BACK TO THE BRINK: POPULATION DECLINE OF THE ENDANGERED GRASSLAND EARLESS DRAGON (TYMPANOCRYPTIS PINGUICOLLA) FOLLOWING ITS REDISCOVERY

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Abstract.—Lizard populations are under serious threat through widespread decline and predictions of multiple extinctions through climate change. Yet detecting specific instances of decline remains problematic in many situations because of inconsistent and sparse data. We assessed the stability of populations of the endangered Grassland Earless Dragons (Tympanocryptis pinguicolla) conducted after its rediscovery using capture rates at 10 sites (from 23 surveyed) and survival and population size estimation at one intensively studied site. We show a gradual non-significant decline in population size across all sites from 1995 followed by a dramatic reduction (88%) from 2006 at the most densely populated site. Using mark-recapture-release approaches, we estimate annual survival at that site to be low (0.017 to one year of age and 0.024 to adulthood) over the three years of the study. Taken together, these data suggest a regional decline among T. pinguicolla populations that place the species in grave jeopardy of becoming the first confirmed reptile extinction in Australia since European settlement. The key factors for basing further hypothesis driven monitoring include drought habitat cover (or the effects of grazing) and habitat fragmentation. We agree with other conservationists that for highly endangered species, there may not be the time required to conduct long-term monitoring. However, by making good use of even disparate past surveys, a case can be made for trends in population size. We urge that even data collected in an ad hoc manner be examined to help plan management programs for rare or endangered species.

Key Words.—Agamid; Grassland Earless Dragon; management; mark recapture; natural temperate grassland; population trend; survival; Tympanocryptis pinguicolla

INTRODUCTION

The accurate estimation of trends in population size is central to identifying species at risk of extinction. Such estimations can be extremely challenging, particularly when populations are small or cryptic (McCulloch and Norris 2001; Melbourne et al. 2004; Humbert et al. An undiagnosed decline may lead to inappropriate management resulting in a failure to prevent extinction. The key issue is gathering data of sufficient quality to obtain the precision necessary to detect a true decline (Fagan et al. 2010) and the demographic and ecological information necessary to be able to identify agents of decline (Hone et al. 2005). The difficulty of doing so is magnified by the smaller population sizes often associated with endangered species (McCulloch and Norris 2001; Melbourne et al. 2004). Furthermore, the use of monitoring data to test for trends as a conservation management practice has been questioned (Marris 2007). On the other hand, longterm monitoring has been identified as having ecological 20% (Sinervo et al. 2010).

value for a range of purposes (Lindenmayer and Likens 2010). In all cases, monitoring that is well designed, consistent, and focused is recommended (Marris 2007; Martin et al. 2007; Lindenmayer and Likens 2010). However, that does not mean that ad hoc data should be overlooked. Many conservation decisions are made on disparate and less than adequate data (Robertson and Evans 2009), so making the best use of even poor quality data becomes a high priority.

However, attempts to identify declining reptile populations are hampered by a lack of duration or consistency in survey data (Pechmann and Wilbur 1994; Engler et al. 2004; see the review by Gibbon et al. 2000 for a few examples). Identifying declining populations is important for all taxa including reptiles, which are often cryptic and difficult to capture or monitor. It is also likely that reptiles will be dramatically impacted by rising temperatures as a result of climate change; by 2080 local extinctions of lizard species are projected to reach 39% worldwide, and species extinctions may reach Lizards globally are



FIGURE 1. Female, gravid Grassland Earless Dragon (*Tympanocryptis pinguicolla*), Australian Capital Territory, Australia. (Photographed by Wendy Dimond).

threatened from increased habitat fragmentation and development, introduced invasive species, environmental pollution, disease, unsustainable use and climate change (Gibbon et al. 2000), and contractions in the distribution of reptiles worldwide are well documented (Díaz et al. 2000; Brown et al. 2008; Chapple et al. 2008; Pike and Roznik 2009; Smith et al. 2009). It is therefore important that all available data be used to undertake adaptive conservation management, even while consistent monitoring is being conducted.

The Grassland Earless Dragon (Tympanocryptis pinguicolla; Fig. 1) is a small (55 mm SVL) agamid that provides a clear example of this issue. Once having a broad distribution in Australia, T. pinguicolla was known from populations in southern Victoria (McCoy 1890; Mitchell 1948), the tablelands in southern New South Wales (NSW), including the Australian Capital Territory (ACT), and as far north as Bathurst (Osborne et al. 1993b). It is currently only known from Cooma in NSW and in the ACT region, and is believed to be in However, there has been little consistent monitoring employed on this species in the past and, in fact, T. pinguicolla were thought extinct in the ACT until an opportunistic observation near Canberra (ACT) in the early 1990s (Osborne et al. 1993a). Subsequently, rapid surveys were employed to investigate the extent of their distribution, but none were repeated in such a way as to provide rigorous estimations of population demographics over time. Consequently, T. pinguicolla is considered endangered nationally (Environment Protection and Biodiversity Conservation Act 1999) and at a state level in the ACT, NSW, and Victoria (Robertson and Cooper, unpubl. report). It is also listed as Vulnerable by the International Union for the Conservation of Nature (IUCN). This species is highly representative of the

conservation issues managers are faced with; that is, a highly cryptic species that is a specialist of an endangered ecological vegetation community (natural temperate grassland; Kirkpatrick et al. 1995).

In this paper we report how population demographics have been investigated for a previously poorly studied population of *T. pinguicolla* in southeastern Australia. We provide systematic data on survival and abundance for comparison with other populations and to provide hypotheses for adaptive management, thus addressing an essential step in effective monitoring (Lindenmayer and Likens 2010). We discuss the direct link between having adequate monitoring practices and the ability to set conservation priorities. Finally, we use this dataset to demonstrate some important considerations in planning and implementing similar studies in the hopes that it will be of use to other researchers.

MATERIALS AND METHODS

Study site.—We report on research by various groups at 23 native grassland sites in the ACT region from September 1993 to March 2009 (Fig. 2). The grassland sites covered in this paper support Austrodanthonia-Austrostipa native grasslands, and all have been used for livestock grazing. These locations vary in their exposure to cultivation from never cultivated to most recently cultivated over 30 years ago. Generally, these sites are characterized by open structured tussock grasslands with little or no trees and shrubs (Osborne et al. 1993a; Osborne et al. 1993b), limited or no fertilization or pasture improvement, and comprising slightly higher ground in well drained areas (Osborne et al. 1993a). All sites are within 13 km of the Canberra International Airport and climate records from the airport (BOM,

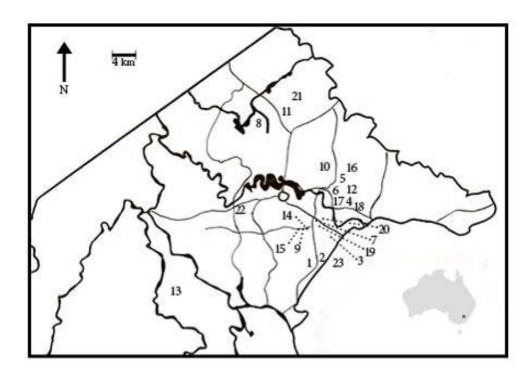


FIGURE 2. Map of the Canberra region of Australia showing the 23 survey sites. Thick lines indicate main rivers, lakes, and the Australian Capital Territory border. Thin lines indicate main arterial roads. 1 Jerrabomberra West (Jerrabomberra Valley Grassland Reserve West); 2 Jerrabomberra East (Jerrabomberra Valley Grassland Reserve East); 3 Bonshaw; 4 Pialligo; 5 Majura (Majura Training Area); 6 Airport (Canberra International Airport); 7 AMTECH (Advanced Manufacturing Technology Estate); 8 Belconnen Naval Base; 9 Callum Brae; 10 Campbell Park; 11 Crace; 12 Malcolm Vale; 13 Urambi Hills NP; 14 Australian Geo Site Office; 15 Therapeutic Goods Association; 16 Avonley; 17 Fairbairn; 18 Dundee; 19 Cookanalla; 20 Fyshwick; 21 Mulanggari Grassland Reserve, 22 Weston 23 Queanbeyan Nature Reserve.

Bureau of Meteorology, data set. Available from http://www.bom.gov.au/ [Accessed 15 June 2011]) show that since 2000, this area has been subject to low winterspring (June-January) rainfall compared to the climate normals (Fig. 3a) and rising mean maximum spring (November-January) temperatures on cloudless days (Fig. 3b).

Data collection.—Data covering 1993 until 2002 were collected from reports and theses (see Appendix 1 for full list of data sources); we collected data from 2003 until 2009. Two types of trap have been used to search for *T. pinguicolla*: pitfalls or tubes (artificial shelters). Pitfalls consisted of a sleeve of PVC piping 9 cm in diameter and 12 cm deep, with a dirt base, shaded by a 200 x 200 mm metal shelter mounted on wire legs. In some surveys, pitfalls were augmented with a short metal drift fence (80 mm tall, 500 mm long). Tubes were made of a piece of capped PVC drain pipe (31 mm diameter x 142 mm deep), lined with brown paint and sand, slipped inside an outer sleeve and shaded by a 200 x 200 mm canvas or metal roof. Both types of traps were embedded vertically into the ground flush with the surface.

Trapping arrays have comprised three main

configurations: (1) Linear transects, which ranged in length from 450 m to just over a kilometer and from one to 11 transects per site with traps placed either 5 m or 10 m apart; (2) Groups, with eight pitfall traps arranged in four pairs (with a 400 x 400 mm cover) 5 m apart in a square; or four tubes arranged on a 14.2 m diagonal; (3) Grids, which took one of two forms: a single grid consisting of 19 x 11 pitfall traps at 5 m intervals covering 0.45 ha, which was placed at one site (used 1993-1996), and a standardized grid system (2002-2009), which comprise tubes placed in a seven by eight grid spaced at 10 m intervals and covering 0.42 ha. Grids were separated by no less than 100 m. These three configurations and two trap types resulted in six trapping methods; see Appendix 1 for method and survey effort at each site, each survey period.

Capture-mark-release methods were employed in all lizard surveys with marking by toe clipping (1994–1996), non-toxic sharpie pen, or photographic pattern recognition. *Tympanocryptis pinguicolla* have dark cross-bars located between three pale longitudinal stripes that run the length of the dorsal surface (Wilson and Swan 2010). This pattern of bars and stripes is unique to each individual and does not change over time. We used a six point coding system based on the pattern of

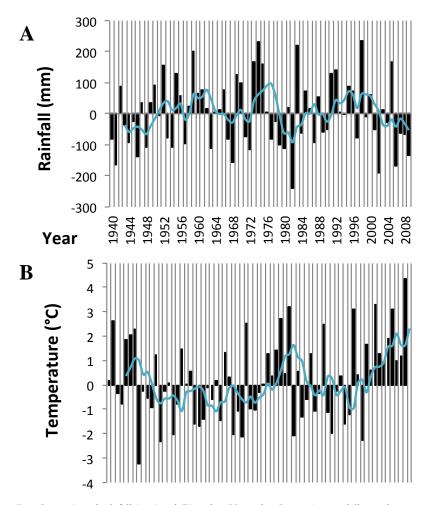


FIGURE 3. (A) Winter (June-January) total rainfall (mm) and (B) spring (November-January) mean daily maximum temperature anomalies at the Canberra Airport, Australian Capital Territory, Australia. Climate normals were calculated from 1961 to 1990. The blue line is the five year running mean.

crossbars and stripes (code available on request) to facilitate identification. A blind trial of 83 reference photos against 140 test photos confirmed this approach as highly accurate (134, 97% correct).

We weighed (g), measured the snout vent length (SVL) and tail length (mm), and determined the sex of all individuals we captured. We defined adults by the size of the smallest gravid female (all individuals > 48.3 mm SVL) identified over all captures, and juveniles by the size of the smallest individual captured during the breeding season (i.e. the period just before hatching, October-November, and in summer, individuals < 38.3 mm SVL). We categorized all individuals between those two size classes as non-breeding sub-adults.

We assigned sex by assessing hemipenal swelling at the base of the tail and by inspection of the cloaca to identify the ends of the hemipenes; visible as red dots on either side of the vent in males. We validated this method by carrying out a blind test of 11 museum specimens that we dissected to confirm sex. We identified 10 of the 11 specimens correctly with the incorrect specimen being a juvenile. Consequently, we report sex here for adults only.

Population trend estimation.—Given the anecdotal evidence suggesting that lizards avoid pitfall traps after being captured once, we standardized all surveys to a common unit of trapping rate calculated as the number of unique individuals per 1,000 trap days. The number of unique individuals does not allow us to include recaptures in the analysis and avoids the problem of trap happiness or shyness. In an attempt to make the best use of non-standard data given the diversity of trapping regimes (see Appendix 1) used over the years, we averaged trap rates between 1994 and 2001 and between 2002 and 2009 at each site, and compared them using a one-tailed sign test ($\alpha = 0.50$) where pluses and minuses were assigned to trapping rates between the two periods.

analyses reported in this study.

To further investigate population trends, established intensive trapping regimes at two populations; Majura 2002–2009 and Jerrabomberra West 2006–2009 (Jerrabomberra West and Majura; Fig. 2). The data for these two sites share a common trap array (seven by eight tubes in a grid spaced at 10 m intervals and covering 0.42 ha) and we monitored them from 2006 to 2009. We estimated population trends using an exponential growth state space (EGSS) model with restricted maximum likelihood (REML) estimates (Dennis et al. 2006; Humbert et al. 2009). This approach assumes both observation error and environmental process noise, and can accommodate missing data. Trend analysis was performed with R 2.10.1 for Windows.

We used an equivalence test based on confidence intervals to test for a significant trend (μ) . This tests whether the true trend is negligible as opposed to nonzero. An equivalence region (b_b, b_u) is defined as that region that includes all values of the trend parameter that are considered negligible (Dixon and Pechmann 2005). We used the bounds suggested by Dixon and Pechmann (2005) that correspond to a doubling or halving time of 10 years (-0.0694, 0.0693) for populations of shorter lived species with large annual fluctuations in abundance. There are no degrees of freedom involved in the Dixon/Pechman equivalence test, as applied to our trend model. Instead, we used a normal distribution for the test statistic:

test statistic: $z = (\mu - b_l)/\sqrt{Var(\mu)}$ $H_1: \mu > b_l$ P-value is area to the right of z in a standard normal distribution

test statistic: $z = (\mu - b_u)/\sqrt{Var(\mu)}$ $H_0: \mu \geq b_u$ $H_1: \mu > b_n$ P-value is area to the left of z in a standard normal distribution

We conclude that a trend is negligible (that is, $\mu \le b_1$ or $\mu \ge b_u$) if both P-values are less than 0.05 or the confidence interval for the trends lie entirely within the equivalence region (Schuirmann 1987).

Survival *estimation.*—The Cormack-Jolly-Seber (CJS) model estimates survival as the probability of surviving between successive surveys given that temporary and/or permanent emigration is > zero (Warner and Shine 2007), and capture probability as the probability of encountering an individual at a particular time. The Multistage Mark Recapture (MSMR) model estimates survival (the probability of surviving between successive surveys in a particular stratum), capture probability (the probability of encountering a live animal at a particular time in a particular stratum) and transition

Unless otherwise stated, we used SPSS 17 for the probability (the probability that an individual moves between stratum; White et al. 2006). We created likely candidate models (as opposed to all possible combinations of the parameters) based on our knowledge of the system and factors that were both likely to affect the population and that were supported by the sparseness of the data (Burnham and Anderson 2001). We selected the most parsimonious models based on Akaike's information criterion corrected for bias (AICc). The notation of Lebreton et al. (1992) is used for model specification. We used the bootstrap approach for goodness-of-fit implemented in MARK (White and Burnham 1999) to investigate the fit of models. The inverse logit link function was used to calculate actual parameters (local survival rates and recapture rates) from untransformed model parameters. We conducted capture sessions when the lizards are most active (February to mid-March and October to mid-November) and therefore most susceptible to encountering artificial burrows. We conducted five trapping periods between February 2006 and March 2008 consisting of 18-20 trapping occasions.

> We used the CJS model on the full complement of adults only (103 individuals) to assess an assumption of no difference in survival between sexes. In that analysis. individuals were recorded as detected when first encountered as an adult (SVL > 48.3 mm). The adult only CJS analysis modeled sources of heterogeneity by considering the effects of sex (g) and time periods (p) on adult survival and recapture probabilities. We created capture histories from all 98 encounter occasions across the three years recognizing nine (five capture, four noncapture) time periods, within and between trapping and resulting in the assessment of six models (Table 1). Of these, two models were tested for goodness of fit:

$$\Phi_{\rm p}$$
, $P_{\rm g}$ and $\Phi_{\rm g}$, $P_{\rm g}$;

TABLE 1. Comparison of Cormack Jolly Seber, survival and resighting models for adult Tympanocryptis pinguicolla only at Jerrabomberra Valley Grassland Reserve West, Australian Capital Territory, Australia, over four grids. Superscripts are aFactors affecting survival (Φ) and recapture (P) probability: g, sex; p, time period; bNumber of parameters in model; Akaike's information criterion; dDelta AIC_c indicating difference in AICc value form that of the best model; and ^eAkaike weight indicating relative support for the model.

Model ^a		- K ^b	AIC, c	$\Delta_{\mathrm{i}}^{\;d}$	w _i e	
Φ	P	K	AiCc	Δ_1	W1	
p	g	11	1305.1	0.0	0.96	
p		10	1311.5	6.4	0.04	
	g	3	1345.3	40.2	0.00	
g	g	4	1346.3	41.2	0.00	
g		3	1349.2	44.1	0.00	
		2	1349.3	44.2	0.00	

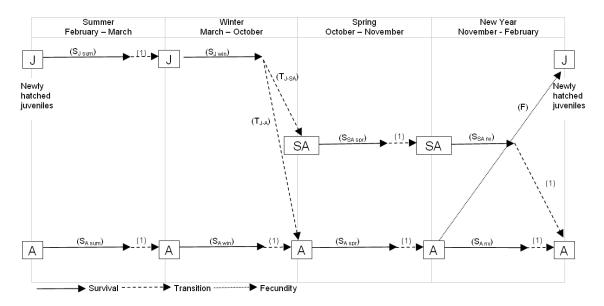


FIGURE 4. Population model outline used to estimate probability of survival and transition for each stage and population viability in Tympanocryptis pinguicolla. Parameters used in population model: $S_{A sum}$, survival of adults in summer; $S_{A win}$, survival of adults in winter; $S_{A spr}$, survival of adults in spring; $S_{A ny}$, survival of adults in new year; $S_{SA spr}$, survival of sub-adults in spring; $S_{SA ny}$, survival of sub-adults in new year; $S_{J sum}$, survival of juveniles in summer; $S_{J win}$, survival of juveniles in winter; T_{SA-J} , transition probability of sub-adults to juveniles T_{J-SA} , transition probability of juveniles to sub-adults; F_{J} , fecundity.

where Φ shows factors affecting survival and P shows factors affecting resighting (Lebreton et al. 1992). We then compared simpler models by removing the effects of sex and time periods so that (.) indicated no difference between time periods or sex.

We used all 220 individuals in the MSMR model, with the lizards produced at the site recorded as first sighted during the summer trapping period. Specifically, we modeled sources of heterogeneity by considering the effects of stage (s), where stage refers to adult, sub-adult or juvenile; time periods (p); and period type (x), where the nine periods were combined into four period types referred to as summer (February-March), winter (March-October), spring (October-November) and new year (November-February). To test for a difference between adult and sub-adult survival and recapture probabilities, we combined adults and sub-adults for some models; in our notation we referred to this as age (a). We fitted a candidate model set of eight models to the encounter histories. Survival (S) and recapture (P) were allowed to vary with period-type, time period, stage and age and interactions of period type with age and stage (x*s) and (x*a) and time period with age (p*a). Survival and recapture models were not allowed to vary with time period as an interactive effect with stage (p*s) because this model required too many parameters to be estimated for the available data. We set transition parameters (ψ) to vary by the interactive model of period type and stage. This provided the only biologically reasonable model for transitioning given our population outline (Fig 3). In every model, we fixed all but nine transition parameters to zero because individuals could not move to a smaller stage. We set seven transition parameters to one; all individuals in the summer and spring periods stay in their stage, in winter and new year periods, all adults stay adults and in the new year period all sub-adults become adults. The only unknown transitions in our model are from juveniles to sub-adults and juveniles to adults, which were estimated in the winter period (Fig. 4). We first compared candidate models for resighting using the most complex survival model S_{p*a} as recommended by Lebreton et al. (1992). We then compared the survival models using the best resighting model. The global model for this analysis was

$$S_{p*a}P_{p*a}, \psi_{x*s}$$
.

We calculated monthly survival for each stage and period from the best MSMR model. We calculated survival to one year as the product of the conditional probabilities of surviving each month.

Population size and density.—We estimated the population size of adults, sub-adults and juveniles on any given day, over the four trapping grids at Jerrabomberra West. We used the best multistrata model,

$$S_{x*a}P_{p*a}, \psi_{x*s}$$

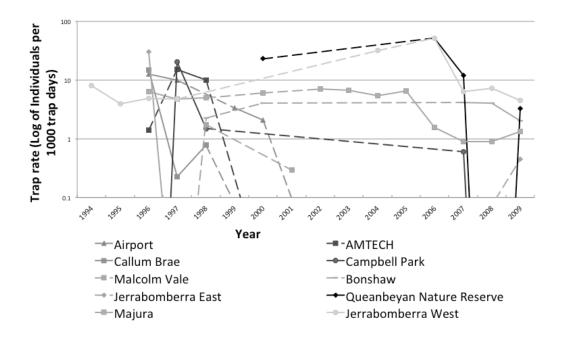


FIGURE 5. Trap rate (log of individuals per 1000 trap days) over time (years) for all sites where *Tympanocryptis pinguicolla* have been detected and which have been surveyed more than once. To show trend more clearly, connecting lines were dashed where there was more than one year between surveys. Zero captures were increased to slightly positive to allow graphing on a log scale (See Fig. 2 for site abbreviations).

to obtain an estimate of resighting probability (P) for each period. The estimated population $\operatorname{size}(\hat{N})$ was given by n/P where n was the average number of individuals seen each day of the trapping period.

To estimate density, we took the daily population estimates and employed White and Shenk's (2001) formulation to estimate density given \hat{N} and the proportion of time radio tracked individuals spent in traps (p_i) . We used radio-tracking data from Stevens et al. (2010), which were collected during the first period of trapping (summer 2006) and occurred while our traps were open. Data were collected at each radio-tracked sighting identifying where the individual was caught (i.e., in a natural burrow, tussock, or artificial burrow; Stevens et al. 2010). Thus $p_i = g_i/G_i$, where p_i is the probability of a location being in an artificial burrow for animal i, estimated by the number of total locations (G_i) divided into the number of locations found in artificial burrows (g_i ; White and Shenk 2001). The mean (\bar{p}) and its variance $[V\hat{a}r(\bar{p})]$ of the p_i s can be used to correct the population estimate (\hat{N}) and its variance $|V\hat{a}r(\hat{N})|$ to obtain an unbiased estimate as

$$D = \hat{N}\overline{p} / A ,$$

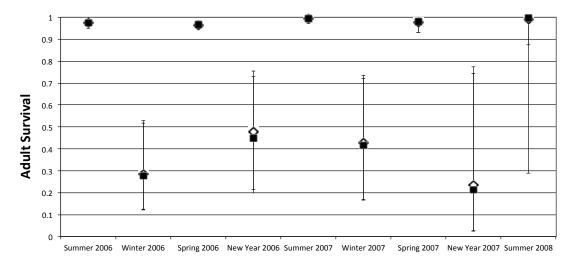
with variance estimated as

$$V\hat{a}r(\hat{D}) = \hat{N}^{2}V\hat{a}r(\overline{p}) + \overline{p}^{2}V\hat{a}r(\hat{N})/A^{2},$$

assuming that \hat{N} and \bar{p} are independent (White and Shenk 2001).

RESULTS

Population size trends.—Between 1997 and 1999, 10 of the 23 sites were found to contain T. pinguicolla. Dramatic changes in trap rates occurred between 1997 and 1999 in populations at the Airport, AMTECH, Callum Brae, Campbell Park, Malcolm Vale, and Jerrabomberra East with all showing a substantial decrease over those years (Fig. 5). These populations do not appear to have recovered from those declines with (Airport, AMTECH, Callum Brae and several Jerrabomberra East) no longer, or only just, detectable by the late 2000s. Conversely, populations at Bonshaw, Jerrabomberra West and Majura showed no clear trend during this initial monitoring. Overall, the majority of populations exhibited decreases in trap rates over the long term, while two populations (Queanbeyan Nature Reserve and Jerrabomberra West) experienced at least one large population spike somewhere between the years 2000 and 2006. Bonshaw was the only site that



Time period

FIGURE 6. Mean adult *Tympanocryptis pinguicolla* survival compared between the two best mark recapture models. Open diamonds are for the model Φp , P. and filled squares are for Φp , Pg, error bars are 95% confidence intervals.

maintained a stable population throughout the 16 years of trapping.

We found average trap rates had decreased at seven of the nine sites for which surveys had been conducted in both periods, giving a marginally non-significant result (P = 0.0898). We estimated declines for both our intensively studied populations at Majura (n = 7; 2003– 2009) and Jerrabomberra West (n = 4; 2006–2009) of μ = -0.18 (95% CI -0.64–0.29) and μ = -0.79 (95% CI -1.41-0.17) respectively. Large confidence intervals, arising from extremely low capture rates in the Majura trend, means that we are unable to say with certainty that the trend is significantly different from the negligible region (i.e. around 0; P = 0.323 and P = 0.148, for b_l and b_{μ} respectively) but it is clear that the trapping rate at the Jerrabomberra West site has declined significantly and is well below the negligible region (P < 0.001 and $P \sim 0$, for b_l and b_u respectively).

Survival.—We found no difference in survival between sexes but some differences in recapture

probability (Table 1). Our goodness of fit tests based on parametric bootstrap simulations and the ratio of observed to expected deviances, indicated that the models, $\Phi_{\rm p}$, $P_{\rm g}$ and $\Phi_{\rm g}$, $P_{\rm g}$, fit the adult encounter data well with under-dispersion (i.e. less variation than expected by chance) detected (GOF test, $\hat{\rm c}=0.68$ and 0.48 respectively). We followed the recommendation of not adjusting $\hat{\rm c}$ when it is less than one (i.e. leave $\hat{\rm c}=1$; Schoener and Schoener 1978; Wolfinger 1996). In addition, our sensitivity test on the models with fluctuations in $\hat{\rm c}$ (0.5–1.5) resulted in minimal change in model rankings.

Comparison of the survival models for adults showed p on its own to be the best model (Table 1), meaning survival was equal for the two sexes but changed with time period. However, comparison of the recapture models showed that g was the best model indicating no difference in resighting probability over time periods but some differences between sexes. The second best model did not include sex in either the survival or recapture models and was much lower weighted than the best

TABLE 3. Monthly survival estimates for each period and stage using the best MSMR model S_{x^*a} , P_{p^*a} , ψ_{x^*s} . aSee Fig. 3 for explanation.

Period		Stage	
Pellou	Adults	Juveniles	Sub-adults
C	0.74	0.48	
Summer	(0.53 - 0.91)	(0.36 - 0.59)	
XX7. 4	0.82	0.86	
Winter	(0.71 - 0.89)	(0.80 - 0.91)	
α .	0.43	, , , ,	0.43
Spring	(0.28 - 0.55)		(0.28 - 0.55)
NI N/	0.78		0.78
New Year	(0.64 - 0.87)		(0.64 - 0.87)

TABLE 2. Comparisons of multistage survival models for all *Tympanocryptis pinguicolla* at Jerrabomberra Valley Grassland Reserve West, Australian Capital Territory, Australia over four grids using the best resighting model (p*a) and transition model (x*s). See text for description of model and Table 1 for superscripts besides aFactors affecting survival (S): p, time period; a, age; s, stage; x, period type

Survival Model ^a	K ^b	AIC _c ^c	Δ_i^{d}	W _i ^e
x*a	15	3399.6	0.0	0.56
X	13	3400.8	1.1	0.32
x*s	17	3403.7	4.0	0.07
p	18	3405.3	5.7	0.03
p *a	23	3408.5	8.9	0.01
S	11	3469.1	69.5	0.00
	10	3470.1	70.5	0.00
a	12	3470.7	71.1	0.00

model (4%; Table 1). The difference in resighting models made little difference to survival (Fig. 6) suggesting that the exclusion of the parameter of adult sex in the final model would have little effect on the survival estimates.

Our goodness of fit test for the multistage, full data analysis indicated that the global model, $S_{p*a}P_{p*a}$, ψ_{x*s} fitted the encounter data well with some underdispersion detected (GOF test, $\hat{c} = 0.68$). As in the first analysis, we left ĉ unadjusted (Wolfinger 1996). The best resighting model was the global model p*a, indicating that resighting changed over time (over all time periods and years) and did not differ between subadults and adults but did between these and iuveniles. Overall, recapture rates were low, ranging from 0.17-0.45. Recaptures increased over time (i.e. with a decrease in individuals captured). Juvenile recaptures were slightly higher than adult recaptures for the summer periods (when juveniles were present and trapped) until summer 2008, when the adult recapture rate was slightly higher (0.30 vs. 0.29).

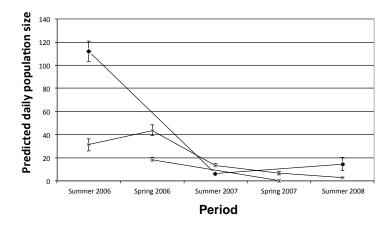
Our best survival models for the multistage analysis showed that while survival did not differ between years, it did vary with period type (x; Table 2). There is also some indication that there was a difference in survival between juveniles and adults (including sub-adults). However, this difference was only slight given that the change in AIC between these two best models is < 3.0 (White and Burnham 1999; Burnham and Anderson 2002).

Overall, monthly survival, calculated from the best survival model (x*a; Table 2) was lowest in spring (0.43) and highest in winter (0.86; Table 3). Juveniles were present only in the summer and winter periods with survival between adults and juveniles comparable in winter (82% adults; 86% juveniles) but 35% higher for adults in summer (Table 3). These monthly survival values result in yearly values of survival in the first year to adulthood being 0.017 and annual adult survival 0.024.

Population size and density.—We revealed a decline in numbers for all stages over the three years of the study at Jerrabomberra West from the average daily population size and density estimates (Fig. 7). In the summer period of 2006, there were approximately 3.5 juveniles for every adult, which dropped to approximately 0.5 juveniles for every adult in the following year (Fig. 7a). Juveniles were the only stage to show a slight increase at the end of the study (summer 2008) reaching a ratio of approximately 5:1 juveniles to adults. As expected from the high recruitment of juveniles in 2006, the number of adults showed a slight increase from summer 2006 to spring 2007. This same recruitment-facilitated increase did not occur in spring 2008 and the numbers of adults continued to decrease into summer 2008. Sub-adults are considered part of the population only in the spring period (Fig. 4) and showed a decline over the two springs sampled in this study to almost none present in spring 2007.

DISCUSSION

Our data demonstrate that T. pinguicolla has experienced a dramatic decline in the ACT between the time of its re-discovery in 1993 to 2009. Over that time, average trapping rates have decreased across all known sites from eight individuals per 1000 trap nights to less than two. Our analyses of trends in two of the most intensely studied populations show this situation to be severe. The extent of the decline is most evident in the largest known population (Jerrabomberra West), where density collapsed from 19.8 individuals per ha in 2006 to 2.4 in 2008. In addition to these unambiguous declines in abundance, presence/absence surveys conducted since 2007 show that T. pinguicolla are no longer detectable at three (30%) of the 10 sites formerly known to contain populations of T. pinguicolla, suggesting that at least three populations are close to, or have become locally extinct (Appendix 1). In all but one (Bonshaw) remaining sites where T. pinguicolla are still present, trapping rates are substantially lower than those rates A



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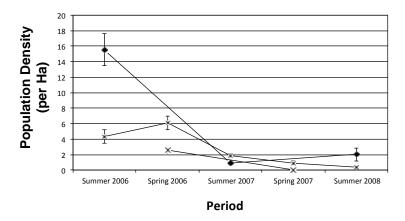


Figure 7. (A) Average daily population size (±1 standard error) over four trapping grids and (B) Population density in numbers per hectare (±1 standard error) of *Tympanocryptis pinguicolla* in each trapping period at Jerrabomberra Valley Grassland Reserve West, Canberra, Australia. Juveniles are depicted by diamonds, sub-adults by crosses, and adults by squares.

observed in previous surveys. Taken together, these data suggest that this species has experienced a decline across its known distribution in the Canberra region that is both sharp and substantial and threatens the very existence of this species.

It is clear *T. pinguicolla* is in decline, but the causes of that decline are not readily identified. As for many lizard species, declines may be closely related to habitat degradation (Driscoll 2004; Gardner et al. 2007; Brown et al. 2008). At Majura, overgrazing reached damaging levels earlier than in the other lowland grasslands (ACT Government 2010). In addition, the airport undergoes regular mowing, Campbell Park was severely overgrazed by 2007, and AMTECH and Callum Brae have increased in weediness (Wendy Dimond and Will Osborne, pers. obs.). Lizards worldwide are being impacted by habitat degradation and fragmentation; however, there are few

published studies that describe the details of these cases in comparison to the concern noted (Gardner et al. 2007). By identifying reduction of vegetation cover in grasslands as a possible factor for the declines of this species, we can formulate an hypothesis that both adaptive management and directed monitoring can be used to test. Focusing on the grassland habitat as well as the lizards broadens the implications of the study to include other grassland specialists. In addition, natural grassland habitats are highly endangered in both Australia and around the world (Kirkpatrick et al. 1995; Chape et al. 2008).

The data indicate declines in *T. pinguicolla* populations across the ACT and the extreme drought conditions experienced in southern Australia (Ummenhofer et al. 2009) suggest that rainfall and temperature have been key drivers of the observed

decline. In particular, it is clear that in the Canberra region, winter/spring rainfall has been below normal levels since 2006 and was below normal for three of the five years before that. In addition, the spring period has experienced higher than normal temperatures in eight of the last 10 years since 2000. As ectothermic animals, lizard survival and reproduction is likely to be highly affected by both temperature and rainfall (Marguis et al. 2008). Winter and spring rainfall have been shown to be positively associated with reproductive output in Uta stansburiana and several Ctenotus species (Hoddenbach and Turner 1968; James 1991). In addition, rainfall preceding the reproductive period has been suggested to influence the timing of reproduction (Bradshaw et al. 1991), number of clutches produced per female each year (Knapp et al. 2006), clutch size (Worthington 1982; Patterson 1991), egg size (Jordan and Snell 2002), and recruitment of lizards (Mayhew 1966; Dickman et al. 1999). Dry conditions have been shown to be an ultimate factor in forcing a lizard population to abandon reproduction altogether (Nagy 1973). Temperature may affect reproduction by modifying time of activity, as when temperatures are high activity can be reduced to prevent overheating (Adolph and Porter 1993). reduction in activity during spring may reduce encounters with members of the opposite sex and hence opportunities for mating. In addition, activity has been shown to be positively related to total annual fecundity (Adolph and Porter 1993). Changes in temperature may also influence the population sex ratio in species with temperature-dependent sex determination (Mitchell and Janzen 2010) by skewing sex ratios, although it is unknown if T. pinguicolla exhibits such a mode of sex determination. Finally, variation in precipitation coupled with temperature may lead to dramatic changes in plant and insect numbers (Hunter et al. 2001: Staley et al. 2007), which in turn may limit the resources available to T. pinguicolla and cause fluctuations in population size and density (Ballinger 1977: Germano and Williams 2005).

Our analysis showed very low survival rates, with survival in the first year to adulthood being 0.017 and annual adult survival 0.024. However, these values did not differ between years during the decline suggesting that actual survival did not change. This may reflect the reduced accuracy caused by the smaller numbers of individuals captured, which would make differences between years harder to detect. Nevertheless, our data do not support the proposition that decreasing survival over years was a key proximate cause of the observed population decline (Fig. 6). Changes in survival often result from seasonality, which can affect many aspects of a lizard's biology and in turn affect its life history and demography (Lemos-Espinal et al. 2003). Our data show that survival among adult and juvenile T. pinguicolla is highest during the winter period when

most individuals enter torpor and movement decreases significantly (Stevens et al. 2010), and is lowest for adults during the spring period when breeding and laying is occurring, and lowest for juveniles during summer (following hatching). This pattern is similar to that seen in the spinifex-inhabiting agamid lizard *Amphibolurus fordi* where most adults died in January after reproducing, when they were one year of age (Cogger 1978).

Although we do not show a reduction in survival across years, survival rates in T. pinguicolla do appear suppressed. In most lizards, mortality among juveniles exceeds annual mortality among adult animals (Rogovin and Semenov 2004), and in stable age populations, annual juvenile survival for lizards is expected to be 13% lower (on average) than adults (Pike et al. 2008). Clearly the Jerrabomberra West population is not stable. as evidenced by the closer to 30% difference between annual adult (0.024) and hatchling to one year of age (0.017) survival. While this could be an artifact of juveniles dispersing to new areas and consequently having lower recapture rates (Pike et al. 2008), our population recapture rates were higher or similar for juveniles as for adults. Pike et al. (2008) report that the average annual adult survival for a range of 20 species of lizards was around 0.4, which is higher than for our population (0.024). However, these values were for populations that were near stable in size unlike those likely to be seen in declining populations of reptiles (Berglind 2000; McCoy et al. 2004; Le Galliard et al. 2005).

It is possible the collapse that we have seen is a shortterm fluctuation in population size typical of such a short-lived, rapidly maturing species and is not indicative of a more permanent or even terminal decline. Such cyclical population fluctuations have been observed in a small number of Sri Lankan agamids with population minima observed at the turn of the year in three species of *Calotes* (Erdelen 1988) and *Xenosaurus* newmanorum (the Mexican Knob-Scaled Lizard) was shown to exhibit variation in life-history traits at both seasonal and annual timescales (Lemos-Espinal et al. 2003). In addition, it is possible that trap shyness may also account for this; however, trap shyness was only observed for bucket pitfalls after first capture (Will Osborne pers. obs.). Bucket pitfall traps were only employed earlier in the study (1990s) and therefore more likely to hide a decline than exacerbate it. In another study, longer term fluctuations were found in populations of *Sceloporus woodi* (Scrub Lizards), where large decreases and increases were found over 10-15 years (McCoy et al. 2004). Nevertheless, in all cases the proportions of different age/size classes staved fairly constant between years and seasons, this was not the case in T. pinguicolla. Taken together, our data suggest a regional decline among T. pinguicolla populations that place the species in grave jeopardy. Should the same process be affecting the only other known extant populations of the species on the Monaro Tablelands 100 km south of the ACT, then the species would be clearly in danger of becoming the first confirmed reptile extinction in Australia since European settlement. This concern is magnified given that the once very extensive population found in Victoria is now considered to be extinct (Robertson and Evans 2009) and the population in the Monaro Tablelands appears to also have declined (Tim McGrath, pers. comm).

Our analysis of population trends in T. pinguicolla enables a refinement of the threatened status of this species. The IUCN red list specifies a reduction in population size of 80% over 10 years or three generations in the past, future, or a combination of these as one criterion by which species can be listed as critically endangered (Hoffmann et al. 2008). The large decline in trapping rates we have demonstrated as occurring in < 10 years leads us to believe that a reduction in population size of this magnitude is likely in at least two of the populations that have been monitored in the ACT, and may well be a feature of all ACT populations. Although it was known that T. pinguicolla inhabited small fragmented populations across its range (Robertson and Cooper, unpubl. report), there has been no effort to determine trends in these populations. We suggest that, given the large number of small, historic populations, a system for regular monitoring of more sites might be applicable for this species. Humbert et al. (2009) found that the robustness of the EGSS model to the absence of more than half of the counts in time series implies that in some cases improved estimates of trend and its variance may be obtained by skipping some consecutive years in a monitoring program and putting the money saved into extending the time series or improving estimates for each year that data are collected. This could also result in extended sampling across more populations by using a staggered sampling method across years and sites or comparisons between sites being used for experimental tests and control sites.

Declines to small numbers can be detrimental to the conservation of this species, because unlike in previous extreme droughts, the grasslands are now smaller and more isolated (ACT Government 2004) so the opportunities for populations to move out of refugia and recolonize localized extinction sites will be few. Without source populations of lizards, isolated blocks of habitat may lose this species during adverse environmental periods. Given climate change predictions, we can expect an increase in frequency and severity of droughts (Karoly, D., J. Risbey and A. Reynolds. 2003. Global warming contributes to Australia's worst drought. Available http://www.wwf.org.au/publications/drought report/. [Accessed 14 July 2010]), which are all too likely to

drive this species to extinction. Recently, it has been shown that climate change has been the cause of 4% of local lizard extinctions worldwide and by 2080 could reach 39% (Sinervo et al. 2010). Adaptive management with the aim to conserve this species will have umbrella effects for other species in grasslands, especially if hypotheses focus on habitat management (in the face of drought and overgrazing) and conservation (through recognizing grassland areas as reserves).

Identification of population decline is an important step in any conservation program. However, obtaining this evidence should not prevent adaptive management, especially when populations are isolated and the species listed. We show here how a focused monitoring program based on well thought out hypotheses can arise from limited data. Implementation of adaptive management will help diagnose the cause(s) of decline, or alternatively, factors limiting growth (Martin et al. 2007), while making inroads to the recovery of a species (Marris 2007).

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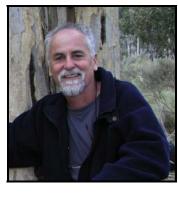
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Dimond et al.—*Tympanocryptis pinguicolla* back from the brink.

APPENDIX 1. Locations, trapping methods, and number of trap nights for *Tympanocryptis pinguicolla* between 1993 and 2009 in the Australian Capital Territory including sources of data from 1993 until 2002. From 2002 until 2009 data were collected by current authors. Site abbreviations are as follows: Jerrabomberra West, Jerrabomberra Valley Grassland Reserve West; Majura, Majura Training Area; AGSO, Australian Geo Site Office; AMTECH, Advanced Manufacturing Technology Estate; Jerrabomberra East, Jerrabomberra Valley Grassland Reserve East; TGA, Therapeutic Goods Association; Airport, Canberra International Airport; Mulanggari, Mulanggari Grassland Reserve; QNR, Queanbeyan Nature Reserve. * One site checked using a fibrescope.

Grassianu Kese	Groups Gr								
Survey	Survey		with	with	of 8	with	Transects	of 4	
Year	Months	Location	pitfalls	pitfalls	pitfalls	tubes	with tubes	tubes	Source
1993-1994 1994	Sep-Feb Jan-May	Jerrabomberra West Jerrabomberra West	16500	8100					(Langston 1996) (Smith 1994)
	Feb-Apr	Jerrabomberra West	10300	17138					(Langston 1996)
1995	Jan-Feb	Callum Brae (AGSO)	1400						(Fletcher et al. 1995)
		AGSO	840				840		(Nelson et al. 1996)
		Airport	1650		672		1650		(Langston 1996; Nelson et al. 1996)
		AMTECH	2160				2160		(Nelson et al. 1996)
		Belconnen Naval Base	1160				1160		(Nelson et al. 1996)
		Callum Brae			672				(Langston 1996)
1996	Feb-Mar	Campbell Park Crace			224 224				(Langston 1996) (Langston 1996)
1,,,0	1 00 11111	Ciucc	220				2004		(Langston 1996;
		Jerrabomberra East	320		224		3904		Nelson et al. 1996)
		Bonshaw	2250		224		2205		(Langston 1996)
		Majura Weston	3250		224		3285		(Nelson et al. 1996) (Langston 1996)
		Weston	2255	0.405			2255		(Langston 1996;
		Jerrabomberra West	3255	9405	448		3255		Nelson et al. 1996)
		Airport					6360	840	(Nelson et al. 1998b)
		AMTECH Callum Brae	5040				8100	600	(Nelson et al. 1998b) (Nelson et al. 1998b)
1997	Feb-Mar	Campbell Park	3040				8100	540	(Nelson et al. 1998b)
		Majura						2520	(Nelson et al. 1998b)
		TGA	990				1020		(Nelson et al. 1998b)
		Jerrabomberra West	1680				1710	600	(Nelson et al. 1998b)
		AMTECH Avonley					585	600	(Nelson et al. 1998a) (Nelson et al. 1998a)
		Callum Brae	2580				5100		(Nelson et al. 1998a)
		Campbell Park	1770				3600	480	(Nelson et al. 1998a)
		Cookanalla	1410				4230		(Nelson et al. 1998a)
1998	Feb-Mar	Dundee Jerrabomberra East					405 750	120	(Nelson et al. 1998a) (Nelson et al. 1998a)
		Fairbairn	660				1320	120	(Nelson et al. 1998a)
		Bonshaw	3150				6300		(Nelson et al. 1998a)
		Malcolm Vale	1320				2640		(Nelson et al. 1998a)
		Majura	1200				2500	2436	(Nelson et al. 1998a)
		Pialligo Airport	1290				2580	600	(Nelson et al. 1998a) (Pinner and Fletcher 1999)
1000	F1.14	Fyshwick						840	(Pinner and Fletcher 1999)
1999	Feb-Mar	Jerrabomberra West/						2856	(Pinner and Fletcher 1999)
		Callum Brae							2.1
2000	Feb-Mar	Majura Bonshaw						2668 1744	(Nelson et al. 2000) (Rowell et al. 2000)
2000	Feb-April	QNR					1900	1/44	(Nelson et al. 2000)
		Crace						780	(Dunford et al. 2000)
2001	Feb-Mar	Malcolm Vale						3390	(Dunford et al. 2000)
		Mulanggari Belconnen Naval Base*					720	690	(Dunford et al. 2000) (Evans and Ormay 2002)
2002	Feb-Mar	Majura				3584	720		(Evans and Ormay 2002)
2003	Feb-Mar	Majura				2688			(=-=== ==== ==== , ====)
	Feb-May	AMTECH					840		
2004	Feb-Mar	Majura				3360	1022		
2005	Feb-Mar	Jerrabomberra West Majura					1022 3060		
2003		Majura				4032	5000		
	Feb-Mar	Jerrabomberra West				4032			
2006	Feb-April	QNR				4400	600		
	Oct-Nov	Majura Jerrabomberra West				4480 4480			
		Majura				4480			
	Feb-Mar	Jerrabomberra West				4480			
		QNR					500		
2007	Mar-Apr	Callum Prac				1680			
	Apr-May Mar-May	Callum Brae Bonshaw				1232 2912			
		Majura				4480			
	Oct-Nov	Jerrabomberra West				4480			
		Callum Brae				4480			
	Feb-Mar	Campbell Park Bonshaw				2240 2240			
2008	reo-iviai	Bonsnaw Majura				4480			
2000		Jerrabomberra West				4480			
		QNR					500		
	Feb-Apr	AMTECH				5824			
		Callum Brae				2240			
2009	Feb-Mar	Jerrabomberra East Bonshaw				2240 4480			
2307	1 00 17101	Majura				6720			
		Jerrabomberra West				6720			
		QNR					500		

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