Maximising trapping efficiency in reptile surveys: the role of seasonality, weather conditions and moon phase on capture success

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Abstract

Context. Designing an appropriate survey protocol requires understanding of how capture rates of target species may be influenced by factors other than on-ground abundance, such as weather conditions or seasonality. This is particularly relevant for ectotherms such as reptiles, as activity can be affected by environmental conditions such as ambient temperature.

Aims. The present study examines factors affecting capture success of reptiles in semi-arid environments of southern Australia, and addresses the following two main questions: (1) what is the influence of weather and seasonal factors on capture rates of reptiles, and (2) what are the implications for developing an effective protocol for reptile surveys?

Methods. We surveyed reptiles using pitfall traps in spring and summer of 2006/07 and 2007/08 at sites ($n = 280$) throughout the Murray Mallee region of south-eastern Australia. We used mixed-effect regression models to investigate the influence of seasonal and weather-related variables on species' capture success.

Key results. Total captures of reptiles, and the likelihood of capture of 15 reptile species, increased with rising daily temperature. Greater numbers of individual species were captured during spring than in summer, even though temperatures were cooler. This probably reflects greater levels of activity associated with breeding. Several species were more likely to be captured when maximum or minimum daily temperatures exceeded a certain level (e.g. *Lerista labialis*, *Delma australis*, *Nephrurus levis*). Other factors, such as rainfall and moon phase, also influenced capture success of some species.

Conclusions. Surveys for reptiles in semi-arid environments are likely to capture the greatest diversity of species on warm days in late spring months, although surveys on hot days in summer will enhance detection of particular species (e.g. *Morethia boulengeri*, *Varanus gouldii*). We recommend trapping during periods with maximum temperatures exceeding 25–30°C and minimum overnight temperatures of 15°C. Finally, trapping during rainfall and full-moon events will maximise chances of encountering species sensitive to these variables (blind snakes and geckoes).

Implications. Selecting the most favourable seasonal and weather conditions will help ensure that reptile surveys maximise the likelihood of capturing the greatest diversity of reptiles, while minimising trap-effort required.

Introduction

Field surveys of fauna are an integral component of wildlife conservation and management. When undertaking such studies it is critical to establish that sampling results adequately reflect species' occurrence at study sites (Caughley 1976). Designing an appropriate sampling protocol requires an understanding of how capture rates of target species are influenced by factors other than abundance, such as weather conditions and seasonality. Reptiles, as ectotherms, depend on external heat sources (primarily solar radiation) for thermoregulation (Heatwole and Taylor 1987; Schmidt-Neilsen 1997). As such, a major factor constraining the activity of ectotherms is their thermal environment. Relative to endotherms that generate heat via metabolism of food (Schmidt-Neilsen 1997; Shine 2005) and often remain active during cool and warm

conditions, the activity of ectotherms is influenced more by daily fluctuations in ambient temperature (Schmidt-Neilsen 1997; Shine 2005). Furthermore, as individual species of reptiles have different thermal preferences (Heatwole and Taylor 1987), the activity patterns of species may differ in response to variation in daily weather conditions.

Both laboratory and field-based studies have identified the preferred body temperature (PBT) or active field body temperatures (FBT) of many species of reptiles (Cogger 1974; Bradshaw *et al.* 1980; Bennett and John-Alder 1986; Henle 1990; Melville and Schulte 2001; Whitaker and Shine 2002). Most agamid species have higher FBTs (range 32.9–37.7°C; Melville and Schulte 2001) than many species of skink (e.g. *Ctenotus* species: range 34.5–36.4°C; *Egernia inornata* 30°C) (Pianka and Giles 1982; Bennett and John-Alder 1986), whereas geckoes

typically maintain much lower active FBTs (range 23.2–28.1°C) than do both skinks or agamids (Pianka and Pianka 1976; Henle 1990).

The activity of reptiles is also affected by variation in other environmental parameters, including fluctuations in relative humidity (Daltry *et al.* 1998; Read and Moseby 2001; Sun *et al.* 2001; Brown and Shine 2002), rainfall (Shine and Koenig 2001; Brown and Shine 2002), wind speed (Sun *et al.* 2001), cloud cover (Van Damme *et al.* 1987; Read and Moseby 2001) and moon phase (Clarke *et al.* 1996; Read and Moseby 2001; Brown and Shine 2002). The season in which reptile surveys are conducted also influences captures, possibly because of seasonal changes in prey availability, reproduction and associated mate-searching activity, or shifts in seasonal environmental conditions (Heatwole and Taylor 1987; Brown *et al.* 2001; Sun *et al.* 2001).

Reptiles are a prominent component of the fauna of semi-arid environments in southern Australia, with high levels of diversity occurring (Cogger 1989; Menkhorst and Bennett 1990). Regional field guides for reptiles (Cogger 2000; Swan and Watharow 2005) suggest that different species are likely to be active under different climatic conditions. For example, blind snakes (Family Typhlopidae) are encountered above ground primarily on wet, humid nights (Swan and Watharow 2005). In the one published study available, Read and Moseby (2001) concluded that daily maximum and minimum temperatures and relative humidity were the most influential factors affecting the activity of semi-arid reptiles and therefore their rate of capture.

The present study examines factors affecting the capture success of reptiles in semi-arid environments of southern Australia. We address the following two main questions: (1) what is the influence of weather and seasonal factors on the capture rate of reptiles across broad spatial scales and (2) what are the implications for developing an effective protocol for reptile surveys?

Methods

Study sites and data collection

The study was carried out in eucalypt-dominated 'mallee' vegetation in semi-arid south-eastern Australia (Fig. 1). Mallee refers to the growth form of eucalypt trees that have multiple stems arising from a basal lignotuber. The term is also used to refer to the region where such mallee trees are widespread. This region supports a diverse herpetofauna, with some 56 species of reptiles defined as 'mallee' inhabitants (Swan and Watharow 2005).

Twenty-eight landscapes, each 2 km in radius (i.e. 12.56 km^2) were selected for the study (Fig. 1). Each landscape included 10 survey sites, with each site comprising a line of 10 pitfall traps (20-L plastic buckets buried flush with the ground) spaced at 5-m intervals, connected by a 50-m drift fence ($n = 280$ pitfall lines). All sites were at least 25 m from roads and at least 200 m apart.

Trapping was carried out for five consecutive nights in spring and in summer during 2006/07 and 2007/08, resulting in 56 000 trap-nights. Trap lines were checked once daily and individuals were released at the point of capture. The 'spring' surveys extended from October to early December, whereas the 'summer' surveys were conducted from January to late March. In November 2006, a fire forced the closure of traps within three landscapes at Gluepot Reserve, South Australia. As a consequence, the affected landscapes were resampled in October 2007.
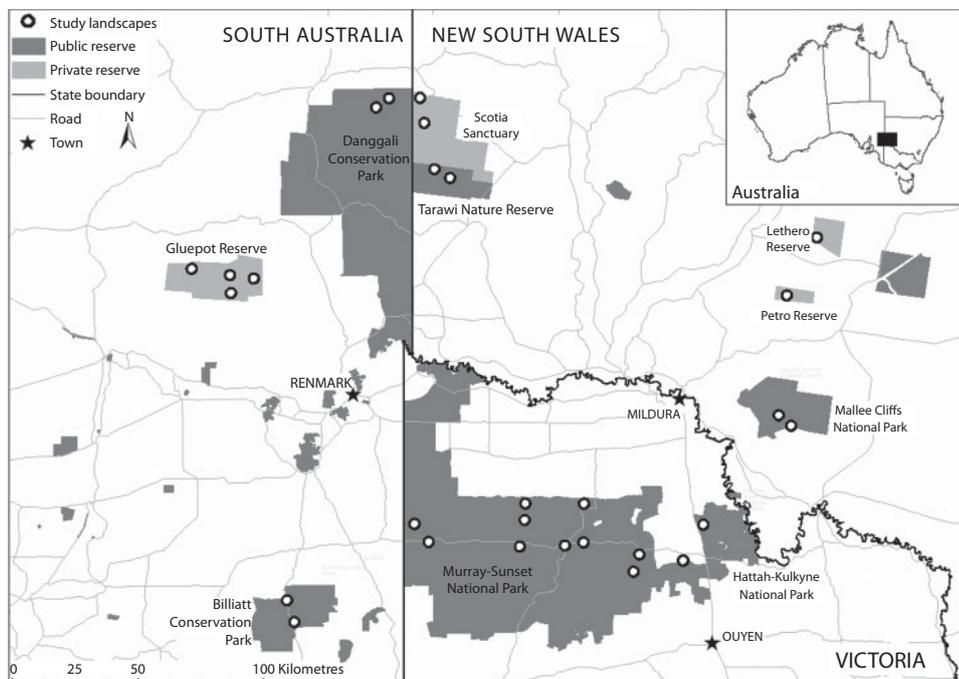

Fig. 1.   The Murray Mallee region of south-eastern Australia. Circles indicate the position of the 28 study landscapes.

Response variables

Reptiles were recorded at each individual site ($n = 280$); however, for analyses in the present study, the data have been collated for the whole landscapes ($n = 28$, Fig. 1). Capture rates were used to explore the influence of weather and moon-phase variables on groups of species and individual species. For groups of species (e.g. all nocturnally active species), the response variable was the number of captures per night of trapping per landscape (each landscape had 20 nights of trapping). For individual species, the response variable was the presence/absence of the species per night of trapping per landscape. Rare species (those present at <10% of sites) were excluded from the analyses because the number of captures was insufficient to perform statistical analysis.

Explanatory variables

Daily weather data were obtained from Bureau of Meteorology Australia (BOM) weather stations ($n = 7$) situated within 100 km of the landscapes. The most representative station for each study landscape was identified by the BOM.

Weather variables obtained were maximum daily temperature (°C), minimum daily temperature (°C), relative humidity (%), wind speed (km h^{-1}) and cloud cover (Oktas or eighths). Cloud cover was a categorical variable with nine categories ranging from 0 (a cloudless sky) to 8 (complete cloud cover). Moon-phase data were obtained from Geoscience Australia (http://www.ga.gov.au/geodesy/astro/moonphases, verified July 2008) and were assigned to three categories following Read and Moseby (2001). Zero (0) represented the two nights before, two nights after or the night of the new moon; a '2' represented the two nights before, two nights after or the night of the full moon; and a '1' represented intermediate moon phases for all nights in between.

Rainfall was recorded at several BOM weather stations in the study area. However, storm activity and light-rainfall events can occur locally. Consequently, rainfall occurring at specific study sites may not have been captured by broadly distributed weather stations. Thus, we recorded evidence of rainfall in the field by documenting characteristic signs of rainfall at each site (such as the presence of moist or disturbed soil) each day. Rainfall was scored categorically as either none (0), light (1) or heavy (2). The night of trapping (numbered one to five for each of four trapping sessions) and season (spring or summer) were also included in analyses, to explore their influence on reptile captures.

Trap lines were checked in the morning only, and so the afternoon/evening before each trap check was considered when exploring the influence of weather on capture rates. Therefore, maximum temperature, humidity, cloud cover, rainfall, wind speed and moon phase were recorded for the afternoon/evening before each trap check, whereas the minimum overnight temperature was recorded for the night preceding the trap-check morning.

Daily data for cloud cover, wind speed and relative humidity at 1500 hours, 1800 hours and 2100 hours were highly correlated (Pearson correlation, $r > 0.6$ in most cases). Therefore, only data from 1500 hours for these variables were used in analyses.

Statistical analyses

We used regression modelling to analyse how capture rates and species presence/absence were influenced by weather variables.

Survey sites were sampled repeatedly over time, resulting in non-independent error structure in the data. Further, exploratory analysis (using scatterplots) indicated that our dataset contained non-linear relationships. As such, we used generalised additive mixed models (GAMMs) (Wood 2006). This flexible form of regression can model non-linear relationships (Wood 2006). Landscape was regarded as a random effect, accounting for the non-independent error structure in the data (Zuur *et al.* 2009), with all predictor variables being fixed effects.

Seven explanatory variables were considered in the modelling process (Table 1); cloud cover was included for modelling diurnally active species only, whereas moon phase was included only for modelling nocturnal species (Cogger 2000; Wilson and Swan 2003; Swan and Watharow 2005).

A Poisson distribution of errors was specified for GAMMs when the response variable was total captures, captures of nocturnal species or captures of diurnal species per landscape, per night of trapping. A binomial error distribution was specified when the response variables were presence/absence data. Significance values (*P*-values) for each explanatory variable were determined using the global (full) model. Adjusted *R*-squared values were used to assess the explanatory power of the models.

Statistical analyses were undertaken in R, version 2.7.2 (Ihaka and Gentleman 1996). We ran GAMMs using the package mgcv (Wood 2009). Additionally, we ran paired Student's *t*-tests in SPSS (Student version 16.0) to test for differences in captures between survey seasons.

Results

General trapping results and weather conditions

The survey effort of 56 000 trap-nights across 28 landscapes captured 55 species of reptiles belonging to seven families. There were sufficient data for analysis for 30 species; for these species, there were 7406 captures in total, comprising 3880 captures of diurnally active species and 3526 captures of nocturnal species (Table 2).

Mean maximum and minimum temperatures were greater for survey days in summer than in spring. However, both spring and summer survey days had similar temperature ranges

Table 1. Explanatory variables used to model the influence of weather and moon-phase conditions on captures of reptiles

Response variable	Explanatory variables used in model
Total captures	Maximum daily temperature (± 0.1°C)
Captures of diurnal species	Relative humidity at 1500 hours (± 1%)
Presence/absence of diurnal species	Wind speed (± 0.1 km h^{-1}) at 1500 hours
	Cloud cover (Oktas) at 1500 hours
	Rainfall (0, 1 or 2)
	Season (spring or summer)
	Night of trapping (1–5)
Captures of nocturnal species	Minimum daily temperature (± 0.1°C)
Presence/absence of nocturnal species	Relative humidity at 1500 hours (± 1%)
	Wind speed (± 0.1 km/h) at 1500 hours
	Rainfall (0, 1 or 2)
	Moon phase (0, 1 or 2)
	Season (spring or summer)
	Night of trapping (1–5)

Table 2. Results of generalised additive mixed models (GAMMs) testing the influence of season, climate and moon phase on captures of reptiles

Models for single species are based on presence or absence within a landscape per night of sampling as the response variable. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. (_) = negative relationship, n.s. = not significant, n.a. = not included, [d] = diurnally active species, [n] = nocturnally active species. For season, reference level = 'summer' and for trap-night reference level = night of trapping five

Response variable	n	Season (spring/ summer)	Max. temp. (°C)	Min. temp. (°C)	Relative humidity (%)	Cloud cover (0–8 oktas)	Rain prev 24 h (0, 1, 2)	Moon phase (0, 1, 2)	Wind speed (km/h)	Night of trapping (1–5)	Adjusted R^2 (%)
Total captures	7406	Spring***	***	n.a.	(***)	(**)	n.s.	n.a.	n.s.	4 (**)	32
Captures of diurnal species	3880	Spring***	*	n.a.	(***)	(***)	n.s.	n.a.	n.s.	4 (**)	15
Captures of nocturnal species	3526	Spring***	n.a.	***	n.s.	n.a.	n.s.	n.s.	n.s.	3 (*)	29
Agamidae											
Amphibolurus nobbi coggeri[d]	377	Spring***	*	n.a.	n.s.	n.s.	n.s.	n.a.	n.s.	1 (*)	5
Ctenophorus fordi[d]	1142	Spring	n.s.	n.a.	n.s.	n.s.	n.s.	n.a.	n.s.	n.s.	<1
Ctenophorus pictus[d]	150	n.s.	n.s.	n.a.	n.s.	(*)	n.s.	n.a.	n.s.	n.s.	<1
Pogona vitticeps[d]	197	n.s.	n.s.	n.a.	n.s.	n.s.	n.s.	n.a.	n.s.	n.s.	<1
Elapidae											
Brachyurophis australis[n]	198	Spring***	n.a.	**	n.s.	n.a.	n.s.	n.s.	n.s.	3 (*)	12
Parasuta nigriceps[n]	72	n.s.	n.a.	n.s.	n.s.	n.a.	n.s.	n.s.	n.s.	n.s.	1
Pseudonaja modesta[d]	59	Spring*	n.s.	n.a.	(*)	n.s.	n.s.	n.a.	n.s.	n.s.	<1
Gekkonidae											
Diplodactylus damaeus[n]	1298	Spring***	n.a.	***	n.s.	n.a.	n.s.	n.s.	n.s.	1, 3*	7
Diplodactylus vittatus[n]	236	Spring*	n.a.	***	n.s.	n.a.	*	n.s.	n.s.	2*	4
Gehyra variegata[n]	69	n.s.	n.a.	***	(**)	n.a.	(**)	n.s.	(*)	1, 3, 4*	1
Nephrurus levis[n]	47	Spring***	n.a.	***	(*)	n.a.	(*)	(***)	n.s.	n.s.	4
Rhynchoedura ornata[n]	81	Spring*	n.a.	**	(*)	n.a.	n.s.	n.s.	(*)	n.s.	<1
Strophurus spp.[n]	195	Spring***	n.a.	n.s.	n.s.	n.a.	*	***	n.s.	n.s.	13
Pygopodidae											
Delma australis[d]	124	Spring***	***	n.a.	n.s.	n.s.	(*)	n.a.	n.s.	n.s.	7
Delma butleri[d]	71	n.s.	***	n.a.	n.s.	n.s.	n.s.	n.a.	n.s.	n.s.	5
Lialis burtonis[d]	70	n.s.	**	n.a.	n.s.	n.s.	n.s.	n.a.	n.s.	n.s.	2
Scincidae											
Ctenotus atlas[d]	315	n.s.	n.s.	n.a.	n.s.	(*)	n.s.	n.a.	n.s.	n.s.	4
Ctenotus brachyonyx[d]	275	Spring***	**	n.a.	n.s.	(*)	n.s.	n.a.	(*)	1 (*)	5
Ctenotus regius[d]	343	n.s.	n.s.	n.a.	n.s.	n.s.	n.s.	n.a.	n.s.	n.s.	2
Ctenotus schomburgkii[d]	259	n.s.	n.s.	n.a.	n.s.	n.s.	n.s.	n.a.	(*)	n.s.	1
Egernia inornata[n]	511	Spring**	n.a.	***	n.s.	n.a.	n.s.	n.a.	n.s.	1**, 4*	3
Lerista bougainvillii[n]	140	Spring***	n.a.	***	n.s.	n.a.	n.s.	n.s.	n.s.	1, 2 (**)	26
Lerista labialis[n]	97	n.s.	n.a.	***	n.s.	n.a.	n.s.	n.s.	n.s.	1, 2 (***), 3, 4 (**)	9
Lerista punctatovittata[n]	474	Spring***	n.a.	***	(**)	n.a.	n.s.	n.s.	*	1, 2, 3(***), 4 (*)	17
Menetia greyii[d]	267	n.s.	n.s.	n.a.	(*)	(*)	n.s.	n.a.	n.s.	1, 2 (*), 4 (***)	5
Morethia boulengeri[d]	64	Spring*	n.s.	n.a.	(*)	n.s.	n.s.	n.a.	n.s.	n.s.	4
Morethia obscura[d]	114	Spring***	n.s.	n.a.	n.s.	n.s.	n.s.	n.a.	n.s.	n.s.	8
Typhlopidae											
Ramphotyphlops bicolor[n]	43	n.s.	n.a.	n.s.	n.s.	n.a.	**	*	n.s.	1, 3 (**)	11
Ramphotyphlops bituberculatus[n]	65	n.s.	n.a.	n.s.	n.s.	n.a.	*	n.s.	n.s.	1 (*)	4
Varanidae											
Varanus gouldii[d]	53	n.s.	n.s.	n.a.	n.s.	(**)	n.s.	n.a.	n.s.	4 (*)	3

(Table 3). Cloud cover, wind speed and relative humidity were similar during survey days in both trapping seasons. The spring surveys were wetter and experienced far fewer warm evenings (minimum overnight temperature >15°C) than did summer surveys. Whereas summer survey temperatures were similar to long-term averages (Table 3), the spring survey period was warmer than long-term averages, with higher mean maximum and minimum daily temperatures. In addition, both the spring and summer survey periods had less monthly rainfall and were less humid than long-term averages (Table 3). The timing of spring surveys resulted in there being more nights with a full moon (52 landscape nights) than in summer surveys (16); conversely,

there were more nights of new moon in summer surveys (77 landscape nights *v.* 31 for spring).

Models of trapping success

Weather and moon-phase variables explained 32% of the variation in total captures of reptiles (Table 2). These variables explained more variation in the capture rate of nocturnally active species (29%) than diurnal species (15%). Furthermore, weather and moon-phase variables were more often significant in models for nocturnally active species than for diurnal species (Table 2).

Season and temperature (maximum or minimum) were the variables that were most frequently significant in models of reptile

Table 3. Seasonal weather averages (±s.e.) and ranges recorded at Bureau of Meteorology (BOM) stations during survey periods in study landscapes
(*n* = 280 landscape nights of trapping per season)

Mean total monthly rainfall (2006–08) was recorded at the BOM weather station at Mildura Airport (34.18°S, 142.20°E). For comparison, long-term averages (1946–2008, recorded at the BOM weather station, Mildura Airport, Victoria) are included. For these long-term averages, data for spring is for all days in September–November each year, and for summer all days in December–February each year

Attribute	Spring surveys		Summer surveys		Spring	Summer
	Mean	Range	Mean	Range	(1946–2008)	(1946–2008)
Daily minimum temperature (°C)	12.44 ± 0.25	1.8–20.1	15.78 ± 0.31	5.0–25.9	9.83 ± 0.17	15.93 ± 0.12
Daily maximum temperature (°C)	29.56 ± 0.34	18.0–41.5	32.98 ± 0.34	20.6–40.9	23.84 ± 0.24	31.26 ± 0.14
Survey days >25°C	200		221			
Survey nights >15°C	29		159			
Survey nights with rainfall	75		41			
Total monthly rainfall (mm)	9.6 ± 4.2		17 ± 8.6		27.2 ± 1.7	21.4 ± 1.9
Daily relative humidity at 1500 hours (%)	24 ± 1	6–90	25 ± 1	9–71	35 ± 1	29 ± 0.5
Daily wind speed at 1500 hours (km h^{-1})	15 ± 0.5	0–38.9	12.7 ± 0.5	0–46.4	19 ± 0.2	17 ± 0.2
Daily cloud cover at 1500 hours (Oktas)	4	0–8	3	0–8	4	3

capture-rates (Table 2). Overall, reptiles were captured in spring at approximately twice the rate for summer (spring mean 16.59 ± 1.11 *v.* summer mean 9.42 ± 0.63 captures per night of trapping per landscape; *t* = 8.81, d.f. = 27, *P* < 0.001), despite the fact that the temperature ranges were similar between the seasons (Table 3). Diurnally active reptiles showed less marked differences between spring and summer than did nocturnally active species. For diurnal species, mean values were 6.78 ± 0.86 captures per night of trapping per landscape in spring *v.* 4.68 ± 0.61 captures per night of trapping per landscape in summer (*t* = 4.99, d.f. = 27, *P* < 0.001); for nocturnal species, mean values were 8.06 ± 0.79 captures per night of trapping per landscape in spring *v.* 4.13 ± 0.41 in summer (*t* = 5.32, d.f. = 27, *P* < 0.001).

The total capture rates, and capture rates of diurnal and nocturnal species, all increased with increasing minimum overnight and maximum daily temperatures (Fig. 2a, b). Total captures of reptiles increase linearly as daily maximum temperatures increased (Fig. 2a). Captures of diurnal reptile species peaked at ~25°C maximum daily temperature (Fig. 2a), whereas captures of nocturnal species increased markedly once minimum temperatures exceeded 10–15°C (Fig. 2b).

Across the study region, all 30 species considered in these analyses were captured in both spring and summer trapping sessions. Although overall species richness of reptiles per landscape was higher in 27 of the 28 study landscapes during spring trapping sessions than during summer sessions, some species were captured in particular landscapes only during summer. Summer trapping added between zero and seven species to species totals for individual landscapes. *Varanus gouldii* (*n* = 9 landscapes), *Ctenophorus pictus* (*n* = 6 landscapes) and *Morethia boulengeri* (*n* = 6 landscapes) were the species that were most commonly captured in landscapes in the summer trapping sessions only.

Capture success for individual species

Sixteen species were captured significantly more frequently in spring than in summer (Table 2). GAMM results indicated that the presence/absence of 15 species (five diurnal and 10 nocturnal) were significantly influenced by either minimum or maximum daily temperature (Table 2). However, the shape of the response curves for each species differed slightly. Some exhibited linear increases in the probability of capture over the range of temperatures experienced during trapping (e.g. the diurnal skink *Ctenotus brachyonyx* and the diurnal agamid *Amphibolurus nobbi coggeri*, Fig. 3a). Others, such as the diurnal legless lizards *Delma australis* and *D. butleri*, showed a marked increase in the probability of capture at temperatures between 25 and 30°C (Fig. 3b).

Among the nocturnally active geckoes that showed a significant response to the minimum overnight temperature, *Diplodactylus damaeus*, *D. vittatus* and *Gehyra variegata* showed a linear increase in capture with increased minimum temperature (Fig. 4a). In contrast, the probability of capture of *Nephrurus levis* appeared to increase markedly once overnight temperatures exceeded 15°C, whereas the probability of capture of *Rynchoedura ornata* peaked at minimum temperatures exceeding 15°C (Fig. 4a). The nocturnal skinks all exhibited considerable increases in the probability of capture with increasing minimum overnight temperature. The probability of capture of *Egernia inornata* and *Lerista bougainvillii* increased markedly once minimum temperatures exceeded 8–10°C (Fig. 4b), whereas the likelihood of capturing *L. labialis* was greatest when minimum overnight temperatures exceeded 15°C (Fig. 4b).

Interestingly, increasing relative humidity had a negative influence on the overall capture rates of diurnally active reptiles and total reptile captures (Table 2). Similarly, increasing relative humidity had a negative influence on the presence of seven species (Table 2).

Examining the raw weather data showed that as maximum temperature increased throughout the trapping period, relative humidity decreased ($y = -1.202x + 62.21$, $r^2 = 0.295$, d.f. = 516, $P < 0.001$). That is, during the trapping periods, the majority of the weather conditions that were 'humid' were also 'cool', rather than 'warm' and humid. As the latter combination (warm and humid) seldom occurred during trapping, it was not possible to model the influence of this combination of factors on capture rates.

As days became more overcast, total captures and captures of diurnal reptiles decreased (Table 2). Following afternoons of almost total cloud cover, captures of diurnal species were only
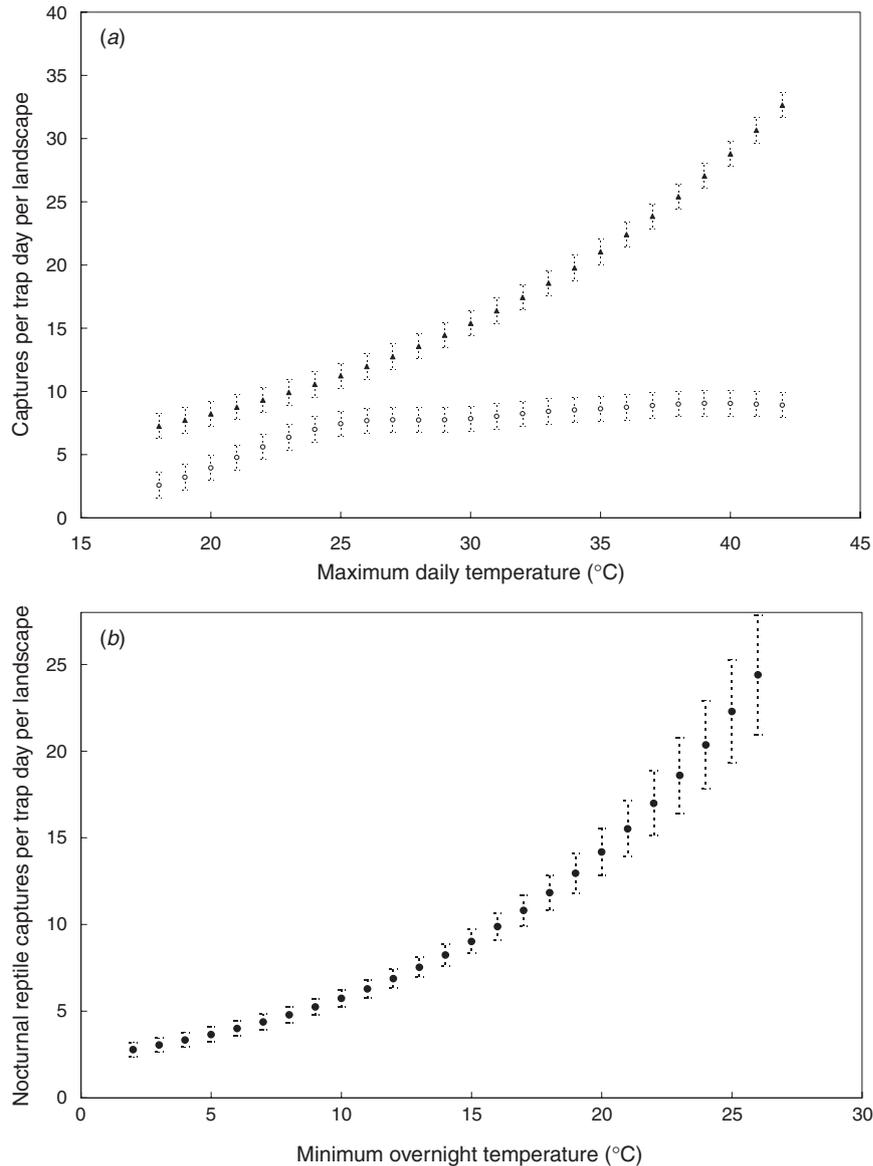
Fig. 2. Changes in the predicted capture rates of (*a*) all reptiles (black triangles) and diurnally active reptiles (open circles), and (*b*) nocturnally active reptiles with increasing daily spring maximum and minimum temperatures. Data points represent the predicted capture rate per day of trapping per landscape ± s.e., generated by using a generalised additive mixed model (GAMM) of captures, with either maximum or minimum temperature and season (= spring) as the predictors.

5.22 ± 0.71 individuals per day of trapping per landscape (*n* = 31 days), whereas on afternoons with no cloud cover (*n* = 57 days), the capture success was 9.21 ± 0.70 individuals per day of trapping per landscape (*t* = 3.65, d.f. = 86, *P* < 0.001). In addition, the presence/absence of five species of diurnally active reptiles was negatively influenced by increasing cloud cover (Table 2).

Seven species of reptiles were influenced by rainfall (Table 2); the probability of capture of four species increased with increasing rainfall (Fig. 5*a*), whereas the probability decreased for three species with increasing rainfall (Table 2). All species that responded positively to rainfall

were nocturnal and represented two families, namely blind snakes (Typhlopidae) and geckoes (Gekkonidae). The blind snakes *Ramphotyphlops bicolor* and *R. bituberculatus* had a probability of capture of <5% on nights with no rainfall, whereas they were more likely to be trapped after rain, with probabilities of capture of >9% after light rain and >15% after heavy rain (Fig. 5*a*). Similarly, the geckoes *D. vittatus* and *Strophurus* spp. had a <30% probability of capture on nights with no rain, but increased to probabilities of >30% after light rain and >40% after heavy rain (Fig. 5*a*).

Moon phase had no influence on the overall capture success of reptiles (Table 2), although it significantly influenced the
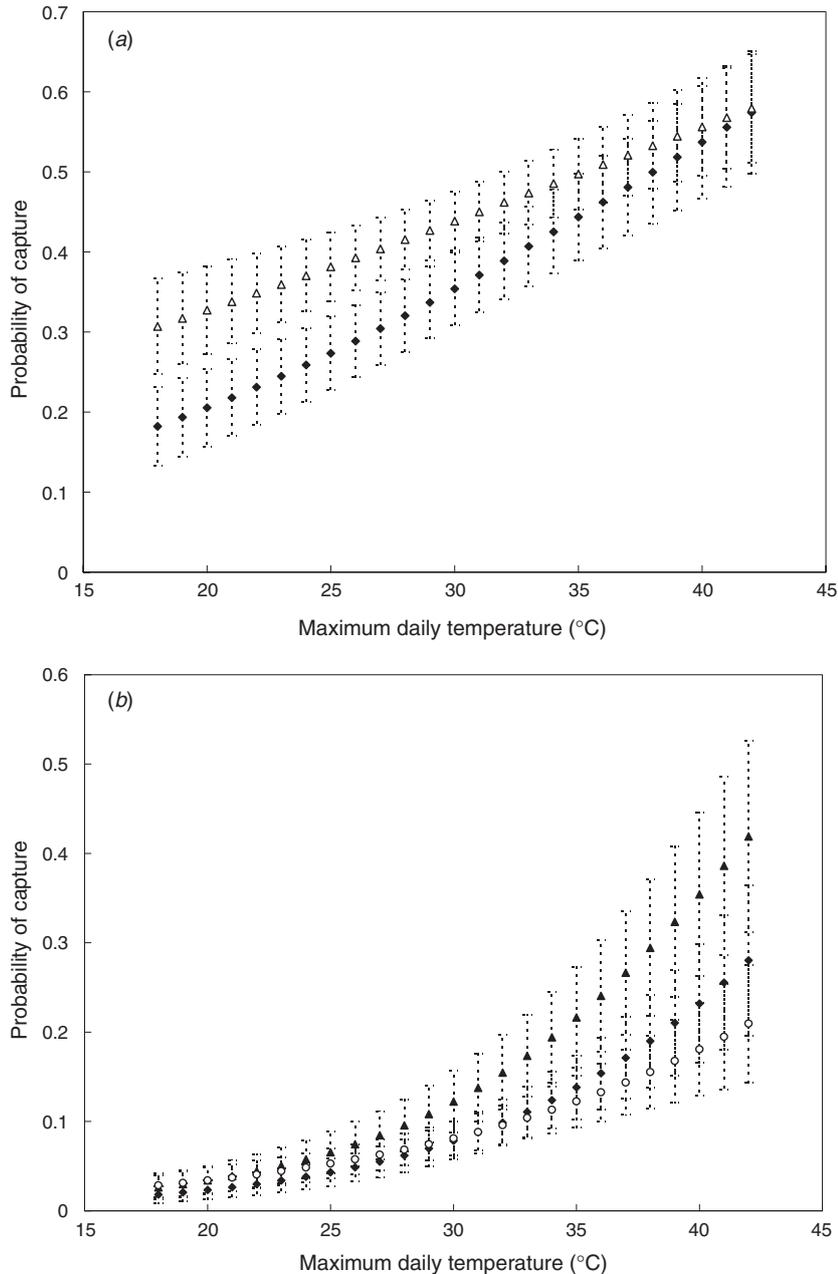
Fig. 3. Changes in the predicted probability of capture of the following diurnally active species: (*a*) *Ctenotus brachyonyx* (black diamonds) and *Amphibolurus nobbi coggeri* (open triangles), and (*b*) legless lizard species *Delma australis* (black triangles), *D. butleri* (black diamonds) and *Lialis burtonis* (open circles), shown to be significantly influenced by maximum temperature, by using generalised additive mixed models (GAMMs). Data points represent the predicted probability of capture of the species ± s.e., generated by using a GAMM of presence/absence data, with both maximum daily temperature and season (= spring) as the predictors.

probability of capture for two gecko species, *N. levis* and *Strophurus* spp., and the blind snake *R. bicolor*. The probability of capturing *N. levis* dropped from 24% on the nights of new moon to 5% on the nights of full moon (Fig. 5*b*). In contrast, the likelihood of capturing *Strophurus*

spp. increased as nights became brighter, from 16% on the new-moon nights to 42% on the full-moon nights (Fig. 5*b*).

Wind speed had no effect on the overall captures of diurnal or nocturnal species. Only four individual species (*Ctenotus brachyonyx*, *C. schomburgkii*, *G. variegata* and *R. ornata*)
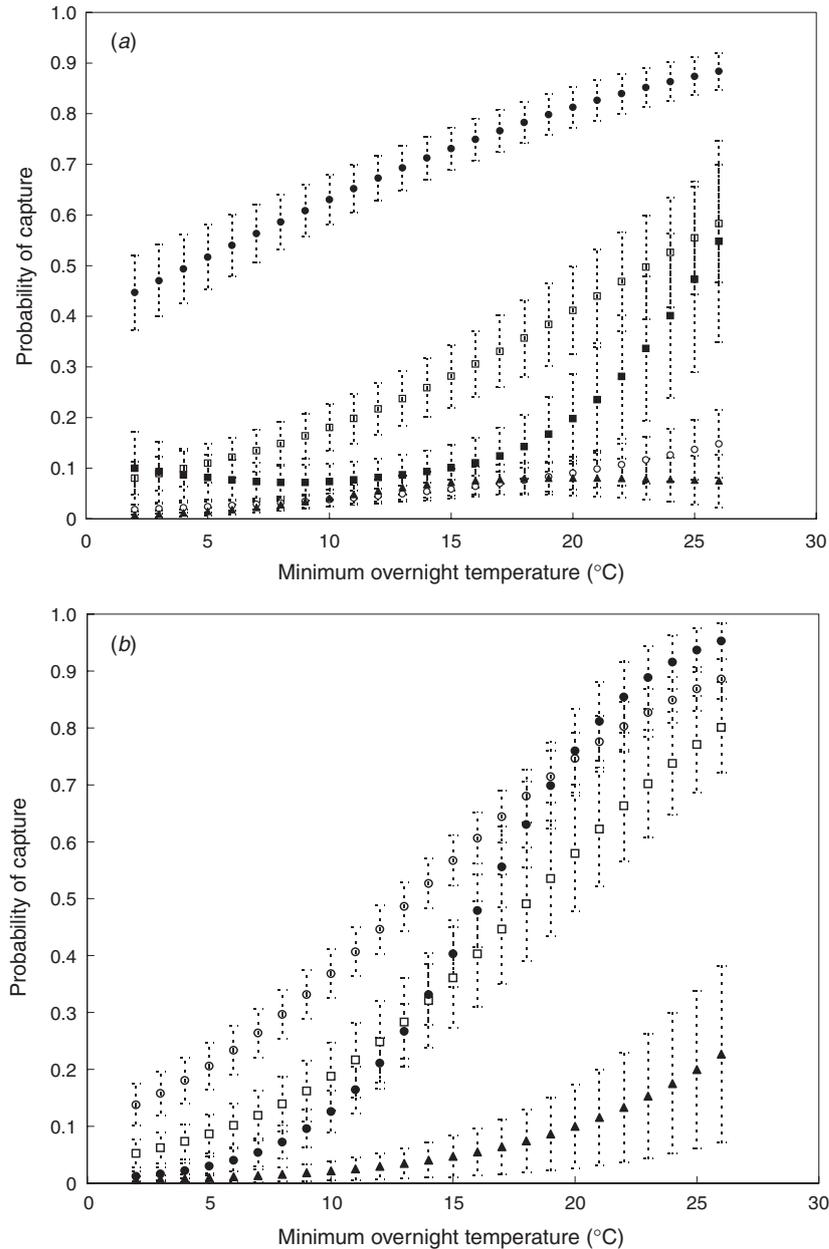
Fig. 4. Changes in the predicted probability of capture of the following nocturnally active species: (*a*) gecko species *Diplodactylus damaeus* (black circles), *D. vittatus* (open squares), *Gehrya variegata* (open circles), *Nephrurus levis* (black squares) and *Rhynchoedura ornata* (black triangles), and (*b*) skink species *Egernia inornata* (open squares), *Lerista bougainvillii* (black circles), *L. labialis* (black triangles) and *L. punctatovittata* (open circles), shown to be significantly influenced by the minimum temperature, by using generalised additive mixed models (GAMMs). Data points represent the predicted probability of capture of the species ± s.e., generated by using a GAMM of presence/absence data, with both minimum temperature and season (= spring) as the predictors.

were less likely to be trapped on days of higher wind speeds (Table 2). In contrast, the nocturnal skink, *Lerista punctatovittata*, was more likely to be captured after days of higher wind speeds (Table 2).

The likelihood of capturing 14 species on a particular trap-night was influenced by how many trap-nights preceded that night within a trapping session (i.e. none to four nights) (Table 2). Some, such as members of the genus *Lerista*, were
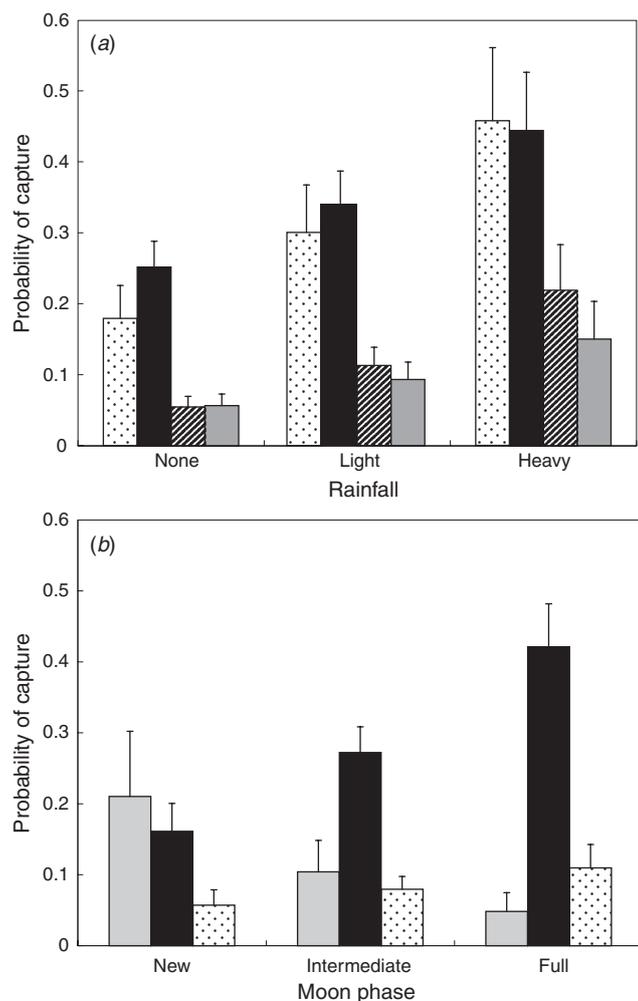
Fig. 5. Changes in the probability of capture of individual species of nocturnal reptiles shown to be influenced by (*a*) rainfall: *Diplodactylus vittatus* (spotted bar), *Strophurus* spp. (black bar), *Ramphotyphlops bicolor* (striped bar) and *R. bituberculatus* (grey bar); or by (*b*) moon phase: *Nephrurus levis* (grey bar), *Strophurus* spp. (black bar) and *R. bicolor* (spotted bar), by using generalised additive mixed models (GAMMs). Data represent the predicted probability of capture ± s.e. of the species generated by using a GAMM of presence/absence, with both rainfall or moon phase and season (= spring) as the predictors.

more likely to be trapped in the later stages of the trapping session (i.e. trap-nights 4 and 5) than in the earlier nights (Table 2), whereas, gecko species such as *D. damaeus* and *D. vittatus* were more likely to be captured on nights earlier in the trapping session (e.g. nights 1–3) (Table 2).

In all, 3 of the 30 species of reptiles included in the analyses did not exhibit a significant response to any explanatory variables (Table 2). Two of these species were diurnal, namely *Ctenotus regius* and *Pogona vitticeps*, with the third species being the nocturnal elapid *Parasuta nigriceps* (Table 2).

Discussion

Reptiles in the semi-arid mallee region exhibited strong seasonality in capture rates. More animals were captured in

spring than summer, despite temperature ranges in both seasons being similar. Previous studies have indicated that cues that drive seasonality in activity of reptiles are related to the timing of reproduction (Brown *et al.* 2001; Sun *et al.* 2001; Brown and Shine 2002). Reproductive cycles in reptile species are thought to result in the birth of young at the most favourable time of year, when food resources are sufficiently abundant for rapid growth of juveniles, which is normally during spring or early summer (Heatwole and Taylor 1987; Cogger 2000; Swan and Watharow 2005). Hence, the strong seasonality observed in the capture success of some reptiles may be associated with breeding activity during the spring sampling periods.

Nocturnally active reptiles were influenced by weather variables to a greater extent than were diurnal reptiles. Similarly, Read and Moseby (2001) found that weather and moon-phase variables accounted for 42% of the variation in capture rates of nocturnal species, but only 25% of the variation for diurnal species. Brown and Shine (2002) found that weather variables accounted for a substantial proportion of the variance in encounter rates of the water python (*Liasis fuscus*) (39%) and the keelback (*Tropidonophis mairii*) (31%), both of which are nocturnal species. This difference between nocturnal and diurnal species is most likely due to differences in thermoregulatory strategies. Diurnal species in the mallee region are almost entirely heliotherms that depend primarily on radiant energy for body heat (Heatwole and Taylor 1987). They can maintain their preferred body temperatures, despite variation in climatic conditions, through behavioural means such as basking, shade-seeking, perching or postural changes (Cogger 1974; Heatwole and Taylor 1987; Melville and Schulte 2001). Some nocturnally active reptiles use behavioural strategies such as repositioning themselves in different microclimates to minimise heat stress or maximise activity (Webb *et al.* 2004; Croak *et al.* 2008). However, as most nocturnal reptiles are predominantly thigmothermic, they depend primarily on heat exchange with substrates to maintain preferred body temperatures. Hence, their activity is more closely correlated with climatic factors such as ambient temperature (Pianka and Pianka 1976; Heatwole and Taylor 1987).

Of all climatic variables, temperature had the greatest influence on the capture rates of reptiles; both the overall captures of reptiles (total, diurnal and nocturnal species) and captures of individual species increased with increasing temperature. This is consistent with studies of snakes (Nelson and Gregory 2000; Sun *et al.* 2001; Brown and Shine 2002) and other reptile species in semi-arid environments (Read and Moseby 2001).

Captures of diurnal reptiles increased with increasing temperature until it exceeded 25°C, after which capture rates remained relatively constant with increasing temperature. Consequently, to maximise captures of diurnal reptiles, trapping periods should include daily temperatures that exceed this threshold (25°C), irrespective of the season. Captures of nocturnal species increased once minimum temperatures exceeded 10–15°C; thus, warm nights favour the capture of these species. There were two common responses to minimum overnight temperature; captures of some species such as *E. inornata* and *L. bougainvillii* increased markedly when minimum overnight temperatures reached 8–10°C, whereas

captures of others, such as *L. labialis* and *N. levis*, increased noticeably only when minimum overnight temperatures exceeded 15°C. Hence, total reptile captures increased with increasing temperature, and capture rates did not plateau or decline in the hottest weather.

Although the likelihood of capture of five diurnal species increased with increasing daily maximum temperature, the shape of their responses differed (Fig. 3). *Ctenotus brachyonyx* and *A. nobbi coggeri* showed a linear increase in the probability of capture with increasing maximum temperature, whereas the probability of capture of the pygopodid species *D. australis* and *D. butleri* increased disproportionately after the temperatures exceeded 30°C. Nothing is known about behavioural thermoregulation, preferred body temperatures (PBT) or critical span of *C. brachyonyx* or the two *Delma* species. However, in laboratory-based thermal gradient studies, *L. burtonis* maintained an average PBT of 35.1°C (Bradshaw *et al.* 1980). This is consistent with its greater probability of capture when temperatures exceed 30°C. Species of *Ctenotus* tolerate a broad range of ambient temperatures (e.g. *C. regius* remains active from 8.7°C to 45.1°C; Bennett and John-Alder 1986). In the present study, *C. brachyonyx* was captured across a broad range of temperatures, with no apparent maximum temperature threshold.

For five species of gecko, the probability of capture increased with increasing overnight minimum temperature (Fig. 4), although the response shapes differed among the species. Whereas *Diplodactylus damaeus*, *D. vittatus* and *G. variegata* exhibited linear responses to increasing temperature, *R. ornata* and *N. levis* showed a preference for temperatures exceeding 15°C. These differences are difficult to explain, given that these species share similar active field body temperatures (Pianka and Pianka 1976). A possible explanation relates to the range of temperatures in which each species is active. *D. damaeus* and *G. variegata* remain active in a broad range of ambient temperatures (7.5–44°C and 6–43.8°C, respectively; Henle 1990), and thus are unlikely to exhibit a threshold response to minimum temperature.

The critical thermal minimum of *E. inornata* (9.5–10.1°C) corresponds with the marked increase in the probability of capture at 8–10°C (Spellerberg 1972). In contrast, the probability of trapping *L. labialis* increased markedly as minimum temperature exceeded 15°C, whereas *L. punctatovittata* showed a linear response to increasing temperature. These findings all highlight the importance of trapping for nocturnal reptiles on warmer nights, preferably above 10°C, and ideally above 15–20°C.

Increasing humidity was associated with decreased captures of nocturnal reptiles. This result was unexpected. Heatwole and Taylor (1987) noted that evaporative water loss in reptiles is influenced by both the temperature and humidity of the surrounding environment. At a given temperature, evaporative water loss occurs more rapidly at lower relative humidities (Heatwole and Taylor 1987), suggesting that species would favour conditions with higher humidity. However, in the present study higher humidity was associated with cooler conditions (rather than warm, wet conditions). Reptile activity is strongly influenced by increasing temperature, so captures are more frequent at higher temperatures, when humidity tends to be lower.

Rainfall and moon phase did not influence overall capture rates of reptiles, although they did affect particular species. Capture success for both species of blind snake increased with rainfall. Although our measure of rainfall was crude (none, light, heavy), the present results support the contention in field guides (e.g. Swan and Watharow 2005) that blind snakes are observed on the surface more often following rain. *R. bicolor* and *R. bituberculatus* feed primarily on the adults, eggs and larvae of ants (Shine and Webb 1990; Webb and Shine 1993). In semi-arid south-western New South Wales, Briese and Macauley (1980) found that the proportion of active ant nests increased markedly after increasing soil moisture (i.e. the addition of water near nest area). Rainfall events may hence be linked with increased availability of food for blind snakes.

Two geckoes, *Strophurus* spp. and *D. vittatus*, were also more likely to be encountered following rainfall. Anecdotally, *Strophurus* spp. is reported to be more active on warm nights after rain (Swan and Watharow 2005). There is no specific information on the activity of *D. vittatus* after rainfall, although Henle (1990) found that congeners (*D. damaeus* and *Diplodactylus tessellatus*) remained active in light to medium rain, with activity of *D. tessellatus* limited by low humidity.

Moon phase influenced the probability of capture of two species; the probability of capture of *N. levis* decreased with increasing fullness of the moon, whereas the opposite was observed for *Strophurus* spp. Other studies have shown that encounter rates of nocturnal reptile species decrease with increasing light at night (Read and Moseby 2001; Brown and Shine 2002). On bright nights, reptiles may be more vulnerable to predators. In addition, their prey may be less active because of exposure to predation (e.g. scorpions, Skutelsky 1996). These explanations may account for the response of *N. levis*, but are inadequate for *Strophurus* spp. In contrast to *N. levis*, which forages in open spaces (Pianka and Pianka 1976), *Strophurus* spp. is primarily arboreal (How *et al.* 1986) and shelters among vegetation that may be less exposed to predators on brighter nights. Differences in visual acuity may also be involved. Werner and Seifan (2006) found that eye size was larger (relative to body size) in terrestrial than in arboreal species of gecko. *Strophurus* spp. are arboreal, and have smaller eyes (Pianka and Pianka 1976) than does the terrestrial *N. levis*. *Strophurus* spp. may forage on brighter nights to maximise hunting success, but be constrained to foraging within vegetation to minimise predation risk.

Only three species were not affected by season, climate or moon phase, namely two diurnal species, *C. regius* and *P. vitticeps*, and one nocturnal elapid, *P. nigriceps*. As mentioned earlier, diurnal heliotherms are likely to be less affected by climate because they can thermoregulate by behavioural means (Heatwole and Taylor 1987).

Although a range of weather and moon-phase variables influence capture rates of many reptile species, much of the variation in capture success remains unexplained. Other studies have reported similar results (Owen 1989; Read and Moseby 2001; Brown and Shine 2002). Other factors that may affect capture rates of reptiles include 'trappability' (i.e. the ability to escape traps or actually get trapped), the likelihood of encountering a trap (e.g. differences in range of movement), the timing of reproduction and aestivation, and the presence of important habitat features.

Conclusions

Given limited time available for surveys, the greatest diversity of reptiles will be gained by concentrating trapping effort predominantly in spring months. Trapping success will be higher if maximum daily temperatures during the survey period are greater than 25–30°C and overnight temperatures are at least 8–10°C, and preferably exceeding 15°C. Trapping success will also be enhanced if some very hot days and warm nights are experienced during the survey as it will increase the probability of capturing species such as the legless lizards *D. australis* and *D. butleri* or the nocturnal species, *L. labialis* and *N. levis*. Finally, rainfall and full-moon events enhance the chances of capturing species such as blind snakes and geckos. Selecting the most favourable seasonal and weather conditions will help ensure that reptile surveys maximise the likelihood of capturing the greatest diversity of reptiles, while minimising the effort required.

Acknowledgements

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