
LIFE HISTORY OF THE COPPERTAIL SKINK (*CTENOTUS TAENIOLATUS*) IN SOUTHEASTERN AUSTRALIA

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Abstract.—The global decline of reptiles is a serious problem, but we still know little about the life histories of most species, making it difficult to predict which species are most vulnerable to environmental change and why they may be vulnerable. Life history can help dictate resilience in the face of decline, and therefore understanding attributes such as sexual size dimorphism, site fidelity, and survival rates are essential. Australia is well-known for its diversity of scincid lizards, but we have little detailed knowledge of the life histories of individual scincid species. To examine the life history of the Coppertail Skink (*Ctenotus taeniolatus*), which uses scattered surface rocks as shelter, we estimated survival rates, growth rates, and age at maturity during a three-year capture-mark-recapture study. We captured mostly females (> 84%), and of individuals captured more than once, we captured 54.3% at least twice beneath the same rock, and of those, 64% were always beneath the same rock (up to five captures). Our growth model estimated that males can reach sexual maturity in as few as 8 mo, whereas females delay maturity until they reach 17 or more months of age. The large body size of females in our population suggests that many individuals were three or more years old. Average monthly survival rate was 86%, which is within the range reported for lizard species in other families. We now have a baseline with which to compare the life histories of other populations of this widespread species, which ranges from temperate to tropical environments. These findings also provide a baseline for examining effects of disturbance or environmental change on life-history traits.

Key Words.—age at maturity; growth rate; mark-recapture; recapture rate; Scincidae; size at maturity; survival; von Bertalanffy growth model

INTRODUCTION

Habitat loss, fragmentation, and degradation caused by anthropogenic activity are responsible for the decline of many reptiles (Gibbons et al. 2000; Böhm et al. 2013). Effective conservation typically requires detailed knowledge of life histories, which allows predictions of population size and growth, and therefore estimates of probability of decline or recovery after habitat restoration (Böhm et al. 2013). Life-history traits, such as growth rate, age and size at maturity, and survival vary widely among reptiles (Pike et al. 2008), often differ between the sexes (Cox et al. 2003), and can determine extinction risk (Tingley et al. 2013). For example, age and size at sexual maturity represent tradeoffs between fast growth with early maturation and slower growth with later maturation (Blueweiss et al. 1978; Stearns 1992; Du et al. 2005). Individuals that mature early are likely to do so at a smaller size; this can be disadvantageous to females, in which body size limits the space that is available for eggs to develop, resulting in fewer and/or smaller eggs laid relative to large females (Blueweiss et al. 1978; Stearns 1992; Du et al. 2005). Males, by contrast,

may be reproductively successful at small sizes, unless large body size confers a fitness advantage, for example during competitive interactions such as defending territories (Cox et al. 2003). Even in cases where large body size is advantageous, alternative mating strategies can sometimes be used by smaller males to successfully reproduce (Keogh et al. 2013). Determining relative sexual size dimorphism can therefore lead to insights into mating systems and ecology.

Detailed knowledge of survival in reptiles, especially juveniles, is extremely limited (Pike et al. 2008). Currently, there are few estimates of natural survival rates of scincid lizards (reviewed by Pike et al. 2008; but see Blomberg and Shine 2001), although some survival rates have been estimated for individuals after manipulation of predator populations (Lettink et al. 2010; Tocher 2010). These studies found high mortality in smaller individuals (Blomberg and Shine 2001) and increased survival was associated with artificially lowered predator abundances (Lettink et al. 2010; Tocher 2010). Knowledge of survival rates is necessary to accurately predict population trends over time, which is becoming increasingly important under current reptile declines



FIGURE 1. The Coppertail Skink (*Ctenotus taeniolatus*) and the rocky habitat in which it lives in southeastern Australia. (Photographed by David A. Pike).

caused by habitat loss and climate change (Gibbons et al. 2000; Böhm et al. 2013). Filling in these knowledge gaps will better allow us to predict population trends and understand lizard life-history evolution, but this is difficult because of the need for detailed field studies, particularly capture-mark-recapture studies, which are time-consuming and often confounded by low recapture rates (Pike et al. 2008).

We studied the Coppertail Skink (*Ctenotus taeniolatus*), a medium-sized (males and females to about 80 mm snout-vent length; SVL) lizard distributed in eastern coastal Australia (Cogger 2014; Fig. 1). This generalist insectivore (Taylor 1986) lives in a variety of habitats, ranging from Coastal Heathlands to Dry Sclerophyll and Wet Montane forests and Granitic Woodlands (Cogger 2014; Swan et al. 2017). Mating occurs in spring, and females lay a single clutch of 1–7 eggs during summer (Taylor 1985, 2004). Hatchlings emerge from the egg after about 55 d of incubation at an average size of 33 mm (± 1.7 standard deviation) SVL and the minimum size at which some individuals reproduce is 43 mm for males and 52 mm for females (Taylor 1985). *Ctenotus taeniolatus* are active foragers that frequently bask and shelter beneath rocks (Goldsbrough et al. 2006; Taylor 1986). By day, skinks use these retreats while actively foraging and resting, whereas during the night, skinks shelter beneath rocks in burrows dug into the soil (Goldsbrough et al. 2006). These burrows offer protection from predator ingress (e.g., nocturnal snakes; Shine 1984) and afford thermal

benefits, due to the heat retention of overlying rock that are exposed to the sun throughout the day (Goldsbrough et al. 2006). Lizard density is positively correlated with the density of suitable rocks, and therefore rock availability may limit population size and gene flow among suitable habitats (Dennison et al. 2012). To clarify the life history of *Ctenotus taeniolatus*, which ranges from temperate to tropical environments, we quantified growth rates and estimated age at maturity and survival rates during a 3-y capture-mark-recapture study. Based on current literature, we expected that: (1) females would grow larger than males because of fecundity benefits associated with large female body size; (2) both sexes would show fidelity to individual rock shelters resulting in high recapture rates; (3) body size would positively influence survival; and (4) survival would be in line with other lizard species (e.g., Pike et al. 2008).

MATERIALS AND METHODS

We studied *C. taeniolatus* along Monkey Gum Plateau, an elevated sandstone ridgeline in southeastern New South Wales, Australia (35°S, 150°E; Fig. 1). The plateau and surrounding valleys are dominated by closed canopy eucalypt forest, except for sun-exposed rock outcrops along cliff edges. These outcroppings contain exfoliated sandstone rocks that reptiles regularly use as shelter (Pike et al. 2011a,b; Fig. 1). The study area consisted of a 5 km stretch of west-facing cliff line with 75 focal rock outcrops containing 1,053 uniquely numbered rocks (see Pike et al. 2011a,b for further details). Each month from May 2007 to November 2009 (31 mo, spanning three autumn-winter-spring periods and two summers), we lifted each rock and attempted to hand capture all *C. taeniolatus*. For each captured lizard, we measured SVL to 1 mm using a plastic ruler, weight to 0.1 g using a spring scale, we determined sex through examination of external tail characteristics (bulging tail in males where the hemipenes are located) and manual eversion of the hemipenes, and we applied a unique toe-clip pattern for identification upon recapture. After we recorded data, we carefully placed back each rock into the position from which it exfoliated from the parent rock and we encouraged lizards with our hands to crawl back underneath.

We used a von Bertalanffy growth model to estimate size (SVL) and age at sexual maturity (Schoener and Schoener 1978) by fitting mark-recapture data using a non-linear, least-squares regression procedure (using JMP 5.0.1; Frazer et al. 1990). The parameters a (asymptotic length) and k (intrinsic growth rate) were first seeded with initial best estimates and allowed to converge on the most parsimonious values (Frazer et al. 1990; Webb et al. 2008). We did not fit models separately for each sex because of similar average body

sizes in our study and a small sample size of recaptured males (see Results).

We used Cormack-Jolly-Seber (CJS) models to estimate monthly survival and recapture probabilities. We performed analyses in program MARK, version 8.2 (White and Burnham 1999) and executed them using the RMark package (Laake 2013) in R statistical software (R Core Team 2019). In CJS models, survival probabilities simultaneously incorporate the probabilities of death and emigration (termed apparent survival), which equates to local persistence in the study area (White and Burnham 1999). Each CJS model separately estimates the probabilities of survival and recapture. We developed a set of candidate models that tested whether survival and recapture rates were constant, time-dependent, or dependent upon body size (SVL at first capture). We tested all additive and interactive combinations of these variables in our model set ($n = 25$ total models; Table 1). We excluded sex as a factor in these models due to the low sample size of recaptured males ($n = 4$). The best-supported models are those that make up the top 90% of Akaike Information Criterion (AIC) weights and have relative deviations from the best model of less than two ($\Delta AIC_c < 2$; Burnham and Anderson 1998). We used ΔAIC_c values to select the best approximating models for the data based on the principles of parsimony and trade-offs between under- and over-fitting models (Burnham and Anderson 1998). The best models were averaged to generate estimates of survival and recapture probabilities.

RESULTS

We captured and marked 120 individual *C. taeniolatus*, with a total of 196 captures. We recaptured 34.2% of marked individuals at least once during our study. We observed a further 83 lizards that escaped before capture. Most captures (84.3%) and recaptures (90.0%)

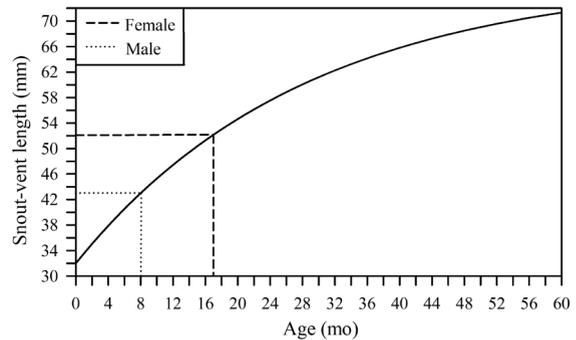


FIGURE 2. Growth curve for the Coppertail Skink (*Ctenotus taeniolatus*) in southeastern Australia generated by fitting mark-recapture data to a von Bertalanffy growth model. Horizontal and vertical lines show the minimum size (snout-vent length; SVL) and age at maturity (months) for females (52 mm SVL) and males (43 mm SVL; Taylor, 1985). The average body size during our study was 68 mm SVL for females and 66 mm SVL for males, and the largest lizard captured during our study was an 85 mm SVL female.

were of females, with males only rarely captured. We found no significant difference in mean SVL between the sexes ($F_{1,105} = 2.96$, $P = 0.088$), although the largest individuals were females. Females averaged 67.7 ± 0.38 (standard error [SE]) mm SVL ($n = 91$) and males averaged 66.0 ± 0.87 mm SVL ($n = 17$). Of individuals that we captured more than once ($n = 42$), 54.3% were captured at least twice beneath the same rock ($n = 22$), and of those, 64% were always beneath the same rock ($n = 14$; beneath the same rock for up to five captures).

We obtained growth data for 36 females and four males, with a mean time between capture and recapture of 6.3 mo (range, 1–28 mo). Our growth model estimated asymptotic length a (\pm SE) to be 76.7 ± 2.6 mm and the intrinsic growth rate k to be 0.035 ± 0.005 . Based on the minimum size of gravid females that we captured (57 mm SVL), lizards in our population likely attain sexual maturity by 24 mo of age (Fig. 2). Based on body size data from dissected museum specimens,

TABLE 1. The top 10 candidate models used to assess the effects of body size and time on the Coppertail Skink (*Ctenotus taeniolatus*) survival (Φ) and recapture (p) probabilities. Models are ranked according to Akaike's Information Criterion (AIC) with adjustment for over dispersion (AIC_c). The four best-supported models have $\Delta AIC_c < 2$ and together explained > 99% of the weight in the model set. Shown are the top 10 models.

Survival	Recapture	Parameters	AIC_c	ΔAIC_c	AIC_c weight
Constant	Constant	2	521.39	0	0.437
SVL	Constant	3	522.23	0.84	0.287
Constant	SVL	3	523.45	2.06	0.156
SVL	SVL	4	524.03	2.64	0.117
Constant	Time	30	532.20	10.81	0.002
SVL	Time	31	532.92	11.53	< 0.001
Constant	Time + SVL	31	534.81	13.42	< 0.001
SVL	Time + SVL	32	535.86	14.47	< 0.001
Time	Constant	30	578.62	57.24	< 0.001
Time + SVL	Constant	31	579.36	57.97	< 0.001

sexual maturity is reached at 43 mm for males and 52 mm for females (Taylor 1985), corresponding to about eight and 17 mo of age in our model, respectively (Fig. 2). Because 64.5% of gravid females had SVLs of 56 mm or larger, many females in our study population appear to be substantially older than 24 mo (Fig. 2). Of captured females, 64.5% were > 70 mm SVL in size, suggesting that individuals can live longer than 3 y. Only 20% of males fell within this size range. Empirical recapture data support these estimates; of the seven individuals recaptured 12 or more months later, five were adults upon initial capture (> 54 mm SVL). We recaptured one adult female after 28 mo, suggesting she was > 50 mo of age. Our model estimates that lizards will reach an asymptotic length of 76.7 mm SVL at > 48 mo of age; we captured 20 individuals larger than this, all of which were females. The largest male we captured was 72 mm SVL.

Four CJS models were supported by our mark-recapture data (Table 1); these models had $\Delta AICc$ values < 2 and together explained > 99% of the weight in the model set. These four models suggested that monthly survival (Φ) and recapture (p) probabilities were constant over time or differed with body size; we did not find strong support that monthly survival or recapture probabilities varied over time (Table 1). The 95% confidence intervals (CI) for beta parameters for SVL in the top four models all included zero, however, which indicates that there was not a significant effect of body size on survival or recapture rates. The beta estimate (and 95% CI) for SVL in the model $\Phi(SVL)p(\text{Constant})$ was 0.011 (-0.008 to 0.030). The beta estimate (and 95% CI) for SVL in the model $\Phi(\text{Constant})p(SVL)$ was 0.001 (-0.019 to 0.021). The beta estimates (and 95% CI) for SVL in the model $\Phi(SVL)p(SVL)$ were 0.014 (-0.008 to 0.036) for survival and -0.006 (-0.029 to 0.016) for recapture. Based on these results, we conclude that lizards had a constant monthly survival rate (\pm SE) of 0.86 ± 0.02 (95% CI = 0.81–0.89), and a constant monthly recapture rate of 0.11 ± 0.02 (95% CI = 0.08–0.15).

DISCUSSION

We studied the life history of *Ctenotus taeniolatus* in a rocky environment in temperate southeastern Australia and found that males can reach sexual maturity in as few as 8 mo, whereas females delay maturity until they reach 17 or more months of age. This suggests that males breed during the summer after their first year, whereas females delay reproduction until the summer of their second year. The large body size of many females in our population suggests that many are more than three years old. Average monthly survival rate was 86%, which is within the range reported for lizard

species in other families (Pike et al. 2008). In temperate Australian lizards, males and females are often similar sizes and reach maturity at an age ranging from 1–5 y (with smaller species maturing more quickly; Greer 1989). The life-history parameters of *C. taeniolatus* thus overlap considerably with those of other temperate Australian lizards (Greer 1989), although little is known about this species in sub-tropical and tropical habitats.

Despite being restricted to isolated rock outcroppings, genetic data demonstrate high levels of regular, long-distance gene flow among ridge tops (Dennison et al. 2012). Our relatively low observed recapture rates (only 34.2% of marked individuals were ever recaptured), low estimated recapture probability for a given sample (11%), and low capture rates of males ($n=4$) also suggest that individuals can move relatively long distances (e.g., outside of our 5 km study area). Capture bias could also explain the disparity in capture rates between the sexes, for example because of different activity periods between males and females (although we sampled our sites randomly with respect to time of day; Moeller et al. 2005) or differences in locomotor speed (e.g., gravid females are often slower; Husak 2006).

We found that male and female lizards reached similar average body sizes, although females become larger than males as older adults, and are likely live longer than males. We estimated age at maturity to be 8 mo for males, but 17 or more months for females with a lifespan of at least 4 y (and likely longer). It is unclear whether this is because females delay reproduction or cannot reproduce until this time. By compounding our average monthly survival estimate of 86%, we can infer a 15% annual survival rate (Pike et al. 2008). This is in line with annual survival rates of juvenile lizards in the families Corytophanidae, Crotaphytidae, Iguanidae, Lacertidae, Phrynosomatidae, Teiidae, and Xantusiidae (mean = 0.31; range, 0.04–0.76; $n=40$ species; Pike et al. 2008). A review of the survival rates of 40 oviparous lizard species (Pike et al. 2008) failed to locate any records for scincid lizards, underscoring the need for detailed studies of life histories of individual species within this diverse family.

Most of our captures (84.3%) and recaptures (90.0%) were females, with males only rarely captured. It is possible that we misidentified sex in the field, but this is unlikely to the degree we observed because mature males of this species have a visible bulge at the base of the tail where the hemipenes are located, and the hemipenes can be everted manually. Instead, we think it is more likely that this disparity in sex ratio is due to the active nature of this species. We suspect that males are more active than females because they are maintaining territories (e.g., Jennings and Thompson 1999; Stapley and Keogh 2004), and thus less likely to be captured sheltering beneath rocks during the day. For example,

we captured 196 individual skinks and observed, but were unable to capture, an additional 83 individuals because they escaped too rapidly. In addition, it is possible that females are more likely to inhabit the burrows we frequently located beneath rocks, especially because these females repeatedly use the same rocks over time. This may make it more likely that we captured and recaptured females, especially because burrows beneath selected rocks provide excellent long-term protection from predators (Goldsbrough et al. 2006) and may also provide suitable nesting sites (as in other scincid lizards that bury eggs beneath rocks; Shine and Harlow 1996). Gravid females may be particularly easy to capture than non-gravid individuals, given their propensity to bask and slower locomotor speed (Husak 2006). Despite these limitations, further understanding of male life-history characteristics is essential for a more holistic picture of the ecology of this species.

We found no differences in body size between the sexes, although the largest and heaviest individuals we captured were all females. Taylor (1985) reported that female *C. taeniolatus*, once past sexual maturity, grow larger and heavier than males. The significance of this is that larger females have a larger volume in which clutches of eggs can develop, leading to increased clutch and/or egg (and therefore offspring) size (Du et al. 2005). Our growth model estimates that lizards will reach the asymptotic length of 76.7 mm SVL at more than 48 mo of age. The largest male we captured was smaller than this (72 mm SVL), again suggesting that females grow larger than males. Taylor (1985) estimated that at sexual maturity, both males and females were most likely to be about two years old or in their third summer, although some males could mature during the second summer of their first year. Female lizards in our population likely attain sexual maturity at close to 24 mo of age, just prior to their second summer (Fig. 1). Of captured females, 64.5% were larger than 70 mm SVL, suggesting these individuals were older than 3 y; by contrast, only 20% of males were within this size range. Based on the size at sexual maturity, males (43 mm SVL; Taylor 1985) are likely to mature just before their second summer (by 12 mo of age), prior to the reproductive season.

Ctenotus taeniolatus relies on exfoliated rocks for shelter, and individual rocks are often repeatedly used over time. Any disturbance of this habitat therefore has important implications for both the persistence and conservation of the species. Reptile collectors often disturb rocks in their searches and do not place them back into their original position where they exfoliated from the sandstone parent rock (Pike et al. 2010). Rock displacement modifies thermal regimes and increases crevice size beneath rocks; two attributes important for site selection by small reptiles (Croak et al. 2010; Pike et al. 2010). In addition, these rocks are often

illegally collected for use in yards and gardens, leading to significant loss of reptile retreat sites from some plateaus (Shine et al. 1998). The high mobility of this species, as evidenced by genetic data, is encouraging because individuals may be able to recolonize disturbed or denuded habitats following restoration (Dennison et al. 2012). Restoration can include manually replacing rocks to their original positions (Pike et al. 2010), or in cases of natural rock removal, adding artificial rocks with appropriate physical characteristics and thermal regimes to provide suitable retreat sites (Croak et al. 2010). The high dispersal of *C. taeniolatus* could facilitate colonization of areas of restored habitat (Croak et al. 2010) because sites with high densities of preferred rocks support more lizards (Dennison et al. 2012). Overall, we now have a much more detailed picture of the life history of this widespread species in eastern Australia and have a baseline with which to compare other populations, which range from temperate through to tropical environments. These data also provide a baseline for examining effects of disturbance or environmental change on life-history traits.

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LITERATURE CITED

- Blomberg, S.P., and R. Shine. 2001. Modeling life history strategies with capture-recapture data: evolutionary demography of the water skink *Eulamprus tympanum*. *Austral Ecology* 26:349–359.
- Blueweiss, L., H. Fox, V. Kudzma, D. Nakashima, R. Peters, and S. Sams. 1978. Relationships between body size and some life history parameters. *Oecologia* 37:257–272.
- Böhm, M., B. Collen, J.E.M. Baillie, P. Bowles, J. Chanson, N. Cox, G. Hammerson, M. Hoffman, S.R. Livingstone, M. Ram, et al. 2013. The conservation status of the world's reptiles. *Biological Conservation* 157:372–385.
- Burnham, K.P., and D.R. Anderson. 1998. *Model Selection and Inference*. Springer-Verlag, New York, New York, USA.
- Cogger, H.G. 2014. *Reptiles and Amphibians of Australia*. CSIRO Publishing, Clayton, Australia.

- Cox, R.M., S.L. Skelly, and H.B. John-Alder. 2003. A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution* 57:1653–1669.
- Croak, B.M., D.A. Pike, J.K. Webb, and R. Shine. 2010. Using artificial rocks to restore nonrenewable shelter sites in human-degraded systems: colonization by fauna. *Restoration Ecology* 18:428–438.
- Dennison, S., S.M. Smith, and A.J. Stow. 2012. Long-distance geneflow and habitat specificity of the rock-dwelling Coppertail Skink, *Ctenotus taeniolatus*. *Austral Ecology* 37:258–267.
- Du, W.-G., J. Xiang, and R. Shine. 2005. Does body-volume constrain reproductive output in lizards? *Biology Letters* 1:98–100.
- Frazer N.B., J.W. Gibbons, and J.L. Greene. 1990. Exploring Fabens' growth interval model with data on a long-lived vertebrate, *Trachemys scripta* (Reptilia: Testudinata). *Copeia* 1990:112–118.
- Gibbons, J.W., D.E. Scott, T.J. Ryan, K.A. Buhlmann, T.D. Tuberville, B.S. Metts, J.L. Greene, T. Mills, Y. Leiden, S. Popy, and C.T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. *BioScience* 50:653–666.
- Goldsbrough, C.L., R. Shine, and D.F. Hochuli. 2006. Factors affecting retreat-site selection by Coppertail Skinks (*Ctenotus taeniolatus*) from sandstone outcrops in eastern Australia. *Austral Ecology* 31:326–336.
- Greer, A.E. 1989. *The Biology and Evolution of Australian Lizards*. Surrey Beatty and Sons, Chipping Norton, Australia.
- Husak, J. 2006. Do female collard lizards change field use of maximal sprint speed capacity when gravid? *Oecologia* 150:339–343.
- Jennings, W.B., and G.G. Thompson. 1999. Territorial behavior in the Australian scincid lizard *Ctenotus fallens*. *Herpetologica* 55:352–361.
- Keogh, J.S., K.D.L. Umbers, E. Wilson, J. Stapley, and M.J. Whiting. 2013. Influence of alternative reproductive tactics and pre- and post-copulatory sexual selection on paternity and offspring performance in a lizard. *Behavioral Ecology and Sociobiology* 67:629–638.
- Laake, J.L. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. Processed Report 2013-01, Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service, Seattle, Washington, USA. 25 p.
- Lettink, M., G. Norbury, A. Cree, P.J. Seddon, R.P. Duncan, and C.J. Schwarz. 2010. Removal of introduced predators, but not artificial refuge supplementation, increases skink survival in coastal duneland. *Biological Conservation* 143:72–77.
- Moeller, B.A., E.C. Hellgren, D.C. Ruthven, III, R.T. Kazmaier, and D.R. Synatzske. 2005. Temporal differences in activity patterns of male and female Texas Horned Lizards (*Phrynosoma cornutum*) in southern Texas. *Journal of Herpetology* 39:336–339.
- Pike, D.A., B.M. Croak, J.K. Webb, and R. Shine. 2010. Subtle - but easily reversible - anthropogenic disturbance seriously degrades habitat quality for rock-dwelling reptiles. *Animal Conservation* 13:411–418.
- Pike, D.A., L. Pizzatto, B.A. Pike, and R. Shine. 2008. Estimating survival rates of uncatchable animals: the myth of high juvenile mortality in reptiles. *Ecology* 89:607–611.
- Pike, D.A., J.K. Webb, and R. Shine. 2011a. Chainsawing for conservation: ecologically informed tree removal for habitat management. *Ecological Management and Restoration* 12:110–118.
- Pike, D.A., J.K. Webb, and R. Shine. 2011b. Removing forest canopy restores a reptile assemblage. *Ecological Applications* 21:274–280.
- R Core Team 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>.
- Schoener, T.W., and A. Schoener. 1978. Estimating and interpreting body-size growth in some *Anolis* lizards. *Copeia* 1978:390–405.
- Shine, R. 1984. Reproductive biology and food habits of the Australian elapid snakes of the genus *Cryptophis*. *Journal of Herpetology* 18:33–39.
- Shine, R., and P.S. Harlow. 1996. Maternal manipulation of offspring phenotypes via nest-site selection in an oviparous lizard. *Ecology* 77:1808–1817.
- Shine, R., J.K. Webb, M. Fitzgerald, and J. Sumner. 1998. The impact of bush-rock removal on an endangered snake species, *Hoplocephalus bungaroides* (Serpentes: Elapidae). *Wildlife Research* 25:285–295.
- Stapley, J., and J.S. Keogh. 2004. Exploratory and antipredator behaviours differ between territorial and nonterritorial male lizards. *Animal Behaviour* 68:841–846.
- Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford University Press, New York, New York, USA.
- Taylor, J.A. 1985. Reproductive biology of the Australian lizard *Ctenotus taeniolatus*. *Herpetologica* 41:408–418.
- Taylor, J.A. 1986. Food and foraging behaviour of the lizard, *Ctenotus taeniolatus*. *Austral Ecology* 11:49–54.
- Taylor, J.E. 2004. Reproduction in sympatric lizards: comparison of two species of *Ctenotus* (Scincidae) in south-eastern Australia. *Australian Journal of Zoology* 52:649–666.
- Tingley, R., R.A. Hitchmough, and D.G. Chapple. 2013.

Herpetological Conservation and Biology

Life-history traits and extrinsic threats determine extinction risk in New Zealand lizards. *Biological Conservation* 165:62–68.

Tocher, M.D. 2010. Survival of Grand and Otago skinks following predator control. *Journal of Wildlife Management* 70:31–42.

Webb, J.K., D.A. Pike, and R. Shine. 2008. Population ecology of the Velvet Gecko, *Oedura lesueurii* in south eastern Australia: implications for the persistence of an endangered snake. *Austral Ecology* 33:839–847.

White, G.C., and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46S:120–138.



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