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Turning ghosts into dragons: improving camera monitoring outcomes for a cryptic low-density Komodo dragon population in eastern Indonesia

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Abstract

Context. Detection probability is a key attribute influencing population-level wildlife estimates necessary for conservation inference. Increasingly, camera traps are used to monitor threatened reptile populations and communities. Komodo dragon (*Varanus komodoensis*) populations have been previously monitored using camera traps; however, considerations for improving detection probability estimates for very low-density populations have not been well investigated.

Aims. Here we compare the effects of baited versus non-baited camera monitoring protocols to influence Komodo dragon detection and occupancy estimates alongside monitoring survey design and cost considerations for ongoing population monitoring within the Wae Wuul Nature Reserve on Flores Island, Indonesia.

Methods. Twenty-six camera monitoring stations (CMS) were deployed throughout the study area with a minimum of 400 m among CMS to achieve independent sampling units. Each CMS was randomly assigned as a baited or non-baited camera monitoring station and deployed for 6 or 30 daily sampling events.

Key results. Baited camera monitoring produced higher site occupancy estimates with reduced variance. Komodo dragon detection probability estimates were $0.15 \pm 0.092–0.22$ (95% CI), $0.01 \pm 0.001–0.03$, and $0.03 \pm 0.01–0.04$ for baited (6 daily survey sampling events), unbaited (6 daily survey sampling events) and long-unbaited (30 daily survey sampling events) sampling durations respectively. Additionally, the provision of baited lures at cameras had additional benefits for Komodo detection, survey design and sampling effort costs.

Conclusions. Our study indicated that baited cameras provide the most effective monitoring method to survey low-density Komodo dragon populations in protected areas on Flores.

Implications. We believe our monitoring approach now lends itself to evaluating population responses to ecological and anthropogenic factors, hence informing conservation efforts in this nature reserve.

Keywords. population monitoring, effective sampling, protected areas, apex predator, reptiles, *Varanus komodoensis*.

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Introduction

Large terrestrial predators are most often at risk from human actions and increasingly require effective conservation actions to ensure population persistence (Gittleman and Harvey 1982; Prowse *et al.* 2015; Penjor *et al.* 2019). The key requirement to establish effective conservation actions for apex predators is to accurately monitor population trends and status (Karanth *et al.* 2011). However, because apex predators are often rare or averse to capture or detect, non-invasive monitoring methods are routinely used to evaluate the effects of threatening processes or conservation actions on their populations (Karanth *et al.* 2004; O'Connell *et al.* 2010). Similarly, the increasing use of hierarchical models such as site occupancy and n-mixture models, which account for imperfect detection, are now among the most common techniques used to provide population-level inference for apex predators (MacKenzie *et al.* 2002, 2006; Royle 2004; Kéry *et al.* 2005). Indeed, these methods are often well suited for threatened predator population studies (du Preez *et al.* 2014; Tan *et al.* 2017; Penjor *et al.* 2019; Searle *et al.* 2020), because threatened predators often persist at low densities where individual-based recapture or resighting probabilities can be too low to allow for the alternate population estimates using mark–recapture type models (Williams *et al.* 2002; Kéry and Schmidt 2008; Couturier *et al.* 2013; du Preez *et al.* 2014; Tan *et al.* 2017; Searle *et al.* 2020).

Non-invasive monitoring techniques such as camera trapping are now increasingly used for monitoring terrestrial reptiles, a taxon with over 11 000 primarily predatory species (Ariefiandy *et al.* 2013; Jessop *et al.* 2013; Welbourne *et al.* 2015; Adams *et al.* 2017; Moore *et al.* 2020). Nevertheless, the use of cameras, as measured by the capacity to achieve adequate detection for robust population-level estimates, remains variable within and among reptile species because of the effects of body size, species habits and environmental factors (Ariefiandy *et al.* 2013; Welbourne *et al.* 2015; Richardson *et al.* 2017; Einoder *et al.* 2018). In the case of large reptiles, lower population densities, greater daily movement capacity, the effects of seasonal climatic variation, and smaller skin surface to ambient air temperature differences can all influence camera-based population monitoring effectiveness (Ariefiandy *et al.* 2013; Jessop *et al.* 2013; Welbourne 2013; Richardson *et al.* 2017; Hu *et al.* 2019). Furthermore, human activities can often disproportionately threaten large-bodied reptiles, causing their populations to be at much lower densities than normal and thus more difficult to monitor (Todd *et al.* 2010; Tingley *et al.* 2019). Thus, addressing these factors by modifying camera sampling designs to increase detection probability is a key consideration to monitor threatened reptile populations effectively. Under such circumstances, there may be compelling reasons to improve camera-based detection using baits or lures (i.e. attractants) to increase detection probability (O'Connell *et al.* 2010; Long *et al.* 2012; Read *et al.* 2015).

Multiple studies have reported that the use of baits or lures as attractants can vastly improve predators' detection sensitivity (du Preez *et al.* 2014; Austin *et al.* 2017; Comer *et al.* 2018). This result is especially important in predator populations where individuals can be cryptic or persist as low-density populations. Hence, attractants or baits may be essential to increase detection to prevent poor quality estimates of population-level parameters (Thompson 2013). For this reason, baited camera traps deployed during appropriate weather conditions can be advocated to optimise large-reptile detection probability (Jessop *et al.* 2013). Although, it is important to note that these benefits may need to consider how baits can affect a species' movement behaviour and create potential biases in any arising population-level estimates (Stewart *et al.* 2019).

The Komodo dragon (*Varanus komodoensis*) is the largest lizard and has an important ecological role as an apex predator (Jessop *et al.* 2006, 2019, 2020). The current distribution of Komodo dragons is restricted to five islands located in Komodo National Park and several fragmented populations on Flores Island (Jessop *et al.* 2007, 2018; Purwandana *et al.* 2014*a*; Ariefiandy *et al.* 2015; Jones *et al.* 2020). Populations on Flores Island have decreased because of anthropogenic activities and are now increasingly reliant on a small number of reserve areas to ensure their persistence (Ariefiandy *et al.* 2015, 2020; Jones *et al.* 2020).

Komodo dragon populations on Flores persist at much lower population densities ($<$1 dragon km^{-2}) than those observed in Komodo National Park ($\sim$10 dragons km^{-2}; Laver *et al.* 2012; Purwandana *et al.* 2014*a*; Ariefiandy *et al.* 2015, 2020). Multiple field methods have been used to estimate population trends of Komodo dragons (Ariefiandy *et al.* 2013, 2014). However, these can vary considerably in their monitoring effectiveness (Jessop *et al.* 2007; Ariefiandy *et al.* 2013, 2014; Purwandana *et al.* 2014*a*, 2015). On Flores, low densities and trap-wary behaviour of Komodo dragons favour wildlife cameras over direct trapping methods as a more effective population monitoring methodology (Ariefiandy *et al.* 2015). However, optimising camera monitoring design is still necessary to allow conservation managers to improve the data used to evaluate these most vulnerable populations (Jones *et al.* 2020). Here, we compare the effect of baited and unbaited camera sampling on the estimates of Komodo dragon detection probability and site occupancy, alongside other measures of monitoring efficacy and project running costs within the Wae Wuul Nature Reserve of Flores. Finally, we discuss the implications of our results for managing Komodo dragons within this protected area and, more broadly, for other populations distributed on the island of Flores.

Materials and methods

Study area

The Wae Wuul Nature Reserve comprises a protected area of 14.84 km^2 located on the western coast of Flores in eastern Indonesia (Fig. 1*a*, *b*). The reserve was established in 1985, aiming to increase protection of Komodo dragons beyond Komodo National Park. The climate is highly seasonal, dominated by a long dry season from March to November and a short wet season. Annual rainfall is less than 2000 mm (Monk *et al.* 1997). The study area comprises a hilly coastal landscape covered in multiple distinct vegetation communities. The two most common vegetation communities are savanna grassland (common species include *Eulalia leschenaultiana* and *Setaria adhaerens*) and savanna woodland (common species include *Borassus flabellifer* and *Zizyphus horsfeldi*) that cover $\sim$80% of the study area (Auffenberg 1981). In valley floors holding permanent or ephemeral watercourses, drier vegetation communities are replaced by open deciduous monsoon forest ($\sim$20% of the study area; dominant species include *Tamarindus indica*, *Schleichera oleosa* and *Cassia javanica*) or bamboo forest. These land cover types are representative of those found across the lowland coastal areas of major islands in this region of eastern Indonesia, including the adjacent Komodo National Park (Auffenberg 1981).

Study design

Twenty-six camera monitoring stations (CMS) were deployed within the Wae Wuul Nature Reserve. These CMS were placed within all key vegetation communities, including deciduous monsoon forest and savanna woodland. A minimum of 400 m separated all sites to improve data independence obtained from cameras (Ariefiandy *et al.* 2013, 2014). This 400-m distance between monitoring sites was based on the radius of the mean home-range area for Komodo dragons (Jessop *et al.* 2018; Purwandana *et al.* 2021). At the commencement of the study, each site was randomly assigned as a baited (n = 13) or non-baited (n = 13) camera monitoring station to ensure equal replicates within each camera method treatment. After the initial sampling period at each station, the assigned camera method

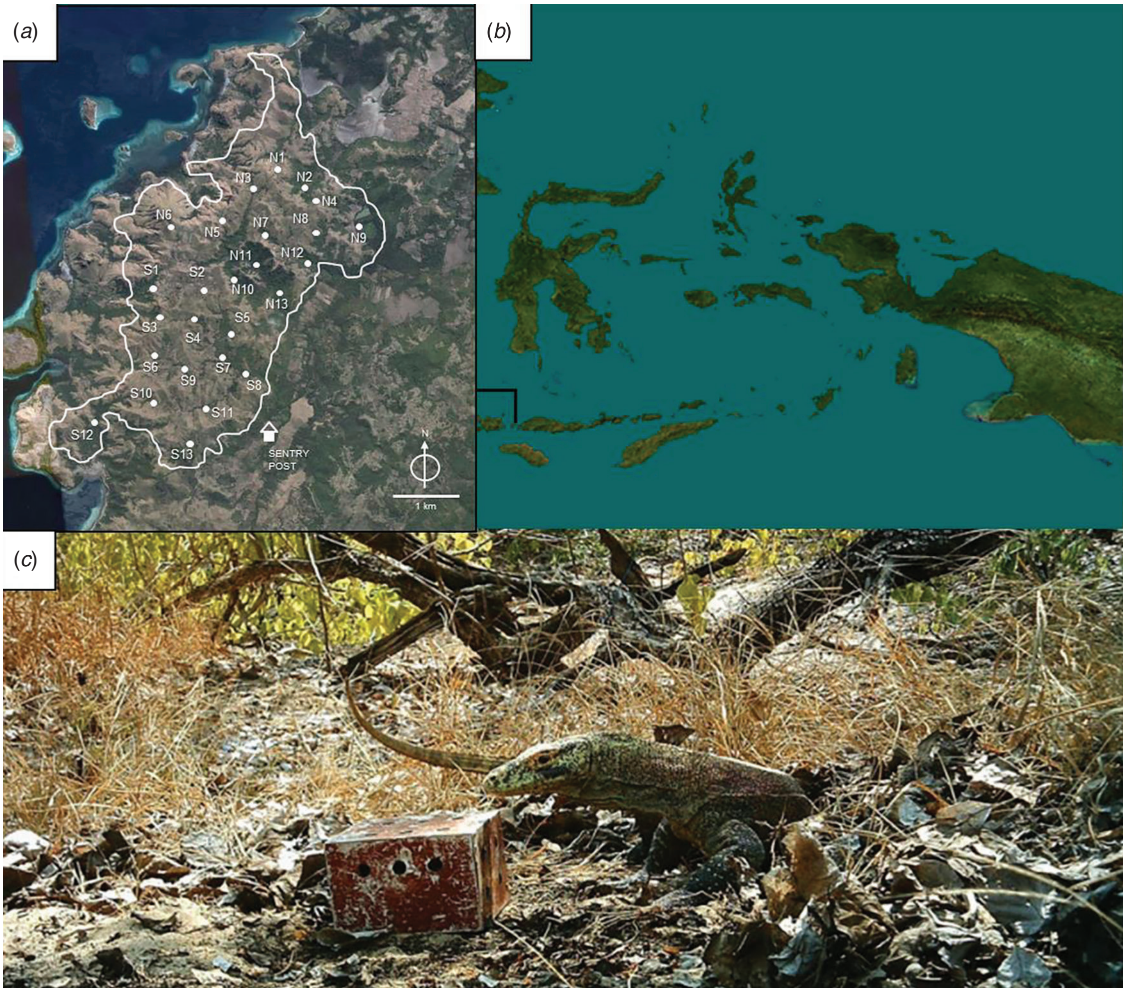

Fig. 1. The study evaluated the effect of bait attractant on Komodo dragon detection probability and site occupancy estimates by using camera monitoring stations deployed across (*a*) the Wae Wuul Nature Reserve located (*b*) on the western coast of Flores in eastern Indonesia. (*c*) An image of a Komodo dragon inspecting the meat attractant contained within a metal bait box.

was reversed to the alternate method to compare estimates of Komodo dragon detection probability and occupancy obtained for each method at each site. The study was conducted during June and July 2017 in the mid-dry season when environmental temperatures permit Komodo dragons to exhibit normal daily diurnal activity patterns and, hence, pending abundance, the potential for good detection probability (Harlow *et al.* 2010*a*, 2010*b*; Jessop *et al.* 2013).

Camera monitoring design

At each CMS, a single outward facing Bushnell camera (Model Trophy Cam HD 119678) was attached to a tree (40 cm above the ground) as described elsewhere (Ariefiandy *et al.* 2013, 2014). Cameras were programmed to take three photos and a 1-min video each time an animal triggered the device. At installation, all cameras were tested to confirm normal functioning. For CMS allocated to the bait treatment, we used two scent lures that comprised a small aluminium box (25 × 15 × 15 cm; L × W × H) and a suspended plastic bag, each containing goat meat that was placed 4 and 2 m in front or above the camera respectively. Baited and unbaited CMS were deployed for 6 and 30 days of monitoring respectively. The uneven durations between treatments reflected our belief that baited cameras would require considerably less sampling effort to produce higher detection probabilities than those obtained from unbaited cameras. As Komodo dragons have been observed to investigate baits at traps for several minutes before entering traps or moving elsewhere, we also used a 30-min camera delay to prevent repeated photography of the same individual lizard (Ariefiandy *et al.* 2014). In addition, a 3-day non-monitoring period was used immediately after the transition from baited to unbaited sites. This waiting period was implemented to remove a potential carry-over bait effect that could have attracted Komodo dragons and inflated detection probability at sites then monitored with unbaited cameras. This research abided by the journal's guidelines on ethical standards.

Estimating detection and site occupancy estimates

We modelled the detectability and occupancy of Komodo dragons by using a single-season occupancy model, using the

Table 1. Model selection results testing effects of baited and non-baited cameras for influencing detection probability (p) and site occupancy (Ψ) of Komodo dragons within the Wae Wuul Nature Reserve in West Flores

K, the number of estimated parameters; logLik, logliklihood; AIC, Akaike information criterion; ΔAIC, the difference in value between AIC of this model and the most parsimonious model; and AIC weights (w_i), a measure of relative model support

Model	K	logLik	AIC	ΔAIC	w_i
Ψ(.) p(bait vs no-bait))	3	365.43	371.43	0.00	0.71
Ψ(bait vs no-bait)) p(bait vs no-bait))	4	365.21	373.21	1.78	0.29
Ψ(.) p(bait vs no-bait))* daily survey variation	62	302.17	426.17	54.74	0.00
Ψ (.) p (.)	2	424.44	428.44	57.01	0.00

software Presence (Hines 2006). Site occupancy models use patterns of detection and non-detection over multiple surveys (sampling occasions) of a sampling unit (CMS) to estimate detection probabilities (p) and, thus, produce unbiased estimates of occupancy (ψ) (MacKenzie *et al.* 2002). We modelled the effect of baits on both the detection probability (p) and ψ relative to those cameras without baits (i.e. p. ψ). We partitioned the unbaited CMS detection probability data into two datasets, given the sampling duration differences between baited and unbaited CMS. One dataset comprised the first six, and the other the full 30 daily sampling events. Models were ranked using AIC, and we considered the effect of bait provision at CMS to be influential if the model AIC was >2 units below that estimated for the null model (Burnham and Anderson 2004).

Detection probability curves, probability of site absences and survey design costs

To assess the expected reduction in sampling effort provided by using baits at CMS, we produced detectability curves for CMS with and without baits. Detectability curves represent the cumulative probability (i.e. rate of increase) that Komodo dragons will be detected after a given number of sampling occasions in a site where the species is present (Wintle *et al.* 2005). Cumulative detection probability curves were estimated as $pk = 1 - (1 - p)^k$, where p is the species' per-survey detection probability within a given treatment and k is the given number of sampling occasions (MacKenzie and Royle 2005).

Next, we estimated the minimum number of sequential sampling occasions, with no detection required to be 95% certain (i.e. $\alpha = 0.05$) that Komodo dragons were absent from a surveyed site by using baited and unbaited cameras (Wintle *et al.* 2012; Ferreras *et al.* 2018). The probability (with $\alpha = 0.05$) of not detecting Komodo dragons after N sampling occasions at a given site is estimated by the formula

$$N > \frac{\log\left(\frac{\alpha}{1-\alpha}\right) - \log\left(\frac{\Psi}{1-\Psi}\right)}{\log(1-\mathrm{p})}$$

Here, values of p and ψ are specific to baited and unbaited CMS site occupancy estimates derived from the 6-day sampling period.

Finally, we compared the costs of sampling for baited and unbaited camera trapping methodology to achieve a similar monitoring outcome (i.e. $\alpha = 0.05$) by calculating protocol-specific costs of each technique, beyond common costs associated with camera purchases, as such we estimated

$$C(m) = \sum (C_d + C_r + C_b \times S_d + C_{bb} \times S_d + C_{cb} \times S_d)$$

where $C(m)$ = method specific survey cost, C_d = cost of camera deployment, C_r = cost of camera retrieval, C_b = cost of bait (US\$0.26 per camera per survey day (S_d)), C_{bb} = cost of bait boxes (US\$10.00 per camera), C_{cb} = cost of camera batteries (US\$0.20 per camera per survey day).

Results

The most parsimonious occupancy model (Ψ (.), p (bait vs no-bait), model weight = 0.71) indicated that the effect of baits placed at CMS vastly improved Komodo dragon detection probability compared with the null model (ΔAIC = 57.01; model weight = 0.00; Table 1). Detection probability estimates for baited cameras (6 daily sampling events) were 15 and 5.5 times higher than those estimated for unbaited (6 daily sampling events) and long-unbaited (30 daily sampling events) camera sampling durations (Fig. 2*a*). Similarly, baited cameras produced 2.3 and 1.3 higher Komodo dragon site occupancy estimates at the equivalent and long-unbaited camera sampling durations (Fig. 2*b*). A goodness-of-fit test on the most parameter-rich model demonstrated that our data were not over-dispersed (i.e. $\hat{c} > 1$).

Effects of bait attractants on monitoring considerations

Baited cameras improved sampling efficacy and reduced monitoring costs compared with sampling using unbaited cameras. First, it was evident that based on cumulative detection probabilities, baited cameras, if deployed sufficiently long enough, could achieve perfect detection at sites with Komodo dragons, with much less survey effort than with unbaited cameras (Fig. 3). Compared with unbaited cameras, baited cameras reduced the sampling effort duration from 184 to 21 days to be certain (with α of <0.05) that Komodo dragons were absent from a site. Finally, because of the much-improved detection probability achieved with baited cameras, it reduced the overall study costs from US\$580.20 to US\$547.60, to obtain similar camera-based detection levels within the study area.

Discussion

The choice of an appropriate sampling method for monitoring threatened predator populations depends on interactions among the program objectives, scale and resources and a species's detection probability (Kéry and Schmidt 2008). We demonstrated that using baited-camera compared with unbaited-camera monitoring greatly improved estimates of Komodo dragon detection probability and site occupancy in the Wae

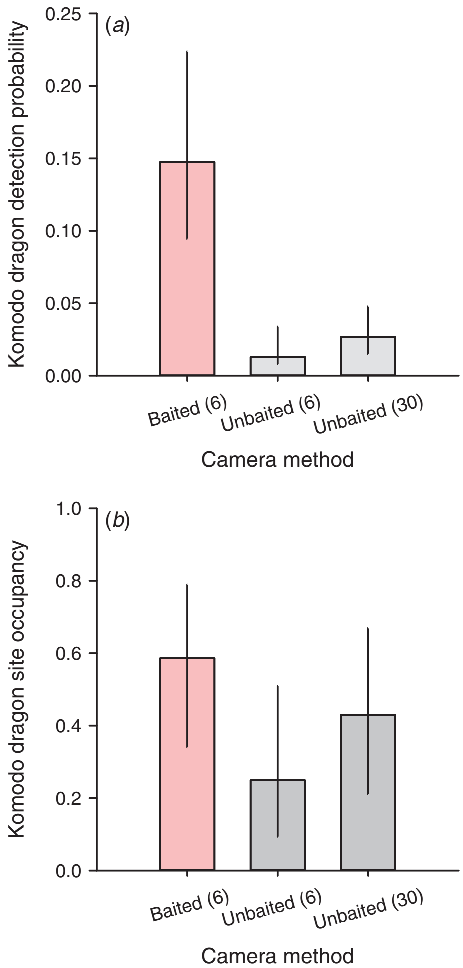

Fig. 2. Komodo dragon (*a*) detection probability and (*b*) site occupancy estimated from baited or unbaited cameras deployed for 6- or 30-day sampling events respectively. The bars report the mean estimate, and the upper and lower 95% confidence intervals are indicated by the error bars.

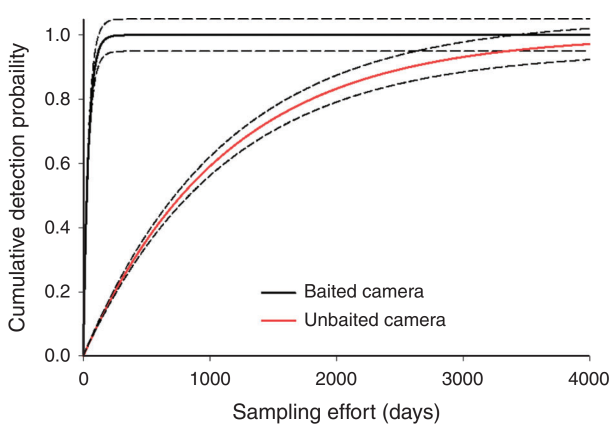

Fig. 3. The cumulative detectability curves for Komodo dragons estimated from baited and unbaited camera occupancy models. These curves represent the probability that Komodo dragons will be detected at least once with each treatment after sequential 1-week sampling period at each camera trap where Komodo dragons are present. The lines report the mean estimate and the dashed upper and lower lower lines are the 95% standard error of the mean.

Wuul Nature Reserve on Flores Island. Indeed, several clear advantages were evident from using baited cameras, including a reduced sampling effort and, ultimately, a more cost-effective monitoring design.

Obtaining a high detection probability is a key requirement to improve site-occupancy estimates for large predators that persist at low density (MacKenzie *et al.* 2006). Such sampling designs should aim to achieve a detection probability exceeding 0.15, so as to allow for better occupancy estimates for predators (O'Connell *et al.* 2010; Otto and Roloff 2011). With camera-based monitoring, there are several ways to increase species detection probability, including increasing the number of cameras deployed for longer survey periods or by also placing cameras in areas that increase detection opportunities of the focal species (e.g. along game trails; O'Connell *et al.* 2010; Geyle *et al.* 2020; Wysong *et al.* 2020). However, the use of attractants such as baits or lures is another common means to improve camera-based detection probability, but their use should be assessed to ensure improved efficacy (Read *et al.* 2015).

It was evident that bait attractants at camera monitoring stations greatly improved Komodo dragon detection probability by 3.5–5 times over similar or extended durations of unbaited camera monitoring. This finding is consistent with those of other studies that indicate similar benefits of using baits or lures at camera monitoring stations (du Preez *et al.* 2014; Austin *et al.* 2017; Tarugara *et al.* 2019). Importantly, these gains in detection probability alongside higher and more robust estimates of site occupancy offset the increased daily sampling costs owing to the purchase of goats as the bait source (Thorn *et al.* 2011).

Another key benefit of baited cameras was the considerable reduction (i.e. 5-fold) in the survey effort needed to achieve adequate Komodo dragon detection within the study area. Reducing survey effort without compromising detection probabilities has many obvious advantages (MacKenzie and Royle 2005). Most importantly, saved survey effort can be allocated into additional sites, survey visits or additional study areas in different ways (Sewell *et al.* 2012). From our perspective, the biggest advantage is that reduced survey effort can be invested into additional camera monitoring activities for more broadly assessing the conservation status of Komodo dragon populations. For example, we have recently used baited camera monitoring surveys beyond this study area to evaluate the distribution of the Komodo dragon across Flores (~400 monitoring stations across 1200 km of coastline; Ariefiandy *et al.* 2021). This feat would not have been possible without using baited cameras to achieve high Komodo dragon detection relative to their survey effort requirements.

It is argued that the use of attractants to increase a species detection must be considerate of any effects on monitoring estimates and arising inference (du Preez *et al.* 2014). For example, if increased estimates of detection at baited cameras arise because of bait effects on animal space-use or daily movements, it could bias parameter estimates. In the case of baited cameras, baits could increase residency times or attract animals beyond their normal home-range area to inflate estimates of detection probability and site occupancy (Stewart *et al.* 2019). This problem could be especially acute if individual animals, particularly those in low-density populations, are detected at multiple camera stations beyond their home range.

Consequently, ensuring spatial independence for camera data is a crucial aspect of monitoring design (Meek *et al.* 2014; O'Connell *et al.* 2010; Geyle *et al.* 2020). We know that the independence of data among camera monitoring sites is largely met for Komodo dragon, because our prior mark–recapture-based studies using traps with similar inter-site distances resulted in a <10% within-study recapture rate of individuals (Ariefiandy *et al.* 2013, 2014).

This study also indicated that estimates of Komodo dragon site occupancy recorded within the Wae Wuul Nature Reserve are significantly lower than those generally recorded for populations in the adjacent Komodo National Park (Purwandana *et al.* 2014*b*; Ariefiandy *et al.* 2015). Adult Komodo dragons, as apex predators, mainly prey on ungulates, particularly Rusa deer (*Rusa timorensis*), wild pig (S*us scrofa*), and, in some locations, water buffalo (*Bubalus bubalis*; Auffenberg 1981; Bull *et al.* 2010; Purwandana *et al.* 2016). Thus, we attribute this lower occupancy estimate to be in part associated with the commensurate reduction of large ungulate prey availability on Flores (Ariefiandy *et al.* 2011, 2015, 2016; Jessop *et al.* 2020). Reduced prey is a presumed consequence of historical and increasingly contemporary human-mediated processes (e.g. fire, poaching, invasive predators) affecting Komodo dragon habitats on Flores (Ariefiandy *et al.* 2020).

Here we advocate that protected-area enhancement actions and community conservation approaches are needed to address the current threats to Komodo dragons on Flores. For example, unlike Komodo National Park, the Wae Wuul Nature reserve is comparatively under-resourced in staff and logistical resources. Thus, aside from ongoing monitoring of Komodo dragon populations, it is necessary to ensure that integrative conservation actions are used to ensure prey and predator persistence in this reserve (Ariefiandy *et al.* 2015, 2020). Thus, this reserve could benefit from additional infrastructure (e.g. ranger posts) and increased patrolling and surveillance measures that would benefit both Komodo dragons and their ungulate prey (Hilborn *et al.* 2006; Ariefiandy *et al.* 2015, 2020). However, as human activities increasingly modify the habitats that directly border this reserve, community-based conservation actions must also be implemented in neighbouring communities (Ariefiandy *et al.* 2015, 2020). For example, implementing conservation awareness meetings in local communities to inform and discuss the value of protecting natural values within this reserve are deemed essential (Kamil *et al.* 2019). Furthermore, working with communities to reduce rates of incursions of village dogs or livestock and stopping villagers from setting fire to habitats within or adjacent to the reserve could be important steps to promote the conservation of Komodo dragons in this key protected area on Flores (Ariefiandy *et al.* 2020).

In conclusion, our study demonstrated that optimising camera survey methods using baits compared with unbaited cameras can provide a better method for estimating Komodo dragon occupancy. This result was particularly important in this study because we aimed to effectively monitor a very low-density population in a key protected area on Flores. We believe our baited camera monitoring approach now lends itself to understanding population responses to ecological and anthropogenic factors, hence informing conservation efforts in this nature reserve (Ariefiandy *et al.* 2015).

Conflicts of interest

The authors declare that they have no conflicts of interest.

Author contributions

Study design and fieldwork: DP, AA, MA, SAN, MS and TSJ; data analysis: TSJ; writing: TSJ.

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References

Adams, C. S., Ryberg, W. A., Hibbitts, T. J., Pierce, B. L., Pierce, J. B., and Rudolph, D. C. (2017). Evaluating effectiveness and cost of time-lapse triggered camera trapping techniques to detect terrestrial squamate diversity. *Herpetological Review* **48**, 44–48.

Ariefiandy, A., Purwandana, D., Coulson, G., Forsyth, D. M., and Jessop, T. S. (2011). Monitoring the primary prey of the Komodo dragon: distance sampling or faecal counts? *Wildlife Biology* **19**, 126–137.

Ariefiandy, A., Purwandana, D., Seno, A., Ciofi, C., and Jessop, T. S. (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., and Jessop, T. S. (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

Ariefiandy, A., Purwandana, D., Natali, C., Imansyah, M., Surahman, M., Jessop, T., and Ciofi, C. (2015). Conservation of Komodo dragons *Varanus komodoensis* in the Wae Wuul nature reserve, Flores, Indonesia: a multidisciplinary approach. *International Zoo Yearbook* **49**, 67–80. doi:10.1111/izy.12072

Ariefiandy, A., Forsyth, D. M., Purwandana, D., Imansyah, J., Ciofi, C., Rudiharto, H., Seno, A., and Jessop, T. S. (2016). Temporal and spatial dynamics of insular Rusa deer and wild pig populations in Komodo National Park. *Journal of Mammalogy* **97**, 1652–1662. doi:10.1093/jmammal/gyw131

Ariefiandy, A., Purwandana, D., Ciofi, C., and Jessop, T. S. (2020). Komodo Survival Program: an NGO's approach to assisting Komodo Dragon conservation and management. In 'Strategies for Conservation Success in Herpetology'. (Eds S. C. Walls and K. M. O'Donnell.) (Society for the Study of Amphibians and Reptiles: University Heights, OH, USA.)

Ariefiandy, A., Purwandana, D., Azmi, M., Nasu, S. A., Mardani, J., Ciofi, C., and Jessop, T. S. (2021). Human activities associated with reduced Komodo dragon habitat use and range loss on Flores. *Biodiversity and Conservation* **30**, 461–479.

Auffenberg, W. (1981). 'The Behavioural Ecology of the Komodo Monitor.' (Florida University Press: Gainesville, FL, USA.)

Austin, C., Tuft, K., Ramp, D., Cremona, T., and Webb, J. K. (2017). Bait preference for remote camera trap studies of the endangered northern quoll (*Dasyurus hallucatus*). *Australian Mammalogy* **39**, 72–77. doi:10.1071/AM15053

Bull, J., Jessop, T. S., and Whiteley, M. (2010). Deathly drool: evolutionary and ecological basis of septic bacteria in Komodo dragon mouths. *PLoS One* **5**, e11097. doi:10.1371/journal.pone.0011097

Burnham, K. P., and Anderson, D. R. (2004). Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research* **33**, 261–304. doi:10.1177/0049124104268644

Comer, S., Speldewinde, P., Tiller, C., Clausen, L., Pinder, J., Cowen, S., and Algar, D. (2018). Evaluating the efficacy of a landscape scale feral cat control program using camera traps and occupancy models. *Scientific Reports* **8**, 5335. doi:10.1038/s41598-018-23495-z

Couturier, T., Cheylan, M., Bertolero, A., Astruc, G., and Besnard, A. (2013). Estimating abundance and population trends when detection is low and highly variable: a comparison of three methods for the Hermann's tortoise. *The Journal of Wildlife Management* **77**, 454–462. doi:10.1002/jwmg.499

du Preez, B. D., Loveridge, A. J., and Macdonald, D. W. (2014). To bait or not to bait: a comparison of camera-trapping methods for estimating leopard *Panthera pardus* density. *Biological Conservation* **176**, 153–161. doi:10.1016/j.biocon.2014.05.021

Einoder, L. D., Southwell, D. M., Lahoz-Monfort, J. J., Gillespie, G. R., Fisher, A., and Wintle, B. A. (2018). Occupancy and detectability modelling of vertebrates in northern Australia using multiple sampling methods. *PLoS One* **13**, e0206373. doi:10.1371/journal.pone.0203304

Ferreras, P., Díaz-Ruiz, F., and Monterroso, P. (2018). Improving mesocarnivore detectability with lures in camera-trapping studies. *Wildlife Research* **45**, 505–517. doi:10.1071/WR18037

Geyle, H. M., Stevens, M., Duffy, R., Greenwood, L., Nimmo, D. G., Sandow, D., Thomas, B., White, J., and Ritchie, E. G. (2020). Evaluation of camera placement for detection of free-ranging carnivores; implications for assessing population changes. *Ecological Solutions and Evidence* **1**, e12018. doi:10.1002/2688-8319.12018

Gittleman, J. L., and Harvey, P. H. (1982). Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology* **10**, 57–63. doi:10.1007/BF00296396

Harlow, H. J., Purwandana, D., Jessop, T. S., and Phillips, J. A. (2010*a*). Body temperature and thermoregulation of Komodo dragons in the field. *Journal of Thermal Biology* **35**, 338–347. doi:10.1016/j.jtherbio.2010.07.002

Harlow, H. J., Purwandana, D., Jessop, T. S., and Phillips, J. A. (2010*b*). Size-related differences in the thermoregulatory habits of free-ranging Komodo dragons. *International Journal of Zoology* **2010**, 921371. doi:10.1155/2010/921371

Hilborn, R., Arcese, P., Borner, M., Hando, J., Hopcraft, G., Loibooki, M., Mduma, S., and Sinclair, A. R. (2006). Effective enforcement in a conservation area. *Science* **314**, 1266. doi:10.1126/science.1132780

Hines, J. E. (2006). 'Program PRESENCE.' Available at http://www.mbrpwrc.usgs.gov/software/doc/presence/presence.html.

Hu, Y., Gillespie, G., and Jessop, T. S. (2019). Variable reptile responses to introduced predator control in southern Australia. *Wildlife Research* **46**, 64–75. doi:10.1071/WR18047

Jessop, T. S., Madsen, T., Sumner, J., Rudiharto, H., Phillips, J. A., and Ciofi, C. (2006). Maximum body size among insular Komodo dragon populations covaries with large prey density. *Oikos* **112**, 422–429. doi:10.1111/j.0030-1299.2006.14371.x

Jessop, T. S., Madsen, T., Ciofi, C., Imansyah, M. J., Purwandana, D., Rudiharto, H., Arifiandy, A., and Phillips, J. A. (2007). Island differences in population size structure and catch per unit effort and their conservation implications for Komodo dragons. *Biological Conservation* **135**, 247–255. doi:10.1016/j.biocon.2006.10.025

Jessop, T. S., Kearney, M. R., Moore, J. L., Lockwood, T., and Johnston, M. (2013). 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, T. S., Ariefiandy, A., Purwandana, D., Ciofi, C., Imansyah, J., Benu, Y. J., Fordham, D. A., Forsyth, D. M., Mulder, R. A., and Phillips, B. L. (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

Jessop, T. S., Ariefiandy, A., Purwandana, D., Benu, Y. J., Hyatt, M., and Letnic, M. (2019). Little to fear: largest lizard predator induces weak defense responses in ungulate prey. *Behavioral Ecology* **30**, 624–636. doi:10.1093/beheco/ary200

Jessop, T. S., Ariefiandy, A., Forsyth, D. M., Purwandana, D., White, C. R., Benu, Y. J., Madsen, T., Harlow, H. J., and Letnic, M. (2020). Komodo dragons are not ecological analogs of apex mammalian predators. *Ecology* **101**, e02970. doi:10.1002/ecy.2970

Jones, A. R., Jessop, T. S., Ariefiandy, A., Brook, B. W., Brown, S. C., Ciofi, C., Benu, Y. J., Purwandana, D., Sitorus, T., and Wigley, T. M. (2020). Identifying island safe havens to prevent the extinction of the World's largest lizard from global warming. *Ecology and Evolution* **10**, 10492–10507. doi:10.1002/ece3.6705

Kamil, P. I., Susianto, H., Purwandana, D., and Ariefiandy, A. (2019). Anthropomorphic and factual approaches in Komodo dragon conservation awareness program for elementary school students: initial study. *Applied Environmental Education and Communication* **19**, 225–237.

Karanth, K. U., Nichols, J. D., Kumar, N. S., Link, W. A., and Hines, J. E. (2004). Tigers and their prey: predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 4854–4858. doi:10.1073/pnas.0306210101

Karanth, K. U., Gopalaswamy, A. M., Kumar, N. S., Vaidyanathan, S., Nichols, J. D., and Mackenzie, D. I. (2011). Monitoring carnivore populations at the landscape scale: occupancy modelling of tigers from sign surveys. *Journal of Applied Ecology* **48**, 1048–1056. doi:10.1111/j.1365-2664.2011.02002.x

Kéry, M., and Schmidt, B. R. (2008). Imperfect detection and its consequences for monitoring for conservation. *Community Ecology* **9**, 207–216. doi:10.1556/ComEc.9.2008.2.10

Kéry, M., Royle, J. A., and Schmid, H. (2005). Modeling avian abundance from replicated counts using binomial mixture models. *Ecological Applications* **15**, 1450–1461. doi:10.1890/04-1120

Laver, R. J., Purwandana, D., Ariefiandy, A., Imansyah, J., Forsyth, D., Ciofi, C., and Jessop, T. S. (2012). Life-History and Spatial Determinants of Somatic Growth Dynamics in Komodo Dragon Populations. *PLoS One* **7**, e45398. doi:10.1371/journal.pone.0045398

Long, R. A., MacKay, P., Ray, J., and Zielinski, W. (2012) 'Noninvasive survey methods for carnivores.' (Island Press.)

MacKenzie, D. I., and Royle, J. A. (2005). Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology* **42**, 1105–1114. doi:10.1111/j.1365-2664.2005.01098.x

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., and Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**, 2248–2255. doi:10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2

MacKenzie, D., Nichols, J., Royle, J., Pollock, K., Bailey, L., and Hines, J. (2006). 'Occupancy estimation and modelling.' (Academic Press: Burlington, MA, USA.)

Meek, P., Fleming, P., Ballard, G., Banks, P., Claridge, A., Sanderson, J., and Swann, D. (2014). Camera Trapping: Wildlife Management and Research. (CSIRO Publishing: Melbourne, Vic., Australia.)

Monk, K. A., De Fretes, Y., and Reksodiharjo-Lilley, G. (1997). 'The Ecology of Nusa Tenggara and Maluku.' (Oxford University Press: Oxford.)

Moore, H. A., Champney, J. L., Dunlop, J. A., Valentine, L. E., and Nimmo, D. G. (2020). Spot on: using camera traps to individually monitor one of the world's largest lizards. *Wildlife Research* **47**, 326–337. doi:10.1071/WR19159

O'Connell, A. F., Nichols, J. D., and Karanth, K. U. (2010). 'Camera traps in animal ecology: methods and analyses.' (Springer Science & Business Media.)

Otto, C. R., and Roloff, G. J. (2011). Using multiple methods to assess detection probabilities of forest-floor wildlife. *The Journal of Wildlife Management* **75**, 423–431. doi:10.1002/jwmg.63

Penjor, U., Tan, C. K. W., Wangdi, S., and Macdonald, D. W. (2019). Understanding the environmental and anthropogenic correlates of tiger presence in a montane conservation landscape. *Biological Conservation* **238**, 108196. doi:10.1016/j.biocon.2019.108196

Prowse, T. A. A., Johnson, C. N., Cassey, P., Bradshaw, C. J. A., and Brook, B. W. (2015). Ecological and economic benefits to cattle rangelands of restoring an apex predator. *Journal of Applied Ecology* **52**, 455–466. doi:10.1111/1365-2664.12378

Purwandana, D., Ariefiandy, A., Imansyah, M. J., Rudiharto, H., Seno, A., Ciofi, C., Fordham, D. A., and Jessop, T. S. (2014*a*). 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, M. J., Rudiharto, H., Seno, A., Ciofi, C., Fordham, D. A., and Jessop, T. S. (2014*b*). 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, M. J., Ciofi, C., Forsyth, D. M., Gormley, A. M., Rudiharto, H., Seno, A., Fordham, D. A., and Gillespie, G. (2015). Evaluating environmental, demographic and genetic effects on population-level survival in an island endemic. *Ecography* **38**, 1060–1070. doi:10.1111/ecog.01300

Purwandana, D., Ariefiandy, A., Imansyah, M. J., Seno, A., Ciofi, C., Letnic, M., and Jessop, T. S. (2016). Ecological allometries and niche use dynamics across Komodo dragon ontogeny. *Naturwissenschaften* **103**, 27. doi:10.1007/s00114-016-1351-6

Purwandana, D., Ciofi, C., Imansyah, M. J., Ariefiandy, A., Rudiharto, H., and Jessop, T. S. (2021). Prey Preferences and Body Mass Most Influence Movement Behavior and Home Range Area of Komodo Dragons. *Ichthyology & Herpetology* **109**, 92–101. doi:10.1643/h2020028

Read, J., Bengsen, A., Meek, P., and Moseby, K. (2015). How to snap your cat: optimum lures and their placement for attracting mammalian predators in arid Australia. *Wildlife Research* **42**, 1–12. doi:10.1071/WR14193

Richardson, E., Nimmo, D. G., Avitabile, S., Tworkowski, L., Watson, S. J., Welbourne, D., and Leonard, S. W. J. (2017). Camera traps and pitfalls: an evaluation of two methods for surveying reptiles in a semiarid ecosystem. *Wildlife Research* **44**, 637–647. doi:10.1071/WR16048

Royle, J. A. (2004). N-mixture models for estimating population size from spatially replicated counts. *Biometrics* **60**, 108–115. doi:10.1111/j.0006-341X.2004.00142.x

Searle, C. E., Bauer, D. T., Kesch, M. K., Hunt, J. E., Mandisodza-Chikerema, R., Flyman, M. V., Macdonald, D. W., Dickman, A. J., and Loveridge, A. J. (2020). Drivers of leopard (*Panthera pardus*) habitat use and relative abundance in Africa's largest transfrontier conservation area. *Biological Conservation* **248**, 108649. doi:10.1016/j.biocon.2020.108649

Sewell, D., Guillera-Arroita, G., Griffiths, R. A., and Beebee, T. J. (2012). When is a species declining? Optimising survey effort to detect population changes in reptiles. *PLoS One* **7**, e43387. doi:10.1371/journal.pone.0043387

Stewart, F. E., Volpe, J. P., and Fisher, J. T. (2019). The debate about bait: a red herring in wildlife research. *The Journal of Wildlife Management* **83**, 985–992. doi:10.1002/jwmg.21657

Tan, C. K. W., Rocha, D. G., Clements, G. R., Brenes-Mora, E., Hedges, L., Kawanishi, K., Mohamad, S. W., Mark Rayan, D., Bolongon, G., Moore, J., Wadey, J., Campos-Arceiz, A., and Macdonald, D. W. (2017). Habitat use and predicted range for the mainland clouded leopard *Neofelis nebulosa* in Peninsular Malaysia. *Biological Conservation* **206**, 65–74. doi:10.1016/j.biocon.2016.12.012

Tarugara, A., Clegg, B. W., Gandiwa, E., and Muposhi, V. K. (2019). Cost–benefit analysis of increasing sampling effort in a baited-camera trap survey of an African leopard (*Panthera pardus*) population. *Global Ecology and Conservation* **18**, e00627. doi:10.1016/j.gecco.2019.e00627

Thompson, W. (2013). 'Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters.' (Island Press.)

Thorn, M., Green, M., Bateman, P. W., Waite, S., and Scott, D. M. (2011). Brown hyaenas on roads: estimating carnivore occupancy and abundance using spatially auto-correlated sign survey replicates. *Biological Conservation* **144**, 1799–1807. doi:10.1016/j.biocon.2011.03.009

Tingley, R., Macdonald, S. L., Mitchell, N. J., Woinarski, J. C. Z., Meiri, S., Bowles, P., Cox, N. A., Shea, G. M., Böhm, M., Chanson, J., Tognelli, M. F., Harris, J., Walke, C., Harrison, N., Victor, S., Woods, C., Amey, A. P., Bamford, M., Catt, G., Clemann, N., Couper, P. J., Cogger, H., Cowan, M., Craig, M. D., Dickman, C. R., Doughty, P., Ellis, R., Fenner, A., Ford, S., Gaikhorst, G., Gillespie, G. R., Greenlees, M. J., Hobson, R., Hoskin, C. J., How, R., Hutchinson, M. N., Lloyd, R., McDonald, P., Melville, J., Michael, D. R., Moritz, C., Oliver, P. M., Peterson, G., Robertson, P., Sanderson, C., Somaweera, R., Teale, R., Valentine, L., Vanderduys, E., Venz, M., Wapstra, E., Wilson, S., and Chapple, D. G. (2019). Geographic and taxonomic patterns of extinction risk in Australian squamates. *Biological Conservation* **238**, 108203. doi:10.1016/j.biocon.2019.108203

Todd, B. D., Willson, J. D., and Gibbons, J. W. (2010). The global status of reptiles and causes of their decline. In 'Ecotoxicology of Amphibians and Reptiles', Second Edition. (Eds D. W. Sparling, C. A. Bishop, and S. Krest.) pp. 47–67. (CRC Press: Pensacola, FL, USA.)

Welbourne, D. (2013). A method for surveying diurnal terrestrial reptiles with passive infrared automatically triggered cameras. *Herpetological Review* **44**, 247–250.

Welbourne, D. J., MacGregor, C., Paull, D., and Lindenmayer, D. B. (2015). The effectiveness and cost of camera traps for surveying small reptiles and critical weight range mammals: a comparison with labour-intensive complementary methods. *Wildlife Research* **42**, 414–425. doi:10.1071/WR15054

Williams, B. K., Nichols, J. D., and Conroy, M. J. (2002). 'Analysis and management of animal populations.' (Academic Press.)

Wintle, B. A., Kavanagh, R. P., McCarthy, M. A., and Burgman, M. A. (2005). Estimating and dealing with detectability in occupancy surveys for forest owls and arboreal marsupials. *The Journal of Wildlife Management* **69**, 905–917. doi:10.2193/0022-541X(2005)069[0905:EADWDI]2.0.CO;2

Wintle, B. A., Walshe, T. V., Parris, K. M., and McCarthy, M. A. (2012). Designing occupancy surveys and interpreting non-detection when observations are imperfect. *Diversity & Distributions* **18**, 417–424. doi:10.1111/j.1472-4642.2011.00874.x

Wysong, M. L., Iacona, G. D., Valentine, L. E., Morris, K., and Ritchie, E. G. (2020). On the right track: placement of camera traps on roads improves detection of predators and shows non-target impacts of feral cat baiting. *Wildlife Research* **47**, 557–569. doi:10.1071/WR19175

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