Time-dependent survival constrained by season improved model support more than five-fold compared to full time dependence (Model 5 vs. 18), but still had over three times less model support than the most parsimonious time-independent survival model (Table 1). The most parsimonious model estimated annual survival rate to be 0.05 ($S_a=0.7776^{12}\rightarrow S_a=0.049$).

Monthly abundance estimates ranged from 11.4 (6.9–26.2) to 50.4 (38.6–75.2) for males and from 13.7 (10.5–24.4) to 41.4 (31.4–63.3) for females within the most parsimonious model (Table 1, Fig. 3). The abundance estimates suggest a fluctuating population size, with a range of ca. 25–91 adult chameleons depending on the time of year (Fig. 3). Abundance fluctuated over the year, with typically 70–75 individuals inhabiting the site during warmer, dryer periods (February–April), dropping to typically 30–40 individuals during colder, wetter periods (June–October) (Fig. 3).

**Multi-Strata Size-Survival Models**

The GoF test showed that the model allowing for body-size, sex specific survival, growth and time-specific recapture (Model 7, Table 2) provided a good fit of the data ($\hat{c}=0.99$, SE=0.039). Three of the four most parsimonious models suggested size-dependent survival rates, accumulating approximately 90% of the model support (Table 2). The top model, with 72% of the model support, suggested size-dependent 30-day survival rates independent of sex or time (Table 2, Fig. 4). Chameleon growth was clearly size-class dependent (Table 2). During 30-day periods, chameleons most commonly grew into the next largest size class; however, growth across two size classes did occur (Table 3). Smaller chameleons were more likely to grow into the next size class than larger individuals.

Given the estimated survival and transition probabilities, chameleons that survived to the beginning of each age class spend on average 1.1 months in size class 40–50 mm, 1.7 months in size class 50–60 mm, 2.5 months in size class 60–70 mm and 6.3 months in size class >70mm. The increased residence times in the larger size classes are a result of both improved survival and a lower probability to transition into the next size class. Overall life expectancy of an individual in size class 1 was 3.4 months.

**DISCUSSION**

**Survival**

Over the one year period, chameleons showed size-dependent survival, where larger adults had higher survival rates than smaller individuals (Fig. 4), corroborating a short-term study on this population (Tolley et al., 2010). Survival was not sex dependent, and contrary to our expectations showed no seasonal effect.

There is no general trend for sex dependent survival across lizard species. Early studies suggest survival rates are not sex dependent (Turner, 1977; Schoener & Schoener, 1982); in contrast, more recent studies found sex dependent survival in a number of species (Andrews & Nichols, 1990; Watkins, 1996; McCoy et al., 2004; Bock et al., 2010; Tolley et al., 2010) and...
suggest underlying mechanisms linked to reproductive 'costs', conspicuous social behaviour and/or sexual size dimorphism (SSD). These more recent studies suggest the above behaviours/attributes increase the risk of predation within one of the sexes (Shine, 1980; Schoener & Schoener, 1982; Watkins, 1996; McCoy et al., 2004; Bock et al., 2010). The discrepancy appears to hinge on the associated reproductive costs, conspicuous social behaviour, and/or SSD within different lizard species and, when present, whether these attributes/behaviours increase the risk of predation. In all Bradypodion studied to date, females are larger than males (Stuart-Fox & Whiting, 2005; Stuart-Fox & Moussalli, 2007; Hopkins & Tolley, 2011), exhibit an aseasonal reproductive cycle and are capable of producing multiple clutches per year (Burrage, 1973; Jackson, 2007). Although Bradypodion reproduction costs and mating systems are not well-studied, other chameleon species (Chameleo chameleon, Furcifer labordi and F. verrucosus) are known to exhibit conspicuous social behaviour (mate-guarding and territoriality) and polygynous mating systems (Cuadrado, 2001; Karsten et al., 2009). The present results indicate a lack of sex dependent survival despite potentially conspicuous social behaviour, again suggesting there is no general trend for lizards.

Annual survival estimates for B. pumilum inhabiting the Noordhoek site are comparable with those for other small-bodied lizards (<100 mm SVL, Φ <0.30; Schoener & Schoener, 1982; Wright et al., 1984; Andrews & Nichols, 1990). Species-specific survival appears to be a function of predation intensity (Schoener & Schoener, 1982; Andrews & Nichols, 1990). Within the current study, RD analysis (omitting the effect of body-size) indicated a constant 30-day survival rate (S=0.78), extrapolated to yield an estimated annual survival rate of approximately 0.05. Bradypodion pumilum’s annual survival rate compares with those of Anolis species (lizards of similar body-size) inhabiting areas experiencing high levels of predation (Wright et al., 1984; Andrews & Nichols, 1990).

Interestingly, 30-day survival estimates within the most parsimonious RD models remained fairly constant throughout the study. Seasonal abiotic factors (temperature) often exert proximate influences on lizard life-history parameters, including survival (Dunham, 1981; Jones et al., 1987). Temperature is often linked to a species’ daily activity period, typically short or non-existent during colder months and longer during the warmer season (Porter & Tracy, 1983; Adolph & Porter, 1993). Populations experiencing warmer climates experience greater daily activity periods and yield lower annual survival rates; this suggests increased mortality in active (vs. inactive) lizards (Adolph & Porter, 1993). Long-term climate data for the city of Cape Town indicates a ±9°C temperature fluctuation between seasons per annum (South African Weather Service, 1961–1990). Although a ±9°C shift in ambient temperature between seasons may appear minimal, a 10°C shift in body temperature typically results in a 33% change in locomotor performance in most ectotherms (Anderson, pers. comm.). Therefore, we would expect to observe a significant decrease in B. pumilum daily activity during the winter; however, Anderson and Deban (2010) suggest that the thermal robustness of chameleon tongue projection enables at least temporary continued daily activity despite lower ambient- and body-temperatures during winter. The thermal robustness of chameleon tongue projection may widen B. pumilum’s thermal niche, leading to relatively constant daily activity periods (for feeding) throughout the year in the mild climate of Cape Town. This phenomenon likely explains the non-season-dependent survival experienced by these chameleons. Alternatively, if the sample size included within the RD models was too low, temporal effects on survival may have gone undetected.

Abundance

There was an increase in abundance observed between the first and second primary capture sessions (November and December 2009), but it is difficult to ascertain whether this effect was real, or rather an artifact of optimizing the CMR survey. Our analysis accounted for variation in capture probability, making the latter explanation less likely. Variation in abundance was therefore probably driven by variation in recruitment. Even though B. pumilum can reproduce at any time of the year, it is likely that recruitment predominately occurs during summer months which could have led to the observed abundance estimates. However, with one year of data, we cannot say whether the observed pattern reflects typical seasonal changes over the long-term, or was an aberrant event.

CONCLUSION

Despite the potential for stochastic events and/or the effects of habitat alteration, chameleons inhabiting the Noordhoek site maintained constant survival and a persistent, stable population. However, B. pumilum experienced low survival compared to larger vertebrates which may increase their sensitivity to perturbations in the system and/or stochastic events. Whether this species exhibits an increased sensitivity predominately hinges on whether their reproduction rate (currently unknown) compensates for their survival rate. The Cape dwarf chameleon exhibits aseasonal reproduction and is capable of producing multiple clutches per year (Jackson, 2007). Year round reproduction should allow for B. pumilum persistence in altered habitats despite low survival because it allows the species to take rapid advantage of suitable conditions. Alternatively, these biological traits may make B. pumilum prone to large demographic fluctuations thus yielding a high risk of local extinction.

This study exemplifies both the necessity and benefits of estimating demographic parameter values for reptile populations inhabiting altered landscapes. Findings such as these can be used in a conservation context because the resilience of a species to transformed habitat is a primary factor in determining IUCN Red List status, and can be used for applied management in restoring or maintaining connectivity in semi-urban areas such as this. Results support many of the initial hypotheses and further our understanding of population demography.
and habitat use for reptiles inhabiting transformed landscapes near urban areas as well as providing empirical data for comparison in future study focused on population demography and stability for small-vertebrate populations. Suggestions for future study include estimating B. pumilum reproduction rates within transformed landscapes, the use of microsatellite markers to estimate temporal genetic variation and stability and investigations focused on vegetation preferences based on body-size and/or sex.

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