

# Capture predicates corticosterone responses and a low recapture likelihood in a varanid lizard

Tim S. Jessop <sup>A,\*</sup> 

For full list of author affiliations and declarations see end of paper

**\*Correspondence to:**

Tim S. Jessop  
Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Waurn Ponds, Vic. 3216, Australia  
Email: [t.jessop@deakin.edu.au](mailto:t.jessop@deakin.edu.au)

**Handling Editor:**

Penny Fisher

**Received:** 27 January 2022

**Accepted:** 13 June 2022

**Published:** 11 July 2022

**Cite this:**

Jessop TS (2023)  
*Wildlife Research*, **50**(7), 517–525.  
doi:[10.1071/WR22013](https://doi.org/10.1071/WR22013)

© 2023 The Author(s) (or their employer(s)). Published by CSIRO Publishing.  
This is an open access article distributed under the Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License (CC BY-NC-ND).

OPEN ACCESS

## ABSTRACT

**Context.** Understanding both the short- and long-term consequences of live animal capture is desirable to limit potential data biases or compromise animal welfare. The short-term elevation of glucocorticoid hormones in animals is an expected short-term stress consequence of trapping and restraint experiences. However, because these hormones also influence behaviour and memory, they may provide a physiological basis through which individuals vary in their recapture responses to subsequent trapping episodes. **Aims.** This objective of this study was to evaluate the interplay among trapping method, corticosterone responsiveness and recapture likelihood in a lizard, the lace monitor (*Varanus varius*). The first aim compared how different capture methods and associated restraint durations influenced plasma corticosterone of lace monitors. The second aim evaluated the relationship between capture methodology, corticosterone response and annual recapture frequency. The third aim measured yearly estimates for the probability of lace monitor recapture. **Methods.** Lace monitors were cage-trapped or noose-captured at 76 sampling sites across three annual sampling periods to measure capture experience, obtain blood samples and estimate recapture probabilities. **Results.** As expected, an increased restraint time and exposure to different capture methods significantly influenced corticosterone concentrations in lace monitors. Lace monitor recapture rates were meagre, suggesting that irrespective of the capture method, restraint duration and corticosterone levels, any form of initial capture experience typically leads to long-lasting aversive behaviour. **Conclusions.** Although plasma corticosterone concentrations may be tell-tale of a lace monitor's duration to short-term capture and restraint, they were not associated with the recapture likelihood in subsequent trapping events. **Implications.** Rapid and seemingly long-lasting trap aversion has apparent implications for the design of population monitoring programs used to study lace monitor population ecology.

**Keywords:** adrenocortical responsiveness, capture stressor, lace monitor, learning, live animal trapping, memory, reptile, restraint.

## Introduction

The capture of individuals through trapping and short-term restraint is often needed to gain essential knowledge of wild animals (Williams *et al.* 2002; Laver *et al.* 2012; Purwandana *et al.* 2014; Molyneux *et al.* 2017). Such practices may provide the only means to gain insights into an individual's health or phenotypic condition and, through recapture of marked animals, permit longer-term estimates of individual, population or community-level processes (Andrews 1982; Madsen and Shine 1996; Pike *et al.* 2008; Bickford *et al.* 2010; Nimmo *et al.* 2012; Stokeld *et al.* 2018). Given that methods of trapping and restraint vary considerably among individuals and species, they can potentially offer different regimes of physiological or psychological stress (Wingfield and Romero 2001; Moore and Jessop 2003; Jessop and Hamann 2005; Langkilde and Shine 2006; Anson *et al.* 2013). The duration of time spent in traps or restraint means that individuals can face exposure to the elements, be deprived of food and water, and endure fear, anxiety

or physiological stress (Broom *et al.* 1993). Because animals are often exposed to novel stressors during the capture process, they can face short- and potentially longer-term consequences (Lynn *et al.* 2003; Wikelski and Michael Romero 2003; Arnemo *et al.* 2006; Breed *et al.* 2019).

Short-term effects associated with the capture and restraint of animals typically include inducing a physiological-stress response (Wingfield and Romero 2001; Romero 2004). In response to stressors, reptiles activate the hypothalamic–pituitary–adrenal/interrenal (HPA) axis. This neuroendocrine pathway results in the release of glucocorticoids (corticosterone) from the inter-renal tissue (Moore and Jessop 2003). Glucocorticoids have system-wide effects on behaviour and physiology; therefore, trapping methods that elevate glucocorticoids could lead to short- and long-term phenotypic changes. For example, glucocorticoids have well known effects on intermediary metabolism (Romero 2004). However, they are also expected to influence cognition and memory consolidation and affect fear conditioning associated with noxious stimuli (i.e. trapping and restraint; Roozendaal 2000; Rodrigues *et al.* 2009). In general, glucocorticoids act on long-term fear memory consolidation in a dose–response relationship (de Kloet *et al.* 1999). In mammals such as humans and rodents, glucocorticoid concentrations appear to influence memory consolidation and learning in a concave up relationship (i.e. memory is most affected at low and high hormone concentrations; de Kloet *et al.* 1999; Diamond *et al.* 2007; Salehi *et al.* 2010). In particular, at low and high plasma concentrations, glucocorticoids have inhibitory effects on memory consolidation, whereas moderate doses produce positive effects. Mammalian studies indicate that glucocorticoids modulate memory consolidation via binding to receptors in multiple brain regions, especially the amygdala, a temporal brain structure associated with emotion and fear (reviewed in McGaugh 2004; Diamond *et al.* 2007; Schwabe *et al.* 2012). Indeed, evidence from the neurobiological literature suggests that trapping animals (a procedure that is likely to elicit both a stress and fear response) could have sustained effects on learning and memory and affect an individual's responses to a repeated exposure to adverse stimuli (Schwabe *et al.* 2012). Furthermore, correlations between stress responsiveness and personality type may influence how individuals experience and learn from novel stressors. For example, individuals with bold personalities are expected to have low-glucocorticoid stress responsiveness that promotes engagement with novel stimuli and reduces aversive learning if such stimuli are generally considered threatening (Cockrem 2007, 2013).

If trapping-induced stress and fear influence an individual's learning and memory to affect their recapture likelihood in future trapping events, it can have significant implications for field studies of wild animals. Whereby differences in HPA axis output promote aversive learning as a result of the initial trapping experience, then sampling

biases may arise if only animals with lower stress responses are recaptured (Biro and Dingemans 2009; Camacho *et al.* 2017). For example, in willow warblers (*Phylloscopus trochilus*) captured by mist-netting, researchers found that the male birds could memorise the first capture event conditions, which caused them to avoid a subsequent recapture by recognising similar conditions and modifying their behaviour (Linhart *et al.* 2012). Thus, addressing the relationship between capture-induced stress and behaviour is essential to avoid confounding data in longer-term field studies (Fowler *et al.* 2013). Indeed, the assumption that individuals demonstrate similar capture probabilities underpins many analytical or statistical techniques used in wildlife ecology (Williams *et al.* 2002; Zuur *et al.* 2009). Thus, the propensity for animals to develop trap-wariness can make it difficult to reliably estimate population parameters (e.g. abundance, dispersal or survival) in long-term wildlife studies (Williams *et al.* 2002; Goñi *et al.* 2003; Purwandana *et al.* 2015; Jessop *et al.* 2018).

Although there may be potential for corticosterone to mediate individual heterogeneity in subsequent capture-related behaviour, there is broad recognition that animals may develop more general patterns of recapture behaviour or other responses (Cubaynes *et al.* 2010; Pradel and Sanz-Aguilar 2012). For example, many studies have reported that wild animal populations, via learning, can develop neophilic (i.e. trappy happy) or neophobic responses (e.g. aversion/trap shyness; Brehm and Mortelliti 2018). These broad-scale responses demonstrate that many animals within a population can rapidly learn to adjust their behaviour to future trapping events (Stryjek *et al.* 2019). Additionally, exposure to trapping may lead animals to suffer from capture-related mortality. For example, individuals of some species suffer from rapid capture-related mortality (e.g. capture myopathy; Breed *et al.* 2019). Here, if individuals undertake intense physical activity associated with the capture process, they may induce metabolic acidosis that causes myocyte necrosis, which can be lethal if sufficiently severe (Paterson 2007).

The objective of this study was to address three aims. The first aim evaluated the effect of noose and cage trap-related capture methods and associated restraint times on plasma corticosterone concentrations in a large monitor lizard, the lace monitor (*Varanus varius*).

Like most reptiles, it would be predicted that both the method of capture and the associated duration of restraint time would increase plasma corticosterone concentrations of lace monitors (Moore and Jessop 2003; Hamann *et al.* 2007; Lancaster *et al.* 2010; Payne *et al.* 2012; Jessop *et al.* 2015).

For the second aim, I evaluated the associations between an individual's first capture experience and corticosterone response at release to see whether it was related to their recapture likelihood in subsequent trapping events. Here, individuals with the most stressful capture experiences and

associated higher corticosterone responses are expected to increase aversive learning and memory consolidation and limit an individual's recapture in subsequent trapping events (Thaker *et al.* 2010). Hence, those individuals who produce greater corticosterone responses at the initial capture are predicted to have a lower likelihood of recapture than have lace monitors that have smaller responses.

For the third aim, in recognition that wild animals may develop distinct patterns of recapture behaviour different from those predicted by their corticosterone responses alone (Cubaynes *et al.* 2010; Pradel and Sanz-Aguilar 2012; Stryjek *et al.* 2019), I assessed the ratio of recaptured to newly captured lace monitors across three annual trapping events to estimate the yearly recapture probability. If the proportion of recaptured to newly captured lace monitor remains low in the second and third trapping events, it could suggest that lace monitors develop aversion (e.g. neophobia or trap shyness) to subsequent annual trapping events. Alternatively, if the proportion of recaptured to newly captured lace monitors disproportionately increases in the second and third yearly trapping events, it could suggest that lace monitors develop a neophilic response to subsequent capture events.

## Methods

### Study species

The lace monitor is a semi-arboreal diurnal reptile that hunts on the ground and in trees (Jessop *et al.* 2010). It is widely distributed in non-arid areas of eastern Australia, and weighing up to 14 kg, it functions as a large native predator (Weavers 1988; Guarino 2001; Smissen *et al.* 2013). It is a generalist predator, and, in southern Australia, its activity is seasonal, with it being predominantly active in warmer months and inactive in winter (Guarino 2002; Jessop *et al.* 2012; Jessop *et al.* 2013a).

### Study area

The study was conducted in the Cape Conran Coastal Park and adjacent Murrungowar State Forest in East Gippsland, Victoria, Australia (37°48'S, 148°52'E). The study area comprised coastal forests covering 42 000 ha of two common vegetation types, namely (1) coastal woodland dominated by *Banksia serrata* and *B. integrifolia*; and (2) lowland forest dominated by *Eucalyptus sieberi* and *E. globoidea*. Here, 76 fixed trapping sites were located within the study area, and a 2-km interval separated each trapping locality. The capture of lace monitors was conducted over three annual trapping events in the summers of December 2007–January 2008, December 2008–January 2009 and December 2009–January 2010. These summer periods of capture coincided

with higher seasonal temperatures favourable to optimising the trapping effort of lace monitors (Jessop *et al.* 2013a).

### Lace monitor capture methods

Lace monitors were captured either by using traps or noose capture. These capture methods are described as below.

#### Traps

Aluminium box traps (2 m × 0.3 m × 0.3 m) were used to capture lace monitors ( $N = 17$ ; mean SVL = 56.67 cm; mean body mass = 3.37 kg; 12 males, 5 females). These traps were purpose-built for lace monitor capture, and the trap design was down-sized from that used for Komodo dragons (Ariefiandy *et al.* 2014). The trap had solid walls of aluminium sheeting, and a single row of ventilation holes was present on each wall of the trap. This design provided a trapped lace monitor with a largely enclosed and darkened internal space. There were no other structures (e.g. hide) inside the trap to provide additional shelter. These traps were positioned randomly within each of the 76 sites. Traps were baited with beef infused with tuna emulsion oil and located 50–100 m off the adjacent forest management track. Traps were always placed in shaded areas (e.g. under tree cover) to limit the risk of overheating to lace monitors. For lace monitors captured in traps, it was impossible to measure the specific capture duration. However, the duration that individuals were exposed to this procedure is likely hours (up to ~4 h) because traps were opened during daylight hours (08:00 am to 06:00 pm) and checked twice daily in the mid- to late morning (09:00 am to 11:45 am) and again mid- to late afternoon (03:00 pm to 06:00 pm). Lace monitors were not confined and could move about inside the trap. Again after capture, each lace monitor was removed from a trap and restrained with electrical tape to close the mouth shut and secure the fore and hind limbs. Post-restraint, trap-captured lace monitors were then immediately blood-sampled, had morphological measures taken and released at their points of capture. The effective trapping effort for each annual survey amounted to ~760 trapping hours per year.

#### Noose capture

During the twice-daily checking of traps, lace monitors were detected using visual search methods along forest management tracks (i.e. used to travel between trap localities) and when walking off the management track to inspect each trap. Once sighted, I approached and attempted to capture each lizard by using a long pole fitted with a noose rope. The noose was placed over the lizard's head and pulled taut to secure the animal. Restraint was initiated by removing each lizard from the noose and binding the mouth and limbs with electrical tape. The combined time for approaching, capturing, and restraining individuals ranged between 90 and 150 s. In the first annual capture event, noose-caught lace monitors ( $N = 36$  individuals; mean SVL = 55.46 cm

mean body mass = 3.22 kg; 25 males, 11 females) were then held for three randomly assigned restraint periods consisting of 3 ( $N = 12$ ), 45 ( $N = 12$ ) or 90 ( $N = 12$ ) min durations to enable comparison of the effect of capture and different restraint periods on plasma corticosterone responses. Lace monitors assigned to the 3 min restraint period were manually restrained, whereas individuals assigned for the 45 and 90 min restraint periods were secured inside an individual hessian sack.

### Lace monitor blood sampling

In the first year of study (December 2008–January 2009), each lace monitor ( $N = 53$ ) after its designated trap-capture or post-nose restraint period had a ~1 mL blood sample taken from its ventral caudal vein with a 21-gauge needle and a 3 mL syringe. Blood samples were then placed into individually labelled lithium heparin containers (BD Microtainer™ Tubes, BD Vacutainer Systems, Franklin Lakes, NJ, USA) and stored on ice. Once back at the camp (~3 h), samples were centrifuged (2100g for 5 min at room temperature) and the plasma was removed and stored at  $-20^{\circ}\text{C}$  until the corticosterone assay was performed (Jessop *et al.* 2012; Smissen *et al.* 2013). These first-year captures provided an initial sample of marked individuals to evaluate the effect of an individual's corticosterone concentration on their recapture likelihood in the two subsequent annual trapping events.

### Lace monitor identification, measurements and sex determination

Across the three annual trapping events, all lace monitors were individually identified with a passive integrated transponder to identify individuals beyond their first capture (Scheelings and Jessop 2011; Jessop *et al.* 2012). A sterile needle and applicator were used to insert the PIT tag laterally between the dermis and the muscle of each individual's upper left hind leg. The PIT-tag insertion site was sealed with surgical glue (Vetbond Tissue Adhesive, 3M, USA). In addition, I recorded each individual's snout to vent length (SVL), measured as the distance between the ventral tip of the snout and the most posterior opening of the cloacal slit. The body mass of each individual was recorded using a digital scale. The sex of individuals was subsequently determined using polymerase chain reaction (PCR) primers that amplified sex-specific alleles from genomic DNA obtained from blood (Jessop *et al.* 2012). On completion of the different capture and restraint durations, lace monitors were released at their capture point.

### Corticosterone radioimmunoassay

Total corticosterone in lace monitor plasma was measured using radioimmunoassay (RIA) techniques identical to those

used elsewhere (Jessop *et al.* 2015). Plasma samples (100  $\mu\text{L}$ ) were extracted for corticosterone concentrations by using a Corticosterone 3H Kit (MP Biomedicals, LLC). Final steroid concentrations were calculated from standard curves and corrected for individual sample recovery, individual plasma volume and the addition of tritiated steroid. Average ( $\pm$ s.e.m.) sample recovery was  $75.7\% \pm 0.028$ , with an intra-assay CV of 7.6% and an inter-assay CV of 13.04%. As reported by the manufacturer, the antibody had 100% cross-reactivity with corticosterone, 11% with 11-dehydrocorticosterone, 7% with 11-deoxycorticosterone, and <1% with the following steroids: progesterone, cortisol, aldosterone, testosterone, pregnenolone and  $5\alpha$ -DHT.

### Data analyses

For Aim 1, a generalised linear mixed model (GLMM) was used to evaluate the effects of different capture methods and their associated restraint time (and blood sampling) on lizard plasma corticosterone concentrations. I also included the effects of sex and body size (SVL) in the model to test whether these predictor variables were associated with significant differences in plasma corticosterone concentrations. The location of an individual's capture was used as a random effect in the model to account for any spatial autocorrelation in plasma corticosterone concentrations related to the proximity of individuals. This model was fitted with a Gaussian distribution and an identity canonical link. For Aim 2, a GLM (with a Poisson distribution and logit link) was used to test for the effects of the capture method, corticosterone and their interaction on the number of captures acquired for each tagged lizard across the study. *Post hoc* tests were conducted to determine where statistical significance was obtained within the main effects. Statistics were performed using SPSS V.22 (IBM).

For Aim 3, I used a Cormack–Jolly–Seber (CJS) model in the program MARK to estimate the annual lace monitor probability of capture (i.e. the proportion of recaptures within the total samples of lace monitors captured in the second and third yearly trapping events; Brownie *et al.* 1993; Nichols and Kendall 1995). This model simultaneously estimates apparent survival ( $\phi$ ) and capture probability ( $P$ ) for marked individuals (White and Burnham 1999). A candidate set of four models was assessed to evaluate capture probability in lace monitors. These models considered temporal and non-temporal variation in  $\phi$  and  $P$ . Models were ranked using the  $\text{AIC}_c$  value. The individual model weights ( $w_i$ ) were estimated to measure relative model support further (Burnham and Anderson 2003).

### Ethical standards

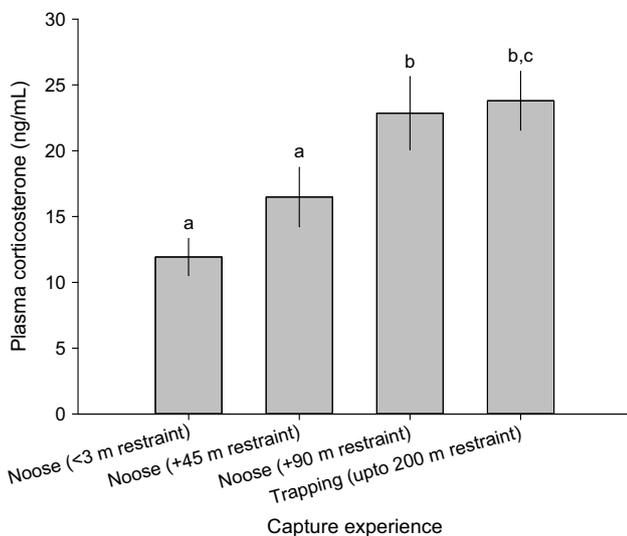
This research abided by the journal's guidelines on ethical standards. The study was conducted under the Department of Sustainability and Environment and a National Parks Act

(1975) research permit 10005037, and a University of Melbourne Ethics Permit 0911328 .

## Results

### Effects of trapping method and restraint duration on plasma corticosterone

Capture method and restraint duration significantly influenced lace monitor plasma corticosterone concentrations (GLMM,  $F_{3,53} = 8.99$ ,  $P < 0.001$ ; Fig. 1). Plasma corticosterone increased across the three post-noosing restraint intervals (i.e. 3, 45 and 90 min). Pairwise *post hoc* tests for individuals captured by noosing indicated that the plasma corticosterone concentrations measured after 90 min of restraint were significantly higher than those reported after 3 ( $P < 0.001$ ) and 45 ( $P = 0.044$ ) min of restraint. Lizards captured in traps and held for multiple hours before blood sampling also exhibited high corticosterone concentrations. These were significantly greater than those exposed to the 3 ( $P < 0.001$ ) and 45 ( $P = 0.035$ ) min restraint periods after noosing. However, there was no significant ( $P = 0.717$ ) difference between the plasma corticosterone concentrations of individuals captured in traps and those of individuals exposed to 90 min of restraint post-noosing. There was no significant effect of sex (GLMM,  $F_{1,54} = 0.17$ ,  $P = 0.685$ ) or body size (GLMM,  $F_{1,54} = 0.13$ ,  $P = 0.72$ ) on lace monitor plasma corticosterone concentrations.



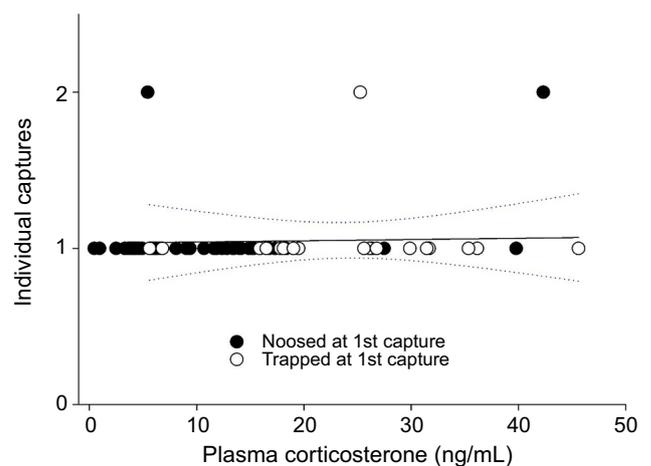
**Fig. 1.** The relationships between trapping method and restraint duration on lace monitor plasma corticosterone. Bars and error bars represent the mean and standard error of plasma corticosterone measured within each category. The superscript letters denote significant *post hoc* differences among groups.

### Effects of capture and plasma corticosterone on lace monitor recapture rates

Variation in the number of recaptures for each lizard across the 3-year study duration was not significantly influenced by an individual's corticosterone concentration on release at first capture (GLM, Wald  $\chi^2 = 0.126$ ,  $P = 0.723$ ). This non-significant relationship between an individual's corticosterone concentration and its number of captures was defined by a nearly flat slope ( $\beta = 0.003 \pm 0.002$ ) and a low coefficient of variation ( $R^2 = 0.01$ ). A power test estimated that a minimum  $R^2$  of 0.23 would be needed with the current sample size. Similarly, neither trapping method (GLM, Wald  $\chi^2 = 0.024$ ,  $P = 0.952$ ) nor the interaction between these two effects (GLM, Wald  $\chi^2 = 0.012$ ,  $P = 0.915$ ; Fig. 2) influenced the number of lace monitor recaptures. These results reflected that just 3 of the 53 individuals captured in the first year of the study were recaptured again in the two subsequent annual sampling events (mean captures =  $1.08 \pm 0.001$  per individual). Two of the three recaptured individuals comprised two large adult males (SVL = 61.45 and 69.55 cm) noosed at their first capture event and caught by trap in the second year of study. The third recapture was a subadult female (SVL = 48.90) captured by a trap in her first capture event and then recaptured by a noose in the third year of study.

### Annual estimates of lace monitor recapture probability

I captured 152 lace monitors, including 53, 48, and 51 individuals in the summers of December 2007–January 2008, December 2008–January 2009 and December 2009–January 2010 respectively. Four recaptures were present among the



**Fig. 2.** The relationships among lace monitor plasma corticosterone recorded at first capture, trapping method and an individual's total number of captures across three annual trapping events. The trend line shows the predicted regression and the associated 95% confidence intervals between corticosterone and individual lace monitor capture rates.

total number of captures, with two tagged individuals captured in the second and third annual trapping events (Fig. 3). The four recaptured lace monitors included the three aforementioned individuals recaptured from the first trapping event. The fourth recapture was an adult male (SVL = 64.58 cm), first captured by a trap in the second trapping event and then retrapped in the third trapping event. The annual recapture probability estimates of previously tagged lace monitors relative to new captures for the second and third annual capture events were  $0.039 \pm 0.027$  and  $0.019 \pm 0.013\%$  respectively (Fig. 3). That top-ranked Cormack–Jolly–Seber model indicated that there was not sufficient evidence of annual differences in the lace monitor probability of recapture for tagged individuals (Table 1).

## Discussion

Lace monitors responded to variation in capture method and the associated restraint duration by increasing plasma corticosterone concentration. This observation validates that field trapping methods activated a physiological stress response in this species (Scheelings and Jessop 2011). Typically, the HPA/I axis can rapidly up-regulate to stressors, causing increased glucocorticoid secretion into the blood plasma within 3–5 min (Romero and Reed 2005). The plasma corticosterone response increased over multiple hours of capture or restraint for lace monitors. Similar, slowly induced capture-related corticosterone responses are consistent with results found in other large reptiles (Lance and Elsey 1986; Jessop 2001; Moore and Jessop 2003; Jessop *et al.* 2004, 2013c). The duration of capture and restraint, as stressful stimuli, are expected to trigger a commensurate increase in glucocorticoids to enable individuals to activate

**Table 1.** Cormack–Jolly–Seber models were used to estimate capture probability for lace monitors.

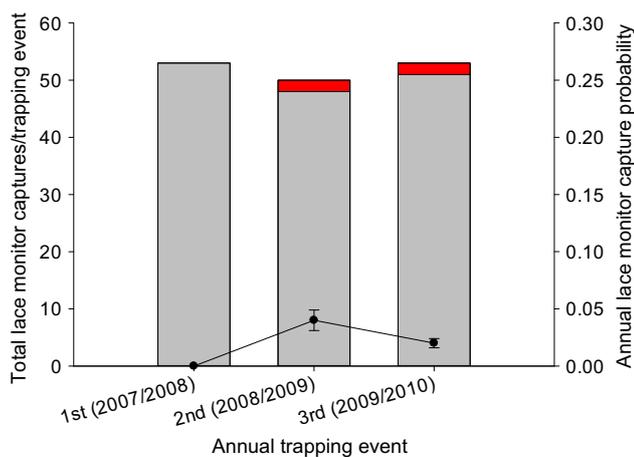
Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>	K	DEV
<b>Φ(.) p(.)</b>	<b>41.07</b>	<b>0.00</b>	<b>0.50</b>	<b>2</b>	<b>0.47</b>
Φ(.) p(t)	43.80	1.73	0.21	3	0.08
Φ(t) p(.)	43.80	1.73	0.21	3	0.08
Φ(t) p(t)	44.97	3.90	0.07	4	0.08

Models are ranked from most to least supported, with the best model in bold. AIC<sub>c</sub>, Akaike information criterion corrected for small sample size; ΔAIC<sub>c</sub>, the difference in value between AIC<sub>c</sub> of this model and the most parsimonious model; AIC<sub>c</sub> weights (w<sub>i</sub>) ranking models by relative support; K, number of estimated parameters; DEV, deviance; Φ, survival probability; p, recapture probability; (.), constant; (t), time dependence.

physiological and behavioural responses to cope with capture experiences (Wingfield *et al.* 1998; Romero 2004).

Further research that can better assess the actual duration of lace monitor restraint within cage traps is needed to discount the effect of the trapping method on this species' corticosterone responses. Other studies comparing different trapping methods have suggested that capture methodology can lead to differences in individuals' acute stress response at similar restraint durations (Lakušić *et al.* 2020). Importantly, for individual lace monitors, given the short duration of the overall trapping event (i.e. acute exposure), it would be expected that any increase in plasma corticosterone would confer short-term benefits rather than pathological or other negative fitness-related consequences typical of either exposure to pervasive acute or chronic stress responses (Jessop *et al.* 2013b; Narayan *et al.* 2015).

The second aim evaluated the correlation between a lace monitor's corticosterone concentration measured at their first capture and the number of recaptures in subsequent annual trapping events. It was evident that differences in trapping method, restraint time, and post-release corticosterone concentration did not influence an individual subsequent recapture rate. This result arose because almost all lace monitors captured in the first year were never recaptured again. However, there is also mixed evidence that experimentally increased plasma corticosterone concentrations can elevate the propensity for aversive, neophobia or fear-related learning behaviours in wild animals (Thaker *et al.* 2010; de Bruijn and Romero 2020). Additionally, other endocrine processes, besides glucocorticoids, are well recognised to influence aversive learning and memory consolidation in vertebrates exposed to stress (Joëls *et al.* 2006; Schwabe *et al.* 2012). Of course, stressful stimuli will also activate the autonomic nervous system to increase catecholamine production, such as norepinephrine (NE), which will rapidly bind to adrenoceptors on vagal afferents to stimulate the prefrontal cortex, amygdala and hippocampus (Schwabe *et al.* 2012). Similar to glucocorticoids, the stimulatory actions of NE can enhance the encoding and processing of stressful stimuli to



**Fig. 3.** The composite bar graph shows the lace monitor total captures and recaptures (red bar) and the scatter and line graph shows the annual recapture probability.

consolidate memories, to allow learning of aversive stimuli (Joëls *et al.* 2006). Thus, catecholamines or other stress-related neurotransmitters (e.g. CRF) may help explain the physiological basis to why lace monitors demonstrate extensive recapture aversion (de Bruijn and Romero 2020). Further study is now required to identify physiological mechanisms, so as to explain what causes this response but also to explain why rapid-onset capture-induced aversion appears so conserved within this lace monitor population.

The third aim confirmed that the annual recapture probability of lace monitors was low (i.e. <5% per year) and similar between the second and third trapping events. This result contrasts with the expectation that increased trapping effort and ongoing tagging of individuals will increase the proportion of recaptures to new captures over time, unless there are mitigating circumstances (Williams *et al.* 2002). For example, high annual recapture probabilities are obtained using similar methods in other lace monitor populations and the congeneric Komodo dragon (*Varanus komodoensis*). Indeed populations of Komodo dragons can obtain annual recapture probabilities greater than 70% after three-yearly trapping events (Laver *et al.* 2012; Ariefiandy *et al.* 2013, 2014; Purwandana *et al.* 2014; Lei and Booth 2018). The extremely low annual lace monitor recapture rate suggests that when this population is exposed to different capture or restraint protocols, they predominantly develop long-term aversive behaviour unrelated to plasma corticosterone responses. Other lizards have shown similar broad-scale and rapid aversion responses to capture or novel stressors (Marcellini and Jenssen 1991; Thaker *et al.* 2010).

Could low annual recapture rates indicate acute or longer-term capture-related consequences such as deferred capture-related mortality? Several reasons suggest this outcome to be unlikely. First, capture myopathy, a potential cause of acute mortality, typically arises when individuals exhibit intense physical activity during capture, confinement or restraint associated with the trapping procedure (Breed *et al.* 2019). Common clinical symptoms of capture myopathy preceding death include lethargy, loss of coordination and impaired movement (Paterson 2007). All lace monitors released in this study exhibited typical escape behaviour (i.e. fleeing or tree climbing) independent of restraint time, capture methods or corticosterone concentrations, suggesting no apparent short-term pathological consequences. Second, in a concurrent study using externally marked lace monitors also captured via trap and noose (i.e. from the same population), who exhibited restricted movement owing to their reliance on anthropogenic food subsidies, it was evident that through repeated resightings, these individuals survived over several weeks, suggesting an absence of long-term lethal trapping consequences (Jessop *et al.* 2012). Thus, most tagged individuals would be expected to persist throughout the study duration to permit recapture. Similarly, the concurrent use of non-invasive trapping methods (e.g. camera-traps and track counts) to measure population

indices in lace monitors over the study duration indicated no evidence of rapid population decline to imply broad-scale mortality as a result of trapping or other environmental processes (Anson *et al.* 2014; Hu *et al.* 2019).

In conclusion, despite the vast amount of literature that posits that increased glucocorticoid concentrations following exposure to stressors can exert a wide variety of behavioural and physiological effects that influence animal performance and fitness (Wingfield and Romero 2001; Romero 2004), the present study indicated that even with increased exposures to lizard-trapping protocols that lead to proportional increases in the plasma glucocorticoid responses, it has little influence on lizard recapture behaviour. Thus, because capture and restraint are often perceived by animals as stressful, using plasma corticosterone as a putative physiological measure of an individual's capture exposure may not correlate well with many short- or longer-term stress-related consequences.

## References

- Andrews RM (1982) Patterns of growth in reptiles. *Biology of the Reptilia* **13**, 273–320.
- Anson JR, Dickman CR, Boonstra R, Jessop TS (2013) Stress triangle: do introduced predators exert indirect costs on native predators and prey? *PLoS ONE* **8**, e60916. doi:10.1371/journal.pone.0060916
- Anson JR, Dickman CR, Handasyde K, Jessop TS (2014) Effects of multiple disturbance processes on arboreal vertebrates in eastern Australia: implications for management. *Ecography* **37**, 357–366. doi:10.1111/j.1600-0587.2013.00340.x
- Ariefiandy A, Purwandana D, Seno A, Ciofi C, Jessop TS (2013) Can camera traps monitor Komodo dragons a large ectothermic predator? *PLoS ONE* **8**, e58800. doi:10.1371/journal.pone.0058800
- Ariefiandy A, Purwandana D, Seno A, Chrismiawati M, Ciofi C, Jessop TS (2014) Evaluation of three field monitoring-density estimation protocols and their relevance to Komodo dragon conservation. *Biodiversity and Conservation* **23**, 2473–2490. doi:10.1007/s10531-014-0733-3
- Arnemo JM, Ahlqvist P, Andersen R, Berntsen F, Ericsson G, Odden J, Brunberg S, Segerström P, Swenson JE (2006) Risk of capture-related mortality in large free-ranging mammals: experiences from Scandinavia. *Wildlife Biology* **12**, 109–113. doi:10.2981/0909-6396(2006)12[109:ROCMIL]2.0.CO;2
- Bickford D, Howard SD, Ng DJJ, Sheridan JA (2010) Impacts of climate change on the amphibians and reptiles of Southeast Asia. *Biodiversity and Conservation* **19**, 1043–1062. doi:10.1007/s10531-010-9782-4
- Biro PA, Dingemanse NJ (2009) Sampling bias resulting from animal personality. *Trends in Ecology & Evolution* **24**, 66–67. doi:10.1016/j.tree.2008.11.001
- Breed D, Meyer LCR, Steyl JCA, Goddard A, Burroughs R, Kohn TA (2019) Conserving wildlife in a changing world: understanding capture myopathy—a malignant outcome of stress during capture and translocation. *Conservation Physiology* **7**, coz027. doi:10.1093/conphys/coz027
- Brehm AM, Mortelliti A (2018) Mind the trap: large-scale field experiment shows that trappability is not a proxy for personality. *Animal Behaviour* **142**, 101–112. doi:10.1016/j.anbehav.2018.06.009
- Broom DM, Johnson KG, Broom DM (1993) 'Stress and animal welfare.' (Springer)
- Brownie C, Hines JE, Nichols JD, Pollock KH, Hestbeck JB (1993) Capture–recapture studies for multiple strata including non-Markovian transitions. *Biometrics* **49**, 1173–1187. doi:10.2307/2532259
- Burnham KP, Anderson DR (2003) 'Model selection and multimodel inference: a practical information-theoretic approach.' (Springer Science & Business Media)

- Camacho C, Canal D, Potti J (2017) Lifelong effects of trapping experience lead to age-biased sampling: lessons from a wild bird population. *Animal Behaviour* **130**, 133–139. doi:10.1016/j.anbehav.2017.06.018
- Cockrem JF (2007) Stress, corticosterone responses and avian personalities. *Journal of Ornithology* **148**, 169–178. doi:10.1007/s10336-007-0175-8
- Cockrem JF (2013) Individual variation in glucocorticoid stress responses in animals. *General and Comparative Endocrinology* **181**, 45–58. doi:10.1016/j.ygcen.2012.11.025
- Cubaynes S, Pradel R, Choquet R, Duchamp C, Gaillard J-M, Lebreton J-D, Marboutin E, Miquel C, Reboulet A-M, Poillot C, Taberlet P, Gimenez O (2010) Importance of accounting for detection heterogeneity when estimating abundance: the case of french wolves. *Conservation Biology* **24**, 621–626. doi:10.1111/j.1523-1739.2009.01431.x
- de Bruijn R, Romero LM (2020) Prior restraint stress inhibits habituation to novel objects in the European starlings (*Sturnus vulgaris*). *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology* **333**, 88–95. doi:10.1002/jez.2327
- de Kloet ER, Oitzl MS, Joëls M (1999) Stress and cognition: are corticosteroids good or bad guys? *Trends in Neurosciences* **22**, 422–426. doi:10.1016/S0166-2236(99)01438-1
- Diamond DM, Campbell AM, Park CR, Halonen J, Zoladz PR (2007) The temporal dynamics model of emotional memory processing: a synthesis on the neurobiological basis of stress-induced amnesia, flashbulb and traumatic memories, and the Yerkes–Dodson law. *Neural Plasticity* **2007**, 60803. doi:10.1155/2007/60803
- Fowler J, Cohen L, Jarvis P (2013) 'Practical statistics for field biology.' (John Wiley & Sons)
- Gofiñ R, Quetglas A, Reñones O (2003) Differential catchability of male and female European spiny lobster *Palinurus elephas* (Fabricius, 1787) in traps and trammelnets. *Fisheries Research* **65**, 295–307. doi:10.1016/j.fishres.2003.09.021
- Guarino F (2001) Diet of a large carnivorous lizard, *Varanus varius*. *Wildlife Research* **28**, 627–630. doi:10.1071/WR01001
- Guarino F (2002) Spatial ecology of a large carnivorous lizard, *Varanus varius* (Squamata : Varanidae). *Journal of Zoology* **258**, 449–457. doi:10.1017/S0952836902001607
- Hamann M, Jessop TS, Schäuble CS (2007) Fuel use and corticosterone dynamics in hatchling green sea turtles (*Chelonia mydas*) during natal dispersal. *Journal of Experimental Marine Biology and Ecology* **353**, 13–21. doi:10.1016/j.jembe.2007.08.017
- Hu Y, Gillespie G, Jessop TS (2019) Variable reptile responses to introduced predator control in southern Australia. *Wildlife Research* **46**, 64–75. doi:10.1071/WR18047
- Jessop TS (2001) Modulation of the adrenocortical stress response in marine turtles (Cheloniidae): evidence for a hormonal tactic maximizing maternal reproductive investment. *Journal of Zoology* **254**, 57–65. doi:10.1017/S0952836901000553
- Jessop TS, Hamann M (2005) Interplay between age class, sex and stress response in green turtles (*Chelonia mydas*). *Australian Journal of Zoology* **53**, 131–136. doi:10.1071/ZO04061
- Jessop T, Sumner J, Lance V, Limpus C (2004) Reproduction in shark-attacked sea turtles is supported by stress-reduction mechanisms. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **271**, S91–S94. doi:10.1098/rsbl.2003.0102
- Jessop TS, Urlus J, Lockwood T, Gillespie G (2010) Preying possum: assessment of the diet of lace monitors (*Varanus varius*) from coastal forests in southeastern Victoria. *Biawak* **4**, 59–66.
- Jessop TS, Smissen P, Scheelings F, Dempster T (2012) Demographic and phenotypic effects of human mediated trophic subsidy on a large Australian lizard (*Varanus varius*): meal ticket or last supper? *PLoS ONE* **7**, e34069. doi:10.1371/journal.pone.0034069
- Jessop TS, Kearney MR, Moore JL, Lockwood T, Johnston M (2013a) Evaluating and predicting risk to a large reptile (*Varanus varius*) from feral cat baiting protocols. *Biological Invasions* **15**, 1653–1663. doi:10.1007/s10530-012-0398-3
- Jessop TS, Letnic M, Webb JK, Dempster T (2013b) Adrenocortical stress responses influence an invasive vertebrate's fitness in an extreme environment. *Proceedings of the Royal Society B: Biological Sciences* **280**, 20131444. doi:10.1098/rspb.2013.1444
- Jessop TS, Anson JR, Narayan E, Lockwood T (2015) An introduced competitor elevates corticosterone responses of a native lizard (*Varanus varius*). *Physiological and Biochemical Zoology* **88**, 237–245. doi:10.1086/680689
- Jessop TS, Woodford R, Symonds MRE (2013c) Macrostress: do large-scale ecological patterns exist in the glucocorticoid stress response of vertebrates? *Functional Ecology* **27**, 120–130. doi:10.1111/j.1365-2435.2012.02057.x
- Jessop TS, Ariefiandy A, Purwandana D, Ciofi C, Imansyah J, Benu YJ, Fordham DA, Forsyth DM, Mulder RA, Phillips BL (2018) Exploring mechanisms and origins of reduced dispersal in island Komodo dragons. *Proceedings of the Royal Society B: Biological Sciences* **285**, 20181829. doi:10.1098/rspb.2018.1829
- Joëls M, Pu Z, Wiegert O, Oitzl MS, Krugers HJ (2006) Learning under stress: how does it work? *Trends in Cognitive Sciences* **10**, 152–158. doi:10.1016/j.tics.2006.02.002
- Lakušić M, Billy G, Bjelica V, Golubović A, Anđelković M, Bonnet X (2020) Effect of capture, phenotype, and physiological status on blood glucose and plasma corticosterone levels in free-ranging dice snakes. *Physiological and Biochemical Zoology* **93**, 477–487. doi:10.1086/711958
- Lancaster P, Jessop TS, Stuart-Fox D (2010) Testing the independent effects of population and shelter density on behavioural and corticosterone responses of tree skinks. *Australian Journal of Zoology* **58**, 295–302. doi:10.1071/ZO10056
- Lance VA, Elsey RM (1986) Stress-induced suppression of testosterone secretion in male alligators. *Journal of Experimental Zoology* **239**, 241–246. doi:10.1002/jez.1402390211
- Langkilde T, Shine R (2006) How much stress do researchers inflict on their study animals? A case study using a scincid lizard, *Eulamprus heatwolei*. *Journal of Experimental Biology* **209**, 1035–1043. doi:10.1242/jeb.02112
- Laver RJ, Purwandana D, Ariefiandy A, Imansyah J, Forsyth D, Ciofi C, Jessop TS (2012) Life-history and spatial determinants of somatic growth dynamics in komodo dragon populations. *PLoS ONE* **7**, e45398. doi:10.1371/journal.pone.0045398
- Lei J, Booth DT (2018) Intraspecific variation in space use of a coastal population of lace monitors (*Varanus varius*). *Australian Journal of Zoology* **65**, 398–407. doi:10.1071/ZO17078
- Linhart P, Fuchs R, Poláková S, Slabbekoorn H (2012) Once bitten twice shy: long-term behavioural changes caused by trapping experience in willow warblers *Phylloscopus trochilus*. *Journal of Avian Biology* **43**, 186–192. doi:10.1111/j.1600-048X.2012.05580.x
- Lynn SE, Breuner CW, Wingfield JC (2003) Short-term fasting affects locomotor activity, corticosterone, and corticosterone binding globulin in a migratory songbird. *Hormones and Behavior* **43**, 150–157. doi:10.1016/S0018-506X(02)00023-5
- Madsen T, Shine R (1996) Seasonal migration of predators and prey: a study of pythons and rats in tropical Australia. *Ecology* **77**, 149–156. doi:10.2307/2265663
- Marcellini DL, Jenssen TA (1991) Avoidance learning by the curly-tailed lizard, *Leiocephalus schreibersi*: implications for anti-predator behavior. *Journal of Herpetology* **25**, 238–241. doi:10.2307/1564662
- McGaugh JL (2004) The amygdala modulates the consolidation of memories of emotionally arousing experiences. *Annual Review of Neuroscience* **27**, 1–28. doi:10.1146/annurev.neuro.27.070203.144157
- Molyneux J, Pavey CR, James AI, Carthew SM (2017) The efficacy of monitoring techniques for detecting small mammals and reptiles in arid environments. *Wildlife Research* **44**, 534–545. doi:10.1071/WR17017
- Moore IT, Jessop TS (2003) Stress, reproduction, and adrenocortical modulation in amphibians and reptiles. *Hormones and Behavior* **43**, 39–47. doi:10.1016/S0018-506X(02)00038-7
- Narayan EJ, Jessop TS, Hero J-M (2015) Invasive cane toad triggers chronic physiological stress and decreased reproductive success in an island endemic. *Functional Ecology* **29**, 1435–1444. doi:10.1111/1365-2435.12446
- Nichols JD, Kendall WL (1995) The use of multi-state capture–recapture models to address questions in evolutionary ecology. *Journal of Applied Statistics* **22**, 835–846. doi:10.1080/02664769524658
- Nimmo DG, Kelly LT, Spence-Bailey LM, Watson SJ, Haslem A, White JG, Clarke MF, Bennett AF (2012) Predicting the century-long post-fire responses of reptiles. *Global Ecology and Biogeography* **21**, 1062–1073. doi:10.1111/j.1466-8238.2011.00747.x

- Paterson J (2007) Capture myopathy. In 'Zoo animal and wildlife immobilization and anesthesia'. (Eds G West, D Heard, N Caulket) pp. 171–179. (John Wiley & Sons, Ltd) doi:10.1002/9781118792919.ch12
- Payne CJ, Jessop TS, Guay P-J, Johnstone M, Feore M, Mulder RA (2012) Population, behavioural and physiological responses of an urban population of black swans to an intense annual noise event. *PLoS ONE* **7**, e45014. doi:10.1371/journal.pone.0045014
- Pike DA, Pizzatto L, Pike BA, Shine R (2008) Estimating survival rates of uncatchable animals: the myth of high juvenile mortality in reptiles. *Ecology* **89**, 607–611. doi:10.1890/06-2162.1
- Pradel R, Sanz-Aguilar A (2012) Modeling trap-awareness and related phenomena in capture–recapture studies. *PLoS ONE* **7**, e32666. doi:10.1371/journal.pone.0032666
- Purwandana D, Ariefiandy A, Imansyah MJ, Rudiharto H, Seno A, Ciofi C, Fordham DA, Jessop TS (2014) Demographic status of Komodo dragons populations in Komodo National Park. *Biological Conservation* **171**, 29–35. doi:10.1016/j.biocon.2014.01.017
- Purwandana D, Ariefiandy A, Imansyah MJ, Ciofi C, Forsyth DM, Gormley AM, Rudiharto H, Seno A, Fordham DA, Gillespie G, Jessop TS (2015) Evaluating environmental, demographic and genetic effects on population-level survival in an island endemic. *Ecography* **38**, 1060–1070. doi:10.1111/ecog.01300
- Rodrigues SM, LeDoux JE, Sapolsky RM (2009) The influence of stress hormones on fear circuitry. *Annual Review of Neuroscience* **32**, 289–313. doi:10.1146/annurev.neuro.051508.135620
- Romero LM (2004) Physiological stress in ecology: lessons from biomedical research. *Trends in Ecology & Evolution* **19**, 249–255. doi:10.1016/j.tree.2004.03.008
- Romero LM, Reed JM (2005) Collecting baseline corticosterone samples in the field: is under 3 min good enough? *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **140**(1), 73–79. doi:10.1016/j.cbpa.2004.11.004
- Roozendaal B (2000) Glucocorticoids and the regulation of memory consolidation. *Psychoneuroendocrinology* **25**, 213–238. doi:10.1016/S0306-4530(99)00058-X
- Salehi B, Cordero MI, Sandi C (2010) Learning under stress: the inverted-U-shape function revisited. *Learning & Memory* **17**, 522–530. doi:10.1101/lm.1914110
- Scheelings T, Jessop T (2011) Influence of capture method, habitat quality and individual traits on blood parameters of free-ranging lace monitors (*Varanus varius*). *Australian Veterinary Journal* **89**, 360–365. doi:10.1111/j.1751-0813.2011.00815.x
- Schwabe L, Joëls M, Roozendaal B, Wolf OT, Oitzl MS (2012) Stress effects on memory: an update and integration. *Neuroscience & Biobehavioral Reviews* **36**, 1740–1749. doi:10.1016/j.neubiorev.2011.07.002
- Smitsen PJ, Melville J, Sumner J, Jessop TS (2013) Mountain barriers and river conduits: phylogeographical structure in a large, mobile lizard (Varanidae: *Varanus varius*) from eastern Australia. *Journal of Biogeography* **40**, 1729–1740. doi:10.1111/jbi.12128
- Stokeld D, Fisher A, Gentles T, Hill BM, Woinarski JCZ, Young S, Gillespie GR (2018) Rapid increase of Australian tropical savanna reptile abundance following exclusion of feral cats. *Biological Conservation* **225**, 213–221. doi:10.1016/j.biocon.2018.06.025
- Stryjek R, Kalinowski A, Parsons MH (2019) Unbiased sampling for rodents and other small mammals: how to overcome neophobia through use of an electronic-triggered live trap: a preliminary test. *Frontiers in Ecology and Evolution* **7**, 11. doi:10.3389/fevo.2019.00011
- Thaker M, Vanak AT, Lima SL, Hews DK (2010) Stress and aversive learning in a wild vertebrate: the role of corticosterone in mediating escape from a novel stressor. *The American Naturalist* **175**, 50–60. doi:10.1086/648558
- Weavers BW (1988) Vital statistics of the lace monitor lizard (*Varanus varius*) in south-eastern Australia. *Victorian Naturalist* **105**, 142–145.
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**, S120–S139. doi:10.1080/00063659909477239
- Wikelski M, Michael Romero L (2003) Body size, performance and fitness in galapagos marine iguanas. *Integrative and Comparative Biology* **43**, 376–386. doi:10.1093/icb/43.3.376
- Williams BK, Nichols JD, Conroy MJ (2002) 'Analysis and management of animal populations.' (Academic Press)
- Wingfield JC, Romero LM (2001) Adrenocortical responses to stress and their modulation in free-living vertebrates. In 'Comprehensive physiology'. (Ed. R Terjung) pp. 211–234. (John Wiley & Sons, Ltd) doi:10.1002/cphy.cp070411
- Wingfield JC, Maney DL, Breuner CW, Jacobs JD, Lynn S, Ramenofsky M, Richardson RD (1998) Ecological bases of hormone–behavior interactions: the “emergency life history stage”. *American Zoologist* **38**(1), 191–206. doi:10.1093/icb/38.1.191
- Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) 'Mixed effects models and extensions in ecology with R.' (Springer Science & Business Media)

**Data availability.** The data that support this study will be shared upon reasonable request to the corresponding author.

**Conflicts of interest.** The author declares no conflicts of interest.

**Declaration of funding.** Support was provided by University of Melbourne Early Career Research Grant to the author.

**Acknowledgements.** I thank Tim Lockwood, Dr Franciscus Scheelings and Dr Jen Anson for assistance in sample collection or laboratory processing. I also acknowledge David Booth and another anonymous reviewer for providing constructive comments that improved the paper.

#### Author affiliation

<sup>A</sup>Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Waurn Ponds, Vic. 3216, Australia.