The effect of camera orientation on the detectability of wildlife: a case study from north-western Australia

Harry A. Moore¹,², Leonie E. Valentine², Judy A. Dunlop³ & Dale G. Nimmo¹

¹Institute for Land, Water and Society, School of Environmental Science, Charles Sturt University, Albury, 2640, New South Wales, Australia
²School of Biological Sciences, University of Western Australia, Crawley, 6009, Western Australia, Australia
³Department of Biodiversity, Conservation and Attractions, Bentley Delivery Centre, Locked Bag 104, Perth, Western Australia, Australia

Keywords
Camera orientation, Camera traps, Camera-trapping, Detectability, Mammals, Reptiles

Abstract
Camera traps are increasingly used to survey and monitor rare or cryptic species, yet few studies consider how camera orientation influences species detectability, among other metrics such as total independent detections and likelihood of missing detections. We used these measures to compare the performance of vertically and horizontally orientated camera traps at 46 sites spread over 10 000 km² in north-west Australia. Data were collected for four taxa, including northern quolls (Dasyurus hallucatus), Rothschild’s rock-walabys (Petrogale rothschildi), feral cats (Felis catus) and varanids (Varanus spp.). Metrics compared included probability of species presence/absence, total independent detections recorded and likelihood of cameras missing or recording nightly detections. We found camera orientation did not impact camera performance across any metric for northern quolls. By contrast, we found horizontal cameras were more efficient at detecting feral cats and Rothschild’s rock wallabies. They also recorded more detections and were less likely to miss detections than vertical cameras for these species. For varanids, vertical cameras outperformed horizontal cameras across all metrics. Studies that use vertical cameras to collect image data better suited for species or individual identification should consider how target species detectability may be compromised by having a reduced detection zone size. However, horizontally orientated cameras may not always be superior to vertically orientated cameras in terms of species detectability, particularly for laterally compressed species such as lizards.

Introduction
Monitoring the occurrence and abundance of animal populations is a challenge in animal ecology (Pollock et al. 2002; Witmer 2005; O’Connell et al. 2010). An array of sampling techniques have been devised to survey animal populations, each varying in reliability and cost (Rabe et al. 2002; Thompson 2013). Among these, passive infrared triggered cameras—often referred to as camera traps—are one of the most popular (Rowcliffe and Carbone 2008; O’Connell et al. 2010), particularly for mammals (Burton et al. 2015). When compared to traditional trapping techniques, such as live trapping, camera traps can be labour and cost effective (Welbourne et al. 2015; De Bondi et al. 2010) and also less invasive (Meek et al. 2014b). However, the use of camera traps to survey an expanding array of fauna groups—now including birds (Brides et al. 2018), and reptiles (Welbourne 2013)—has led to variability in the way cameras are deployed (O’Connell et al. 2010). For example, camera trigger type (Rovero et al. 2013), trigger sensitivity (Heiniger and Gillespie 2018), flash (Meek and Pittet 2013) and focus settings (Welbourne et al. 2019) are all factors that can influence camera performance in terms of the quantity and quality of images collected. Each of these factors must be considered by the camera trap user with a specific research objective in mind. One of the most basic factors influencing camera trap performance is the direction that cameras face (horizontal or vertical), here termed ‘orientation’ (Meek et al. 2012; Taylor et al. 2014). Aside from influencing the quantity and quality of images collected, camera orientation also affects the angle from...
which animals are photographed; hence it can affect user capacity to distinguish between individual animals of the same or different species (Muneza et al. 2019).

Individually identifying animals is important because most methods used to estimate animal abundance, such as mark-recapture methods, rely on repeated observations of individuals to derive abundance estimates (Robson and Regier 1964; Seber 1982; Wilson and Delahay 2001). The suitability of image data for individual identification relies on the way cameras are orientated in relation to features that are used to tell individuals apart. In the case of animals where individual markings are located on the dorsal surface, such as goannas (Varanidae spp.) (Moore et al. 2020), numbatbs (Myrmecobius fasciatus) (Thorn per commms, 2019), and quolls (Dasyurus spp.) (Diete et al. 2016), orientating cameras in a vertical position (i.e., downward facing) above a target individual is likely to produce images that allow individual identification. Further, for species that can be identified from both a horizontal and vertical perspective (e.g., quolls), vertically orientated cameras may be preferable because they remove the need to capture both left and right lateral sides of an animals to confirm its identity, as is required for study designs using horizontally orientated cameras. However, given many camera traps are designed to be positioned horizontally, positioning them vertically can reduce the area within the ‘detection zone’ of sensors (Welbourne et al. 2016). For example, the detection zone of Reconyx cameras is made up of two horizontal bands that cover roughly 30% of the camera’s field of view (Reconyx 2013) (Appendix S1). When focused toward the horizon, Reconyx cameras are capable of detecting animals moving within these bands at a distance of 30.5 meters (Reconyx 2013), translating to a total detection zone of 324 m² (Meek et al. 2012). When positioned vertically, the detection range of cameras is limited by the height above the ground at which cameras are positioned, and thus the total detection zone size is substantially reduced.

A reduced detection zone can reduce the number of detections recorded by a camera (Meek et al. 2012); for example, Nichols et al. (2017) found horizontally positioned cameras recorded 1.5 times more detections of feral cats (Felis catus) and mustelids (Mustela furo, M. erminea and M. nivalis) in New Zealand, and Taylor et al. (2014) found that horizontally oriented cameras had greater detectability than vertically orientated cameras for several medium-sized mammals in eastern Australia. Low detection rates can be problematic when attempting to estimate abundance, as it may result in sparse data, especially for rare or cryptic species (Thompson 2013). Hence, for species with dorsal markings, a trade-off may exist requiring users to choose between (i) increasing detection rates and forfeiting the ability to identify individuals and (ii) risking lower detection rates but maintaining the ability to identify individuals.

Here we compare the effectiveness of vertically and horizontally orientated camera traps at detecting three species of mammal as well as a group of reptiles using paired cameras in north-western Australia. Given horizontal cameras permit a larger detection zone than vertical cameras, for all species, we hypothesised;

a Horizontal cameras would have a higher nightly probability of detecting species than vertical cameras.

b Horizontal cameras would record more detections than vertical cameras.

c Horizontal cameras would be less likely to miss detections than vertical cameras.

Materials and Methods

Study area

This study was carried out across four properties situated within the Pilbara bioregion in north-west Western Australia. These were Indee Station, Mallina Station, Pippin-garra Station and Yandeyarra Indigenous Reserve (Fig. 1). Yandeyarra Indigenous Reserve is also a working cattle station. The study area encompassed the Karayarra and Nya- mal indigenous language groups. Vegetation across all study sites is dominated by hummock grasslands (ESCAVI 2003). This habitat class is characterized by open ground cover comprising of spinifex (Triodia spp.) hummock grasses that cover roughly 30–50% of the ground surface. Geology is characterised by largely flat sand plains scattered with greenstone ridges and granite (Withers 2000). Climate within the study area is characterized by high temperatures and low annual rainfall. Average daily temperature maximums across the study period ranged from 28.4°C (August 2017) to 44.1°C (December 2018) (Australian Bureau of Meteorology 2019).

Taxa

Taxa targeted in this analysis included two native mammals, the northern quoll (Dasyurus hallucatus), Rothschild’s rock-wallaby (Petrogale rothschildi), one introduced mammalian predator, the feral cat (Felis catus), and four native varanids (Varanus gigan-teus, Varanus panoptes, Varanus gouldii and Varanus pilbaren-sis). Target taxa were selected to include species commonly recorded using camera traps within the Pilbara bioregion that vary in size, morphology, and behaviour. To increase statistical power, detections from all varanid species were pooled and classed as the group ‘varanids’.
Survey methods

Forty-six camera sites were established within 23 study landscapes, with two sites, separated by at least 300 m, assigned to each landscape. Landscapes were 0.79 km² in size. Six landscapes were established on Indee station, four on Pippingarra, four on Mallina, and nine on Yandeyarra Indigenous Reserve (Fig. 1). All study sites were positioned within rocky outcrops using ArcGIS 10.6 (ESRI 2011), as this habitat was most suitable for target taxa (Menkhorst and Knight 2010; Wilson and Swan 2017).

Two Reconyx PC900 Hyperfire covert cameras were deployed at each site. Camera one was attached to a wooden tree stake 1.5 m above the ground and was orientated in a vertical position, with the camera lens, and PIR sensors focused directly at the ground surface using a bookshelf bracket (Fig. 2). Camera two was attached to a second tree stake 50 cm above the ground, located 2.5 m north from camera one (as recommended by Meek et al. 2012 for medium sized mammals), and was orientated in a horizontal position. The camera lens and PIR sensors were focused at a 10° angle toward the ground surface, in the direction of camera one (South) (Fig. 2). Horizontal cameras were positioned to face south to avoid intense sunlight exposure to the camera lens. A PVC canister containing 150 g of pilchards (fish) was attached to the bottom of the tree stake supporting camera one, within the centre focus of both cameras (Fig. 2).

Sites were sampled for 200 days each. Twenty four sites were sampled between August 2017 and March 2018, and the remaining twenty-two sites were sampled between August 2018 and March 2019. Cameras were set to high sensitivity, and five images were taken at one-second intervals per trigger. To assess the rate at which a camera trap was visited by animals, we defined independent detection events for all taxa as detections separated by 15 mins (Diete et al. 2016). Five cameras failed, leaving 41 functioning sites. Failures were mainly due to cameras being knocked out of focus by animals. One camera failed as a result of battery failure.

Statistical methods

We examined the effect of camera orientation on three response variables: the nightly probability of detecting a given species, the total number of independent detections over the duration of sampling, and the paired detection likelihood (outlined below). In each case, we used generalized linear mixed models (GLMMs). Each taxa was modelled separately, and camera orientation was included as a fixed effect in all models. To account for non-independence between cameras positioned at the same site (pair), all models included ‘Site’ as a random variable. We report if \( P < 0.05 \). Models were fit using the lme4 package (Bates et al. 2007) in R version 3.5.3 (R Core Team 2013).
To model the nightly probability of detecting a species, our response variable was the proportion of nights a species was detected over the sample period, which we modelled as two vectored response variables indicating the number of nights each species was and was not detected over the first 60 nights of sampling. This type of proportion data can be modelled using a binomial distribution, with the number of nights detected/not detected modelled as the number of success and failures in a fixed number of Bernoulli trials (Crawley 2012). The output of these models is the probability that a given species will be detected using a given camera trap orientation on a randomly selected trap night. We restricted this analysis to the first 60 nights to account for declining species detectability over time as a result of reduced bait effectiveness.

We then generated cumulative nightly detectability curves for each taxon based on the detectability estimates derived from these models, using the following formula:

\[ P = 1 - \prod_{i=1}^{n} (1 - p_i) \]

where \( P \) is the cumulative nightly detection probability, \( n \) is number of nights and \( p \) is the nightly detection probability. For each taxon, we then calculated the minimum number of nights per site necessary to be 95% confident that the site is unoccupied:

\[ N_{\text{min}} = \log(\alpha)/\log(1-p) \]

where \( \alpha = 0.05 \) and confidence is equal to \( 1-p \) (Kery 2002).

Next, we modelled the number of independent detections of each species in relation to camera trap orientation. We restricted this analysis to sites with at least one detection on each camera for two reasons. Firstly, because we had already modelled the probability of detecting a species and how it relates to camera orientation. Secondly, because data including all sites were zero-inflated, and removal of sites without detections allowed the data to be modelled using a Poisson distribution.

Finally, to further compare the effect of camera orientation on detections, we modelled the likelihood of a horizontal or vertical camera detecting a species on a trap night, given its corresponding paired camera detected that species on the same trap night. We termed this measure ‘paired detection likelihood’. For each camera, we coded every night a species was detected as one, and every night a species wasn’t detected, but was detected by its corresponding paired camera, as zero. Next, we used a GLMM with a binomial distribution to model the probability that a detection occurred in one camera type (i.e., horizontal or vertical), given it was detected on the other camera type on the same night. Model outputs show the percentage likelihood that either horizontally or vertically orientated cameras will record a species on a given night, given that the camera it was paired with recorded a detection.

**Results**

A total of 6473 independent detection events were recorded for 105 species over 14 640 trap nights, including 1318 detections for study taxa. The most detected species was the northern quoll (820 detections, horizontal = 426, vertical = 394), followed by varanids (211 detections, horizontal = 80, vertical = 131), Rothschild’s rock-wallaby (165 detections, horizontal = 119, vertical = 46), and feral cats (127 detections, horizontal = 89, vertical = 38).

**Detection probability**

Camera orientation had a significant effect on nightly probability of detection for all species except for northern...
quolls (Fig. 3). Horizontal cameras had higher nightly detection probabilities for feral cats and Rothschild’s rock wallabies, and vertical cameras had a higher nightly detection probability for varanids (Fig. 3). For horizontal cameras, northern quolls required the least number of nights to be 95% confident of sites being unoccupied (24 nights, 95% CI 14 – 41 nights), followed by Rothschild’s rock wallabies (44 nights, 95% CI 50 – 141 nights), feral cats (69 nights, 95% CI 44 – 110 nights) and varanids (85 nights, 95% CI, 51– 141 nights) (Fig. 4). For vertical cameras, northern quolls required the least number of nights to be 95% confident of sites being unoccupied (32 nights, 95% CI 19 – 57 nights), followed by varanids (49 nights, 95% CI 32 – 78 nights), Rothschild’s rock wallabies (129 nights, 95% CI 67 – 248 nights), and feral cats (142 nights, 95% CI 78–258 nights) (Fig. 4).

**Total independent detections**

Camera orientation had a significant influence on the total number of independent detections recorded at sites for all taxa except northern quolls (Fig. 5). For feral cats, the predicted total number of independent detections for horizontal cameras (2.48, 95% CI 1.80 – 3.43) was over double the predicted total number of independent detections for vertical cameras (1.04, 95% CI 0.70 – 1.57). Similarly, for Rothschild’s rock wallaby, the predicted total number of independent detections for horizontal cameras (3.81, 95% CI 2.36 – 6.15) was almost three times higher than the predicted total number of independent detections for vertical cameras (1.34, 95% CI 0.79 – 2.28). Total predicted independent detections for varanids was higher for vertical cameras (2.52, 95% CI 1.72 – 3.69) than for horizontal cameras (1.54, 95% CI 1.02 – 2.30) (Fig. 5).

**Paired detection likelihood**

GLMM results indicated paired detection likelihood was significantly influenced by camera orientation for all species except for northern quolls (Fig. 6). Horizontal cameras had a 82.1% (95% CI 73.2%–88.5%) probability of detecting feral cats if a feral cat was detected on a paired camera on the same night, and vertical cameras had a 35.6% probability (95% CI 26.5%–45.9%). Similarly, for Rothschild’s rock wallaby, we found horizontal cameras had a 89.2% probability (95% CI 81.7%–93.8%) of detecting an animal if it was detected on a paired camera on the same night, but vertically orientated cameras had only a 34.6% probability (95% CI 26.5%–45.3%) of detecting an animal if it was detected on a horizontal camera (95% CI 25.2%–45.3%). Horizontal cameras had a 51.9% probability (95% CI 43.5%–60.3%) of detecting varanids if they were detected by a paired camera on the same night. Vertical cameras had a 75.0% probability (95% CI 67.1%–81.5%) of detecting varanids if an animal was detected by a paired camera on the same night (Fig. 6).
Discussion

Camera traps are the primary means of surveying an increasingly diverse range of animal taxa (Rowcliffe and Carbone 2008; Trolliet et al. 2014; Burton et al. 2015), yet studies rarely consider how camera orientation affects survey data (Rovero and Zimmermann 2016). Our results suggest camera orientation does not significantly affect camera performance in terms of any of the detection metrics measured in this study for northern quolls. Conversely, we found horizontally orientated cameras were more efficient at detecting both feral cats and Rothschild’s rock-wallabies, and vertically orientated cameras were better at detecting varanids.

Species detectability

As horizontal cameras have a larger detection zone—an important factor in maximising species detectability (Meek et al. 2015; Fancourt et al. 2018)—we predicted they would have higher nightly detection probabilities than vertical cameras. Our results supported this prediction for feral cats and for Rothschild’s rock-wallabies, concurring with findings of Nichols et al. (2017) who found a similar result for cats, and Taylor et al. (2014) for smaller species of macropods.

In addition to detection zone size, the attractiveness of baits to different mammal species may also have influenced this result. Bait type has previously been shown to alter species detectability (Diete et al. 2016), and bait preferences vary between species (Paull et al. 2011). In our study, we used a meat-based bait and therefore vertical cameras may have been less likely to detect Rothschild’s rock-wallaby, which is less likely than carnivorous species to have been drawn to the bait. Cameras themselves may also act as a deterrent or attractant to species, by emitting novel visual and acoustic cues which can be received by animals (Meek et al. 2014a). While still poorly understood, the capacity of animals to receive and respond to these cues is likely to vary with species (Meek et al. 2016). Because vertical cameras are positioned directly above the bait lure, cues emitted by the vertical cameras may influence the likelihood of species entering the vertical detection zone, and ultimately the probability of presence being recorded on vertical cameras.

Interestingly, we found camera orientation did not significantly influence whether northern quolls were detected...
at sites, nor the number of nights required to be 95% confident of sites being unoccupied. We suspect this result is reflective of bold foraging behaviour; that is, despite the novelty of the camera trap set-up, quolls readily approach bait canisters at close proximity, and thus are equally likely to breach both horizontal and vertical camera detection zones. This behaviour could be expected from northern quolls in the Pilbara, given they are generally not considered shy or neophobic.

Previous studies using camera traps to detect lizards have employed horizontal (Ariefiandy et al. 2013) and vertical cameras (Welbourne et al. 2015; Richardson et al. 2018; Moore et al. 2020), but our study is the first to compare how camera orientation influences lizard detectability. Contrary to our prediction, we found vertical cameras were more likely to record presence for varanids and required less survey effort to be 95% confident sites were unoccupied. The most likely explanation for this result may be that vertically orientated cameras are more suited to detecting a lizard morphology. Squamates, including lizards, have a laterally compressed body type, with a larger dorsal, than lateral, surface area (Thompson and Withers 1997). This type of morphology is more visible from a top-down perspective when compared to a horizontal perspective, and thus likely more exposed to vertical camera sensors, despite the larger detection zone of horizontal cameras.

Maximising the total number of independent detections is a priority in many ecological studies, because the total number of species detections can determine the variety and power of techniques available for subsequent statistical analysis (Foster and Harmsen 2012; Forcino et al. 2015; Lashley et al. 2018). We predicted horizontal cameras would record a significantly greater number of total independent detections than vertical cameras for all species, and we found this to be true for feral cats and Rothschild’s rock-wallabies, concurring with the results of previous studies (Taylor et al. 2014; Nichols et al. 2017). Like other behaviourally cryptic species, rock-wallabies and feral cats can be difficult to detect using camera traps, even at sites where presence has previously been confirmed (Bluff et al. 2011; Glen et al. 2016; Comer et al. 2018; Turpin et al. 2018). Maximising the total number of independent detections by orientating cameras appropriately may therefore be especially important for these species, given the risk of small samples sizes precluding the use of advanced analysis techniques already being high. For northern quolls and varanids, results were consistent with our probability of presence analysis — camera orientation did not influence the total number of independent detections recorded for northern quolls, and vertical camera recorded a higher number of varanid detections than horizontal cameras. For quolls, this result is again likely product of bold foraging behaviour. For varanids, increased total independent detections on vertical cameras is likely due to their laterally compressed morphology.

**Paired detection likelihood**

We found that horizontal cameras were significantly more likely to detect feral cats and Rothschild’s rock wallabies than vertical cameras (42.9% and 55.9% respectively). We also found horizontal cameras missed between 11.1% and 48.6% of detections across all focal species. This result was unexpected, as we presumed that animals would not have been able to enter a vertical detection zone without having already entered the horizontal detection zone. A possible explanation for missed detections by horizontal cameras could be the distance at which they were placed from the bait cannister. For example, Taylor et al. (2014) positioned their horizontal cameras two metres away from bait cannisters and found they outperformed vertical cameras, whilst Smith and Coulson (2012) used a distance of three metres and recorded the opposite result using the same species. We used a distance of 2.5 meters, as recommended by Meek et al. (2012) for detecting medium sized mammals. Using a reduced distance may have limited the

---

**Figure 5.** Output from generalized linear mixed models testing the effect of camera orientation on the total number of detections recorded for northern quolls (*Dasyurus hallucatus*), feral cats (*Felis catus*), Rothschild’s rock wallabies (*Petrogale rothschildi*), and varanids (*Varanus spp.*). Black points represent total number of predicted detections and blue error bars represent 95% confidence intervals. Treatment (horizontal or vertical camera orientation) was used as the fixed effect. Site was included as a random effect. ***P < 0.001.
number of detections missed by horizontal cameras, although it may also have reduced total detections by reducing the detection zone immediately surrounding bait cannisters. Another explanation for missed horizontal detections may be that even though camera sensitivity was set as high as possible, camera sensitivity may still not have been high enough to always detect species moving within the detection zone. For example Heiniger and Gillespie (2018) found Reconyx PC850 cameras with similar sensor capabilities to cameras used in this experiment frequently missed detections when bait was being removed 1.5 metres away by medium sized species such as the northern quoll and northern brown bandicoot (*Isoodon macrourus*). We also cannot discount that animals evaded detection from horizontal, or vertical cameras, by moving under or over camera detection bands (Meek et al. 2014b; Apps and McNutt 2018), which cover less than half of the cameras field of view for Reconyx cameras (Reconyx 2013) (Appendix S1).

**Conclusions**

We found that horizontal cameras performed better than vertical cameras in terms of detecting feral cats and Rothschild’s rock wallabies, but no significant differences were observed for northern quolls. We also found vertically orientated cameras were better at detecting varanids. Given the clear differences in detectability performance, it is important to consider the practicality of using horizontal or vertical cameras on a species by species basis. For example, whilst orientation made no difference to the probability of cameras detecting northern quolls, wildlife managers may still be inclined to use vertically orientated cameras given they generally capture image data more suited to individually identifying northern quolls, which are most easily distinguished from their dorsal surface (although see Hohnen et al. 2013). By contrast, individual cats and possibly rock wallabies can be distinguished from their ventral surfaces, which are better captured using horizontal cameras (Bengsen et al. 2012; McGregor et al. 2015), and thus there would be no reason to reduce detectability by using vertical cameras for these species. Vertical cameras were better at detecting varanids, and have been shown to be well suited to species and individual identification for lizards (Welbourne 2013; Moore et al. 2020; Welbourne et al. 2019), and therefore would be a more logical approach in most situations.
Overall our results demonstrate that neither horizontally or vertically orientated cameras are best suited to all taxa, and both orientations are susceptible to missing detections at times. We recommend future studies that use vertical cameras to collect image data better suited for species or individual identification should consider how target species detectability maybe compromised by having a reduced detection zone size.

Acknowledgments

We acknowledge and thank the Karayarra and Nyamal people whose land this study was conducted on. Data collection was assisted by Sian Thorn, Darcy Watchorn, Rainer Chan, Daniel Bohorquez Fandino, Jacob Champney, Hannah Kilian, Mitch Cowan, Gasten Stewart, John Stewart and Nathaniel Herbert. Camera-trap deployment was also completed with the assistance of the Yandeyarra Indigenous ranger program facilitated by Pip Short and Greening Australia. Technical support was provided by Neal Birch, Brent Johnson, Hannah Anderson, Russell Palmer, Alicia Whittington and Jo Kuiper from the Western Australian Department of Biodiversity, Conservation and Attractions (DBCA), as well as Deb Noy from Charles Sturt University. Stephen Van Leeuwen from DBCA provided assistance with the project conception and also provided support throughout. Equipment and operational costs were provided by DBCA, Roy Hill and Charles Sturt University. Roy Hill also covered the costs of flights, fuel and freight. Harriet Davie from Roy Hill provided technical support throughout, along with the Roy Hill rail team in Port Hedland. We thank Colin Briery, Betty Briery and Graham for providing access to Indee station, Ben and Lindsey for access to Mallina and Troy Eaton for access to Pippinagara. Belinda Barnett from BHP assisted with site access. H.A.M is supported by a scholarship from the Institute of Land, Water and Society and Charles Sturt University. L.E.V. was funded by the Australian Government’s National Environmental Science Program through the Threatened Species Recovery Hub. D.G.N. was supported by an Australian Research Council Early Career Researcher Award (DECRA). This project was supported by the Holsworth Wildlife Research Endowment – Equity Trustees Charitable Foundation and the Ecological Society of Australia, as well as the Western Australian Department of Biodiversity, Conservation and Attractions as well as environmental offsets and public good funding provided by BHP, Rio Tinto, Atlas Iron, Fortescue Metals Group, Roy Hill, Process Minerals International, Metals X and Main Roads Western Australia. Research ethics was granted through the Charles Sturt University Animal Ethics Committee (permit Number A17031), and the Western Australian Department of Biodiversity, Conservation and Attractions (permit Number 08-002376-1).

We are grateful to two reviewers and the topic editor who provided valuable and detailed comments on the manuscript and improved it to the version presented here. We also thank Susan Blackburn, Anna Cresswell and George Cresswell for their contributions in the way of comments and suggestions.

Data accessibility

Data and code is available on dryad.

Conflict of interests

No authors report any conflict of interests.

References

Apps, P., and J. W. McNutt. 2018. Are camera traps fit for purpose? A rigorous, reproducible and realistic test of camera trap performance. Afr. J. Ecol. 56, 710–720.

Ariefiandy, A., D. Purwandana, A. Seno, C. Ciofi, and T. S. Jessop. 2013. Can camera traps monitor Komodo dragons a large ectothermic predator? PLoS ONE 8, e58800.

Australian Bureau of Meteorology. (2019) Climate Data Online. Australian Bureau of Meteorology.

Bates, D., D. Sarkar, M. D. Bates, and L. Matris. 2007. The lme4 package. R Package Version 2, 74.

Bengsen, A., J. Butler, and P. Masters. 2012. Estimating and indexing feral cat population abundances using camera traps. Wildl. Res. 38, 732–739.

Bluff, L. A., L. Clausen, A. Hill, and M. D. Bramwell. 2011. A decade of monitoring the remnant Victorian population of the brush-tailed rock-wallaby (Petrogale penicillata). Aust. Mammal. 33, 195–201.

Brides, K., J. Middleton, K. Leighton, and A. Grogan. 2018. The use of camera traps to identify individual colour-marked geese at a moultng site. Ringing Migr. 33, 19–22.

Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, et al. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. J. Appl. Ecol. 52, 675–685.

Comer, S., P. Speldewinde, C. Tiller, L. Clausen, J. Pinder, S. Cowen, et al. 2018. Evaluating the efficacy of a landscape scale feral cat control program using camera traps and occupancy models. Sci. Rep. 8, 5335.

Crawley, M. J. 2012. The R book. John Wiley & Sons.

De Bondi, N., J. G. White, M. Stevens, and R. Cooke. 2010. A comparison of the effectiveness of camera trapping and live trapping for sampling terrestrial small-mammal communities. Wildl. Res. 37, 456–465.

Dieta, R. L., P. D. Meek, K. M. Dixon, C. R. Dickman, and L. K.-P. Leung. 2016. Best bait for your buck: bait preference
for camera trapping north Australian mammals. Aust. J. Zool. 63, 376–382.

ESCAVI E. S. C. f. A. V. I. 2003. Australian Vegetation Attribute Manual: National Vegetation Information System Version 6.0. Department of Environment Executive Steering Committee for Australian Vegetation Information, Canberra, Australian Capital Territory.

ESRI. 2011. ArcGIS Desktop: Release 10.

Forcino, F. L., L. R. Leighton, P. Tweryd, and J. F. Cahill. 2015. Reexamining sample size requirements for multivariate, abundance-based community research: when resources are limited, the research does not have to be. PLoS ONE 10, e0128379.

Foster, R. J., and B. J. Harmsen. 2012. A critique of density estimation from camera-trap data. J. Wildl. Manag. 76, 224–236.

Glen, A., D. Anderson, C. Veltman, P. Garvey, and M. Nichols. 2016. Wildlife detector dogs and camera traps: a comparison of techniques for detecting feral cats. New Zealand J. Zool. 43, 127–137.

Heiniger, J., and G. Gillespie. 2018. High variation in camera trap-model sensitivity for surveying mammal species in northern Australia. Wildl. Res. 45, 578–585.

Hohnen, R., J. Ashby, K. Tuft, and H. McGregor. 2013. Individual identification of northern quolls (<i>Dasyurus hallucatus</i>) using remote cameras. Aust. Mammal. 35, 131–135.

Huy, M. 2002. Inferring the absence of a species: a case study of snakes. J. Wildl. Manag. 330–338.

Lashley, M. A., M. V. Cove, M. C. Chitwood, G. Penido, B. Gardner, C. S. DePerno, et al. 2018. Estimating wildlife activity curves: comparison of methods and sample size. Sci. Rep. 8, 4173.

McGregor, H. W., S. Legge, J. Potts, M. E. Jones, and C. N. Johnson. 2015. Density and home range of feral cats in north-western Australia. Wildl. Res. 42, 223–231.

Meek, P., and A. Pittet. 2013. User-based design specifications for the ultimate camera trap for wildlife research. Wildl. Res. 39, 649–660.

Meek, P. D., D. Fleming, and G. Ballard. 2012. An introduction to camera trapping for wildlife surveys in Australia. Invasive Animals Cooperative Research Centre Canberra, Australia.

Meek, P. D., G.-A. Ballard, P. J. Fleming, M. Schaefcr, W. Williams, and G. Falzon. 2014a. Camera traps can be heard and seen by animals. PLoS ONE 9, e110832.

Meek, P. D., P. Fleming, G. Ballard, P. Banks, A. W. Claridge, J. Sanderson, et al. 2014b. Camera trapping: wildlife management and research. CSiro Publishing Melbourne, Australia.

Meek, P. D., G.-A. Ballard, and P. J. Fleming. 2015. The pitfalls of wildlife camera trapping as a survey tool in Australia. Aust. Mammal. 37, 13–22.

Meek, P., G. Ballard, P. Fleming, and G. Falzon. 2016. Are we getting the full picture? Animal responses to camera traps and implications for predator studies. Ecol. Evol. 6, 3216–3225.

Menkhors, P., and F. Knight. 2010. Field guide to the mammals of Australia. Oxford University Press.

Moore, H., J. Champney, J. Dunlop, L. Vantline, and D. Nimmo. 2020. Spot on: Using camera traps to individually monitor one of the world’s largest lizards.

Muneza, A. B., W. Ortiz-Calo, C. Packer, J. J. Cusack, T. Jones, M. S. Palmer, et al. 2019. Quantifying the severity of giraffe skin disease via photogrammetry analysis of camera trap data. J. Wildl. Dis. 55, 770–781.

Nichols, M., A. S. Glen, P. Garvey, and J. Ross. 2017. A comparison of horizontal versus vertical camera placement to detect feral cats and mustelids. N. Z. J. Ecol. 41, 145–150.

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

Paul, D. J., A. W. Claridge, and S. C. Barry. 2011. There’s no accounting for taste: bait attractants and infrared digital cameras for detecting small to medium ground-dwelling mammals. Wildl. Res. 38, 188–195.

Pollock, K. H., J. D. Nichols, T. R. Simons, G. L. Farnsworth, L. L. Bailey, and J. R. Sauer. 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. Environmetrics 13, 105–119.

R Core Team R. 2013. R: A language and environment for statistical computing. R Foundation for statistical computing. Vienna.

Rabe, M. J., S. S. Rosenstock, and Jr J. C. deVos. 2002. Review of big-game survey methods used by wildlife agencies of the western United States. Wildl. Soc. Bull. 46–52.

Reconyx. 2013. Hyperfire™ high performance cameras instruction manual. Reconyx, Inc Holmen, WI, USA.

Richardson, E., D. G. Nimmo, S. Avitabile, L. Tworkowski, S. J. Watson, D. Welbourne, et al. 2018. Camera traps and pitfalls: an evaluation of two methods for surveying reptiles in a semi-arid ecosystem. Wildl. Res. 44, 637–647.

Robson, D., and H. Regier. 1964. Sample size in Petersen mark–recapture experiments. Trans. Am. Fish. Soc. 93, 215–226.

Rovero, F., and F. Zimmermann. 2016. Camera trapping for wildlife research. Pelagic Publishing Ltd.

Rovero, F., F. Zimmermann, D. Berzi, and P. Meek. 2013. “Which camera trap type and how many do I need?” A review of camera features and study designs for a range of wildlife research applications. Hystrix 24, 148–156.

Rowcliffe, J. M., and C. Carbone. 2008. Surveys using camera traps: are we looking to a brighter future? Anim. Conserv. 11, 185–186.
Seber, G. A. F. 1982. *The estimation of animal abundance and related parameters*. Blackburn press Caldwell, New Jersey.

Smith, J. K., and G. Coulson. 2012. A comparison of vertical and horizontal camera trap orientations for detection of potoroos and bandicoots. *Aust. Mammal.* 34, 196–201.

Taylor, B. D., R. L. Goldingay, and J. M. Lindsay. 2014. Horizontal or vertical? Camera trap orientations and recording modes for detecting potoroos, bandicoots and pademelons. *Aust. Mammal.* 36, 60–66.

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

Thompson, G. G., and P. C. Withers. 1997. Comparative morphology of western Australian varanid lizards (Squamata: Varanidae). *J. Morphol.* 233, 127–152.

Thorn, S. (2019). Unique markings on Numbats. *Remote Sens. Ecol. Conserv.* 2, 77–83.

Welbourne, D., A. Claridge, D. Paull, and F. Ford. 2019. Improving terrestrial squamate surveys with camera-trap programming and hardware modifications. *Animals* 9, 388.

Wilson, G. J., and R. J. Delahay. 2001. A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. *Wildl. Res.* 28, 151–164.

Wilson, S. K., and G. Swan. 2017. *A complete guide to reptiles of Australia*. Reed New Holland, Sydney.

Witmer, G. W. 2005. Wildlife population monitoring: some practical considerations. *Wildl. Res.* 32, 259–263.

**Supporting Information**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** The position of detection bands for Reo-nyxTM camera, adapted from (Reconyx 2013). (A) Image from vertically orientated camera, (B) horizontally orientated camera.