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Effective conservation of any species is difficult without a clear picture of population trends. We aimed to improve monitoring of Lumholtz's tree-kangaroo, a species that is typically hard to detect, showing that thermal imaging technology is more cost-effective than traditional survey methods. This information can improve the conservation outlook for the tree-kangaroo as well as many other hard-to-detect species.

Cost-effectiveness of thermal imaging for monitoring a cryptic arboreal mammal

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Abstract

Context: The development of reliable and cost-efficient survey techniques is key to the monitoring of all wildlife. One group of species that presents particular challenges for monitoring is the arboreal mammals. Traditional techniques for detecting these species often yield low detection probabilities (detectability) and are time-consuming, suggesting the potential for novel methods to enhance our understanding of their distribution, abundance and population trajectories. One relatively new technique that has been shown to increase detectability in a range of terrestrial species is thermal imaging, though it has rarely been applied to arboreal species. The true conservation status of Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi*) is uncertain due to low detectability under typical survey techniques, and a more suitable method is required to enable effective monitoring of the species, making it an ideal candidate for this study.

Aims: We aimed to compare the success and cost-effectiveness of surveys utilising thermal imaging to two traditional methods – spotlighting and daytime surveys – in order to optimise monitoring of *D. lumholtzi*.

Methods: We carried out surveys at ten sites in Queensland (Australia) where *D. lumholtzi* was known to occur using each method, and modelled both the detectability of *D. lumholtzi* and the cost-effectiveness of each technique.

Key results: Detectability of *D. lumholtzi* was significantly higher with the use of thermal imaging compared to the other survey methods, and thermal detection is more cost-effective. In average survey conditions with a trained observer, the single-visit estimated detectability of *D. lumholtzi* was 0.28 [0.04, 0.79] in a transect through rainforest using thermal imaging. Using only spotlights, the detection probability was 0.03 [0, 0.28] under the same conditions.

Conclusions: These results show that incorporating thermal technology into monitoring surveys will greatly increase detection probability for *D. lumholtzi*, a cryptic arboreal mammal.

Implications: Our study highlights the potential utility of thermal detection in monitoring difficult-to-detect species in complex habitats, including species that exist mainly in dense forest canopy.

Introduction

Monitoring is central to good management and conservation of all species. Detecting population changes in a timely manner allows appropriate actions to be taken (Ogutu *et al.* 2006; Spehar *et al.* 2015). Population estimates derived from statistical analysis of field survey data are generally used to monitor changes over time, as exact population size is seldom known (Lee and Bond 2016). Where estimating population size is not considered feasible, due to low density, cryptic nature of a species or difficulties in distinguishing between individuals, presence-absence data can be used to estimate the occupancy state of sites (i.e. occupied by the species, or not) and characterise the distribution of species (Gálvez *et al.* 2016). Temporally- and/or spatially-replicated occupancy survey methods can produce estimates of both occupancy and detectability, the probability of detection of the species (Whittington *et al.* 2015). Through monitoring programs, occupancy data can provide an indication of the proportion of a region occupied by a species, or the distribution of the species across a region (when environmental covariates are included), and how these change over time (Einoder *et al.* 2018).

Researchers have a wide array of techniques that can be used to detect species, and the most suitable method is situation-specific, based on species and habitat characteristics (Wintle *et al.* 2005). Most survey methods for most species are affected by imperfect detection – where a target species is not always detected, even when present at a site (Mackenzie and Royle 2005). This can lead to false absences if not properly accounted for, with implications for the management of habitat and threatened populations. In recent times, occupancy modelling approaches have been developed that account for imperfect detection in such a way to reduce bias in predictions and inferences (Mackenzie *et al.* 2002; Tyre *et al.* 2003; Mackenzie and Royle 2005).

Detectability is the probability of a species being detected at a site, on a particular survey occasion, given presence (Mackenzie *et al*. 2002). Detectability differs for all species, based on their characteristics, and can be affected by site variables such as vegetation type, altitude and patch size, or survey covariates such as temperature, precipitation, time of day, season, the expertise or experience of the surveyor, and the time spent at the survey (Wintle *et al.* 2005; Garrard *et al.* 2008; Wintle *et al.* 2012; Guillera-Arroita 2017). Importantly, different survey methods will return different values for a species' detectability, depending largely on the species and habitat in question, and this should be a consideration of any monitoring design. There are likely to be important trade-offs in sampling design around the costs of a given survey method and the number of surveys that can be conducted, as the method considered best for detecting a species may not always be the cheapest.

Ever-improving technology is reshaping the way researchers think about biological surveys. Greater availability and decreasing costs are increasing access to tools that may improve monitoring effectiveness, including established technology becoming more accessible (e.g. thermal imaging, acoustic monitoring, drones) or more novel tools such as environmental DNA. Improvements to monitoring through the use of such technologies can be achieved in several (related) ways: increasing detectability for a given effort, improving precision of counts, reducing false positive observations, collecting more data within a given survey time, allowing access to remote sites or covering a greater area than is feasible with more traditional techniques (Gill *et al.* 1997; Claridge *et al.* 2010; Koh and Wich 2012; Hodgson *et al.* 2016). Innovation in monitoring is especially important for species that are cryptic or lacking in accurate population data (Spehar *et al*. 2015). However, careful comparison of the cost-effectiveness of survey methods and their capacity to deliver the required information with the required accuracy and precision is crucial to avoid wasting the limited resources available for conservation monitoring, especially when considering a shift to a new technique. Various studies have compared traditional and novel methods for surveying cryptic species. Greene *et al*. (2016) showed camera trapping to be more efficient than the live trapping methods typically used to estimate numbers of fox squirrels (*Sciurus niger*) throughout south-eastern USA. Other recent studies have compared survey methods for monitoring giraffes, moose, dolphins and sea turtles, with variable findings, suggesting that novel methods may not always improve survey accuracy (Mansson *et al.* 2011; Mancini *et al.* 2015; Lee and Bond 2016; Tyne *et al.* 2016). For this reason, it is essential that new methods with the potential to improve survey success are trialled systematically to assess their effectiveness and cost-efficiency.

The cost of thermal imaging technology has recently decreased to the point that it can be widely considered as a monitoring tool in ecology and conservation. It has been applied in wildlife surveys, with promising results. Thermal imaging detects the far- or mid-infrared radiation of objects, allowing the visualisation of heat signatures (Sabol and Hudson 1995; Gill *et al.* 1997; Longmore *et al.* 2017). This is especially useful for carrying out surveys at night, to detect nocturnal species or species that are less active during daylight (Sabol and Hudson 1995; Gill *et al.* 1997). Endotherms will stand out against relatively cool background environments when viewed through a thermal scope or camera, giving this technology obvious potential in detecting such species (Gill *et al.* 1997; Morelle *et al.* 2012). Such an increase in detectability would reduce the likelihood of missing the species during a survey. By effectively increasing species detectability, thermal technology decreases the impact of imperfect detection and is likely to increase the accuracy of occupancy or population estimates. Various studies have shown improved detection rates of terrestrial species with thermal imaging compared to traditional methods (Focardi *et al.* 2001; Collier *et al.* 2005; Ditchkoff *et al.* 2005; Betke *et al.* 2008; Mills *et al.* 2011), though none have explicitly compared the cost-effectiveness of survey method alternatives, and the utility of thermal imaging in surveying arboreal mammals is unclear.

Until recently, the use of thermal imaging for population surveys has been limited by the substantial cost of equipment. Thermal imaging devices vary greatly in cost, with basic units usually priced upwards of AU$800 (e.g. FLIR Scout TK Thermal Vision Monocular) and more advanced equipment over AU$14,000 (e.g. FLIR T530 Thermal Imaging Camera), though costs keep dropping rapidly. The two major differences between high-end and low-end models are resolution and whether a model is radiometric. Radiometric units can provide absolute temperature values, and are generally more expensive than non-radiometric models, which only display relative temperatures. To assess the effectiveness of this survey tool, Morelle *et al.* (2012) conducted surveys of three game species under varying levels of forest cover (14-46%) in Belgium using expensive and mid-range thermal imaging devices. This study found no difference in detection rate between the two models, suggesting that lower-cost thermal imagers may be more cost-effective than more expensive ones (Morelle *et al*. 2012). In recent years, small thermal imaging units have even been mounted on drones and used to successfully detect terrestrial species including kangaroos, deer and rabbits (Witczuk *et al*. 2018; Burke *et al*. 2019; Brunton *et al*. 2020).

In this study, traditional survey methods (daytime and spotlight surveys) are compared with thermal imaging in surveying a cryptic arboreal mammal, Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi*). We provide a comparison of the cost-effectiveness of traditional and thermal imaging methods for monitoring tree-kangaroos. We survey rainforests of far north Queensland, Australia, using multiple detection approaches (spotlighting, daytime surveys and thermal imaging) to estimate detection rates of the competing approaches. We combine these estimates with the cost-efficiency of each method, with the aim of guiding survey design for regional monitoring of *D. lumholtzi* and similar arboreal species.

Methods

Study species

Dendrolagus lumholtzi is one of at least 14 species of tree-kangaroos making up the *Dendrolagus* genus in the Macropod family. *D. lumholtzi* is confined to part of the wet tropics region of northern Queensland, Australia, from the Carbine Tablelands in the north to the Cardwell Range in the south (Winter *et al.* 1991). Only one other species of tree-kangaroo, Bennett's tree-kangaroo (*D. bennettianus*), is found in Australia; the remaining species occur in Papua New Guinea (Flannery *et al.* 1996; Newell 1999c). *D. lumholtzi* individuals spend most of their time in trees but will come to ground to move between habitat patches or when they feel threatened (Flannery *et al.* 1996).

Population estimates of *D. lumholtzi* are uncertain due to their cryptic nature, occurrence in dense habitat in remote areas and a lack of effective survey methods (Newell 1999a, b, c; Heise-Pavlov and Meade 2012). Past studies have attempted to address this, trialling scat counts and scratch marks on trees as an alternative to the more typical method of spotlight surveys, but these have displayed various limitations (Heise-Pavlov and Meade 2012). Consequently, the true conservation status of the population is uncertain, with the species currently listed as Near Threatened according to both the Queensland Nature Conservation Act (1992) and the International Union for the Conservation of Nature (IUCN) Red List (Woinarski and Burbridge 2016). In fragmented habitat, dog attacks and collisions with vehicles are threats that *D. lumholtzi* faces when moving between patches (Newell 1999a). The impact of climate change is predicted to be detrimental to the species, by reducing suitability of food plant species through the impacts of increased CO_2 levels on foliar chemistry, severe weather events and rising temperatures (Kanowski 2001). Due to the lack of reliable data around population numbers, and the species' reported low detectability under traditional survey techniques (mainly spotlight surveys), we consider it a prime candidate for this study.

Study area

This study is based on the Atherton Tablelands, where most work on *D. lumholtzi* has taken place and the population is believed to be at its highest density (Newell 1999a, c). The Tablelands are located approximately 60km south-west of Cairns, in northern Queensland, Australia, covering an area of 32,000km^2 and a range of altitudes from 500m to over 1,200m above sea level (Figure 1). The landscape lies on highly-fertile volcanic soils, and has been subjected to high levels of habitat fragmentation, as large areas have been converted for agricultural purposes since the 1870s (Newell 1999b; Turton 2009; Heise-Pavlov *et al.* 2011). The elevation of the region gives it a distinct climate to the surrounding lowland areas. The lower temperatures and humidity on the Atherton Tablelands have resulted in a different flora and fauna composition to nearby regions, and provide seemingly preferable conditions for *D. lumholtzi*, which occurs at much lower densities outside of the Tablelands (Newell 1999b; Kanowski *et al.* 2001).

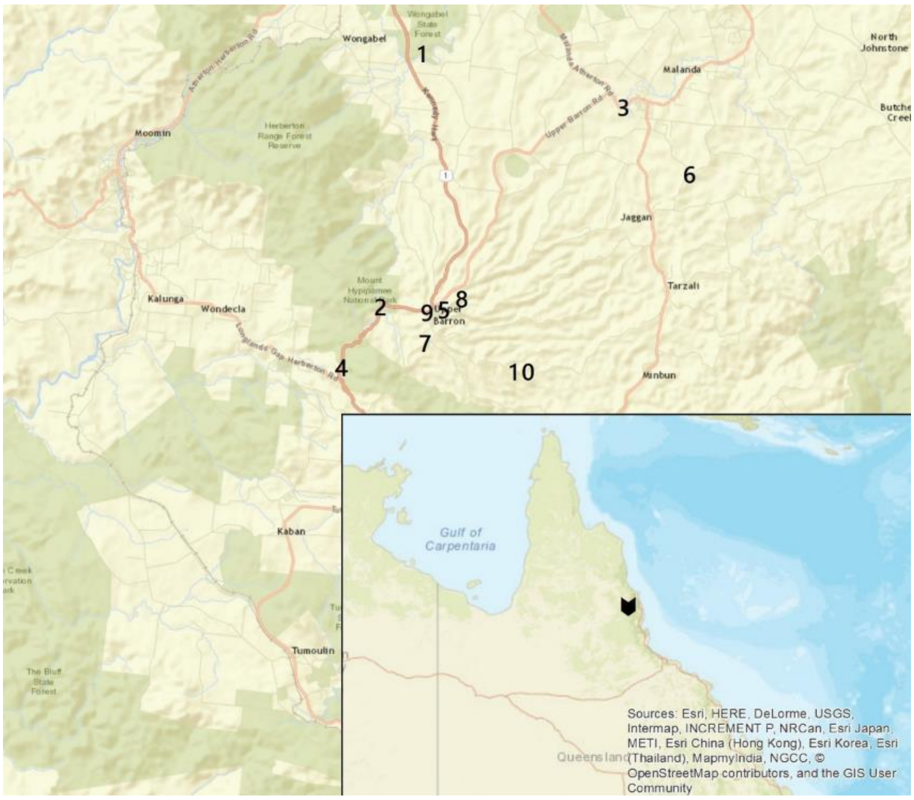

Figure 1 - *Location of study sites, with sites numbered according to Appendix 1. Inset map shows the location of the study area within Queensland, north-eastern Australia.*

Ten sites on the Atherton Tablelands were selected for transects based on size, accessibility and reliable recent reports of *D. lumholtzi* presence. The sites are mostly based around Upper Barron region, consist of both private and public land and include five transects that are along edges of fragments (*edge sites*) and five transects on tracks within forest patches (*interior sites*). The interior sites consisted of a combination of standard walking tracks and wider tracks that were suitable for vehicles. The length of transects ranged between 619-1066m. The substrate is mostly basalt, with a rhyolitic base layer at one site. Most sites are classed as notophyll vine forests, with mesophyll forest and secondary rainforest complexes present at some sites. The ten sites were all used for surveys in 2016, while a subset of six were used for further surveys in 2017 (Appendix 1).

Survey methods

Surveys included (i) daytime surveys, (ii) spotlight surveys at night and (iii) spotlight surveys with the addition of a handheld thermal imager, also at night (hereafter denoted as 'thermal surveys'). Each method was used three times at each of the ten sites between June and September 2016, except for a single missed daytime survey at site 5. In 2017, a subset of sites (numbers 1, 2, 5, 6, 7 and 9; half of them edge sites) were surveyed again under each method, between June and July (Appendix 1). Time was a limiting factor in the 2017 field season, and a large proportion of available survey nights were unsuitable due to heavy rain. Within the reduced timeframe, multiple surveys at a subset of sites was preferred over a single repeat of each method at all ten sites. The sites that were surveyed in 2017 (a relatively small proportion of surveys compared to 2016) were selected based on site type (three edge and three interior), only including sites where tree-kangaroos were detected in 2016 (i.e. not site 3), and included sites with a range of detection rates. As explained in next section, the focus of our study was detectability, and we did not estimate occupancy; hence choosing sites with known high probability of presence (in 2016 and 2017) was not a concern in terms of introducing bias in the model. In total, 26 surveys were carried out in 2017 consisting of eight daytime surveys and nine each of spotlight and thermal surveys.

All surveys were completed by two surveyors – at least one of whom was experienced with the methods and target species. The second surveyor was either another experienced surveyor, or an inexperienced volunteer who was briefed on the survey methods and aims. Daytime surveys took place from late morning to early afternoon, while spotlight and thermal surveys were not started until it was dark enough to clearly see eye-shine and vegetation had cooled sufficiently to allow endothermic animals to be clearly distinguishable through the thermal imager. Where surveyors completed two surveys in one night, the same site was not surveyed twice in one night, and a break (~30-60 minutes) was taken in between surveys to minimise observer fatigue.

In daytime surveys, the surveyors walked the transect at a slow, steady pace, approximately 5-10m apart, looking up and down the entire extent of vegetation present along the transect – one side of the transect for edge sites and both sides for interior sites. Spotlight surveys were performed in much the same way, with each surveyor using a headlamp (LED Lenser H7R.2, maximum brightness 300 lumens) to allow eye-shine detection. Whenever an inexperienced volunteer was present, the experienced surveyor walked in front, such that they were in a better position to see any animal that may flee in response to human presence. This gave the greatest chance of positively identifying the species. The same method was followed for the thermal surveys, except the surveyor at the front was looking through a handheld thermal scope (Pulsar Quantum XD19S; Figure 2) when scanning the transect. Headlamps were still required to positively identify the species after a thermal detection. No surveys were performed in significant rain, due to the difficulties of spotlighting with heavy rainfall. Table 1 shows the survey-specific information collected in surveys, including temperature which was recorded with digital thermometers at the time of survey (Digitech QM-1679 or Mastercool 5224-A Infrared Thermometers).

Figure 2 - *Image of D. lumholtzi as viewed through the Pulsar Quantum XD19S scope, captured using a smartphone camera.*

Table 1 - *Summary of candidate covariates. The second column shows the categories considered in categorical variables.*

Parameter	Categories
Start time	N/A
Survey method	Day, Spotlight, Thermal
Surveyor experience	Experienced/Experienced, Experienced/Inexperienced
Temperature (°C)	N/A (continuous)
Presence of rain	1 (Rain), 0 (No Rain)
Presence of fog	1 (Fog), 0 (No Fog)

Moon percentage	N/A (continuous)
Site Type	Interior, Edge
Soil Type	Barron, Maalan, Pin Gin, Mixed
Vegetation Class	Complex notophyll vine forest, Mixed, Cleared/Regrowth
Base Layer	Basalt, Rhyolite

Detectability modelling

Since our interest is in evaluating detectability under different monitoring options, we do not estimate occupancy (a priori believed to be close to 1 in our set of selected sites) using a classic occupancy-detection model (Mackenzie 2018). Instead, we model detectability of *D. lumholtzi* using survey data from the on-foot surveys to construct a generalised linear model (GLM) in R (R Core Team 2015). The model follows a logistic regression of the following form, for site i and visit j:

$$d_{i,j} \sim Bernoulli(p_{i,j}) \qquad (Equation\ 1)$$

$$logit(p_{i,j}) = \beta_0 + \sum \beta_k x^{[k]}$$

where d_{ij} is the survey detection data (1 if the species is detected in a survey, 0 if not detected) and $p_{i,j}$ is the probability of detection of the species in one visit. Through the logistic regression, detectability can be related to an intercept (β_0) and k covariates $x^{[k]}$. Covariates were either site-specific, $x_i^{[k]}$ (site type, transect length, altitude, soil type, vegetation class and base layer) or visit-specific, $x_j^{[k]}$ (start time, survey method, surveyor experience, temperature, moon percentage, rain and fog). β_k represents the slope or magnitude of the effect of variable $x^{[k]}$ on detectability as a linear effect on the logit scale.

All data from sites with detections were included in the modelling data. Any site that did not record a detection was not included due to the true occupancy state being uncertain; this strategy allows modelling to focus on detectability. Only one site (Site 3) had to be removed from analysis for this reason. Continuous variables were standardised with a mean of zero and standard deviation of one. Candidate models were formulated systematically by beginning with a full model (including all possible covariates) and subsequently trialling different combinations with one change per step. We plotted continuous variables against observations to assess whether any non-linear relationships existed, and found no evidence of such relationships. Candidate models were compared based on their Akaike Information Criterion (AIC) values to determine which combination of covariates most parsimoniously predicted detectability. Models with an AIC value within two units of the best-fitting model (i.e. ΔAIC ≤ 2) were considered a good fit to the (see Table 2).

Cost-effectiveness analysis

A simple cost-effectiveness analysis was carried out to compare the return from each method for given budgets at sites of unknown occupancy. Each method carries unique costs to be considered, and for a set budget there is a trade-off between the number of sites that can be covered and the number of repeat visits per site. In this case, we aimed to represent cost-efficiency by the number of sites for which the occupancy status can be defined with a confidence level of at least 0.95.

First, the number of repeat visits required per site to achieve this condition was calculated for each method. This was defined as the number of visits needed to be 95% confident that the species will be detected if present. This value was calculated using (Wintle *et al.* 2012):

$$k_{min} = \frac{\log(0.05)}{\log(1 - p_m)} \qquad (Equation\ 2)$$

where k_{min} is the minimum number of repeat visits per site and p_m is the estimated detectability of the species of interest using method m. We used the average of predicted detectability for interior and edge sites, which makes the results indicative of a situation where survey sites comprise half of each type. k_{min} values were rounded up to the nearest whole number. We break the costs into initial (investment in equipment) and time (travel and participant time) costs as follows. Time cost was defined as AU$30/hr, while the initial costs, at the time equipment was purchased, were AU$290 for spotlight surveys (cost of two LED Lenser H7R.2 headlamps) and AU$3,940 for thermal surveys (one Quantum Pulsar XD19S thermal scope plus two LED Lenser H7R.2 headlamps). There was no initial cost associated with day surveys. This information was used to calculate the number of surveys that could be carried out with each method for a given budget and, thus, the number of sites that could be visited the minimum number of times as defined by Eq.2. Results were plotted for a situation where the purchase of equipment was required, as well as without equipment purchase.

Results

Survey detections

Table 2 shows the number of *D. lumholtzi* detections recorded for each site, with each survey method. The following non-target species were also detected: coppery brushtail possum (*Trichosurus vulpecula johnstonii*), Herbert River ringtail possum (*Pseudochirulus herbertensis*), green ringtail possum (*Pseudochirops archeri*), lemuroid ringtail possum (*Hemibelideus lemuroides*), fawn-footed melomys (*Melomys cervinipes*), long-tailed pygmy possum (*Cercartetus caudatus*), giant white-tailed rat (*Uromys caudimaculatus*) and striped possum (*Dactylopsila trivirgata*). Four of these species (*M. cervinipes*, *C. caudatus*, *U. caudimaculatus* and *D. trivirgata*) were only detected in thermal surveys, while the other species were recorded in both thermal and spotlight surveys.

Table 2 - *Number of surveys with D. lumholtzi detection (and total number of surveys in brackets) for each survey method at each survey site*

Site	**Surveys with *D. lumholtzi* detection (no. of surveys)**			
	Day	**Spotlight**	**Thermal**	**TOTAL**
1	0 (4)	0 (5)	3 (4)	3 (13)
2	1 (4)	0 (4)	5 (5)	6 (13)
3	0 (3)	0 (3)	0 (3)	0 (9)
4	0 (3)	0 (3)	3 (3)	3 (9)
5	0 (4)	0 (4)	1 (4)	1 (12)
6	2 (5)	5 (5)	3 (4)	10 (14)
7	0 (4)	3 (4)	4 (5)	7 (13)
8	1 (3)	3 (3)	3 (3)	7 (9)
9	1 (4)	3 (5)	4 (5)	8 (14)
10	1 (3)	1 (3)	3 (3)	5 (9)
TOTALS	**6 (37)**	**15 (39)**	**29 (39)**	**50 (115)**

Detectability modelling

The model ranked as AIC-best predicted detectability as a function of survey method, site type, temperature and soil type, giving the following logistic regression for detectability (Table 3; Table 4):

$$\text{logit}(p_{i,j}) = -3.662 - 2.520D_j + 2.702T_j + 4.613E_i + 0.567t_j + 1.538B_i + 2.457M_i + 0.048P_i \ (Equat$$

where D_j and T_j are indicator functions that take value 1 when survey *j* is day or thermal respectively (and 0 otherwise); together, they code for the 3 possible methods, the default (reference) being spotlight (when both D_j=0 and T_j=0). Hence, D_j and T_j represent the incremental effect of daytime and thermal surveys compared to spotlighting. Similarly, B_i, M_i and P_i take value 1 when the soil type at site *i* is Barron, Mixed or Pin Gin respectively, compared to a reference soil type of Maalan. $E_i = 1$ if site i is an edge site, 0 if an interior site, and t_j is temperature at visit j. 19 other models were identified within 2 AIC units of the top one, indicating that they had some support compared to the AIC-best model (Burnham and Anderson 2002). The closeness of the AIC values for a wide range of models indicates that several other factors could be important in determining detectability on any given survey night, and model averaging (based on the Akaike weights) could be used when determining ideal survey conditions or predicting detectability under a range of survey conditions. The AIC weights presented in Table 3 support the closeness of suitability of these models as well, with the top three models all weighted similarly. However, for the sake of simplicity, in further analysis only the single AIC-best model is used.

Table 3 - *Summary of the AIC-best candidate GLMs to predict D. lumholtzi detectability, where model rank 1 is the best-supported model, model rank 2 is second best-supported, and so on.*

Rank	**Variables**	**ΔAIC**	**AIC Weight**
1	Method + Site Type + Temperature + Soil Type	0	0.093
2	Method + Site Type + Temperature + Soil Type + Moon Percentage	0.02	0.092
3	Method + Site Type + Temperature + Transect Length	0.10	0.088
4	Method + Site Type + Temperature + Soil + Cars	0.73	0.065
5	Method + Site Type + Temperature + Soil Type + Start Time	1.13	0.053
6	Method + Site Type + Temperature + Soil Type + Moon Percentage + Start Time	1.25	0.050

7	Method + Site Type + Temperature + Soil Type + Moon Percentage + Cars	1.30	0.048
8	Method + Site Type + Temperature	1.43	0.045
9	Method + Site Type + Temperature + Soil Type + Transect Length	1.46	0.045
10	Method + Site Type + Temperature + Soil Type + Moon Percentage + Fog	1.64	0.041
11	Method + Site Type + Temperature + Cars	1.65	0.041
12	Method + Site Type + Temperature + Soil Type + Altitude	1.70	0.040
13	Method + Site Type + Temperature + Soil Type + Moon Percentage + Transect Length	1.70	0.040
14	Method + Site Type + Temperature + Soil Type + Vegetation Class	1.72	0.039
15	Method + Site Type + Temperature + Moon Percentage	1.72	0.039
16	Method + Site Type + Temperature + Soil Type + Tourists	1.80	0.038
17	Method + Site Type + Temperature + Soil Type + Moon Percentage + Tourists	1.85	0.037
18	Method + Site Type + Temperature + Soil Type + Moon Percentage + Altitude	1.87	0.036
19	Method + Site Type + Temperature + Soil Type + Fog	1.90	0.036
20	Method + Site Type + Temperature + Soil Type + Moon Percentage + Vegetation Class	1.92	0.036

Table 4 - *Summary of detectability model coefficients for the most parsimonious model (model 1) in Table 2. The intercept corresponds to a spotlight survey at an interior site on Maalan soil. Asterisks indicates statistical significance at 0.05 significance level.*

	Estimate	***Standard error***	***Z***	***p***	
Intercept	-3.6618	1.3999	-2.616	0.0089	*
Method = day	-2.5201	0.9129	-2.761	0.0058	*
Method = thermal	2.7018	0.9269	2.915	0.0036	*
Site type = edge	4.6133	1.4380	3.208	0.0013	*
Standardised temperature	0.5672	0.3778	1.501	0.1333	
Soil type = Barron	1.5384	1.4365	1.071	0.2842	
Soil type = Mixed	2.4569	1.4707	1.671	0.0948	
Soil type = Pin Gin	0.0479	0.7336	0.065	0.9479	

The estimated detectability values at interior sites were 0.025 (SE=0.034) for spotlight surveys, 0.277 (SE=0.231) for thermal surveys and 0.002 (SE=0.003) for day surveys. At edge sites, these values increased to 0.721 (SE=0.122) for spotlight, 0.975 (SE=0.025) for thermal and 0.172 (SE=0.103) for day surveys (Figure 3). All of these estimates are calculated for the average temperature value (18.6°C), and the most common soil type at our study sites (Maalan).

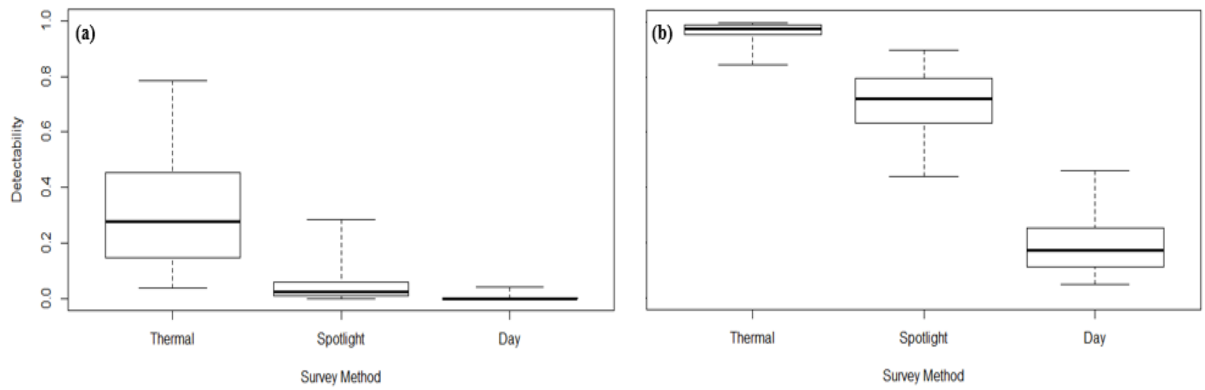

Figure 3 - *Predicted D. lumholtzi detectability for the three survey methods considered, according to the top ranking model in Table 3, for average temperature and sites on Maalan soil at (a) interior sites and (b) edge sites.*

Cost-effectiveness

Cost-effectiveness calculations suggest that, when equipment needs to be purchased, spotlight surveys would be the preferred method up to a budget of AU$13,078.29, above which thermal surveys allow the occupancy state of a greater number of sites to be defined with 95% confidence. Day surveys achieve 95% confidence at less than one site up to a budget of AU$797.34, at which point spotlight surveys can have achieved this at two sites, meaning that day surveys would not be recommended in any case (Figure 4).

When equipment is already available (i.e. no initial purchasing costs associated with any method) thermal surveys are clearly the most cost-effective technique, as expected given their higher detection probability. With only time costs, thermal surveys returned a cost of AU$133.67 to achieve 95% probability of detecting the species if present at a site, compared with AU$187.06 for spotlight surveys and AU$797.34 for day surveys (Figure 4).

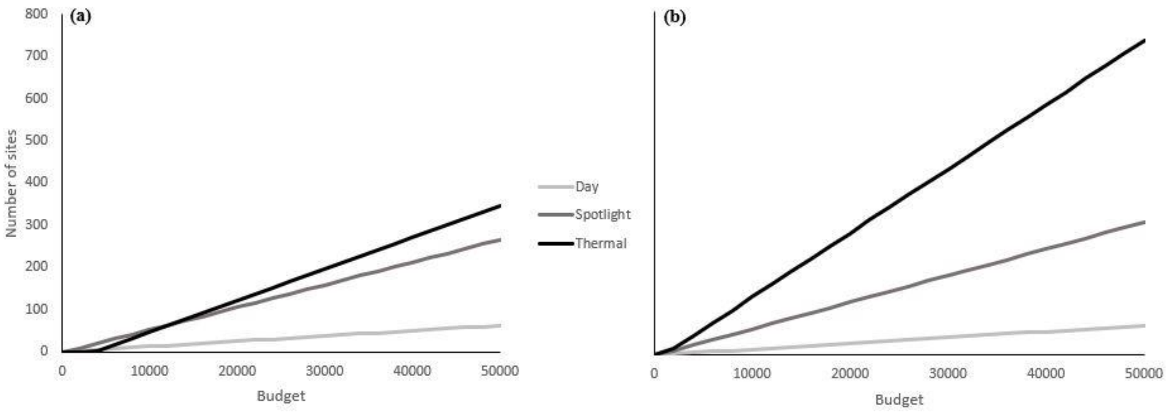

Figure 4 - *Expected number of sites at which D. lumholtzi occupancy could be determined with 95% confidence (false negative rate 5%) for the three survey methods considered, with increasing budget, where equipment purchase (a) is and (b) is not required.*

Discussion

Results from comparisons of survey methods suggest that thermal surveys are preferable to either daytime or spotlight surveys. The increased detection rates with the thermal scope may be due to a combination of factors. The thermal hotspot from a mammal is much more conspicuous than the eye-shine of *D. lumholtzi* when spotlighting, due to the contrast with the cooler surrounding environment. Furthermore, detecting eye-shine relies on the target animal facing the observer; thermal imaging does not have this limitation. Day surveys yielded very little success in detecting *D. lumholtzi*, without the benefit of either eye-shine or thermal imaging. This was expected, due to the species' tendency to be more active during dusk and night than during the day, and to occupy lower sections of the canopy at night (Newell 1999b; Martin 2005); daylight surveys are not routinely used as a method for monitoring of this species.

The improved detectability of *D. lumholtzi* with a thermal sensor is consistent with much of the literature relevant to terrestrial mammals (Focardi *et al.* 2001; Collier *et al.* 2005; Ditchkoff *et al.* 2005; Betke *et al*. 2008; Mills *et al*. 2011), though the detection of arboreal mammals has to date been less well documented This study comprehensively supports the use of thermal imaging for detecting *D. lumholtzi*, a cryptic, mid-sized arboreal mammal living in dense forest canopy, a result that is likely to be applicable to similar species in other parts of the world. Although there was no effect of observer experience on detectability in this study (likely due to at least one observer in each survey being classed as experienced), this is a potential issue in spotlight surveys that we believe will be mitigated by utilising thermal technology.

When interested only in detecting the presence of a species at a site, a survey can logically end as soon as the species is detected. Our results show that thermal imaging can decrease survey times in this situation, as a much greater number of animals were detected with this method. As many wildlife monitoring programs are focussed on identifying habitat where a species is present, thermal imaging may thus increase cost-efficiency by decreasing the time required to detect target species and, therefore, overall cost. On the flipside, this technology may increase survey time in some cases (e.g. habitats with a diverse mammal community) due to the need to positively identify animals with a spotlight after detection with the thermal scope. Familiarity with the study species and any other species in the area that may cause "false" detections can counteract this to an extent, as the size or shape of the thermal signature, along with how an animal moves or sits, can hint at the identity of the species. In this study, the species most likely to cause false positives was *T. v. johnstonii* as, of the non-target species detected, it is the closest in size to *D. lumholtzi*; given a clear view, most other non-target species were readily distinguishable from *D.lumholtzi* through the thermal scope due to a size discrepancy. However, even animals that appeared small through the thermal scope may have been a partially-obscured *D. lumholtzi*, hence the need for all thermal detections to be confirmed visually with a spotlight in this study.

The extra cost of thermal imaging compared to spotlights seems minor when considering the significantly greater detection rates, making thermal imaging a relatively efficient option for conducting region-wide surveys. With the purchase of equipment factored in, thermal imaging surveys will allow the occupancy status of *D. lumholtzi* to be determined at a greater number of sites than either day or spotlight surveys at any budget above AU$13,078.29. This result assumes a relatively arbitrary time cost of AU$30/hr of survey time, which may be an underestimate when access to more remote sites is required. By only taking the cost of one thermal scope into account, this comparison is limited to the case that only one observer is using the scope, so for multiple surveys to be carried out simultaneously there will be added cost. The costs of thermal imaging technology are likely to decrease over time however, further improving the cost-effectiveness of this method. Once a thermal imaging device has been purchased, this method will allow *D. lumholtzi* presence to be determined at more sites in subsequent surveys, making this technology a worthwhile investment.

It is not completely clear whether the observed increased detectability at edge sites reflects a preference of *D. lumholtzi* towards the edges of forest fragments, or whether animals at the edge of fragments are inherently easier to detect, because the line of sight to animals is less obscured by vegetation, and observers can move more freely to advantageous observing positions. Previous observations have reported the species to be a generalist folivore, unlikely to favour edges simply due to availability of particular food species (Newell, 1999b; Martin, 2005). Home range estimates of *D. lumholtzi* based on radio telemetry demonstrated that on over 90% of occasions, tagged individuals were not visible by spotlighting along forest edges (Newell 1999b), indicating that we observed a detection effect, rather than a preference for edges.

The effect of temperature was not considered statistically significant, but did improve the AIC value (without temperature, ΔAIC = 14.08 compared to the AIC-best model). The estimated increase associated with temperature may be behavioural, with anecdotal accounts of individuals often found lower in the canopy when temperatures are high (R. Martin, pers.

comm.). Similarly, including soil type improved the AIC value slightly (without soil type, ΔAIC = 1.43 compared to the AIC-best model) but did not return a statistically-significant effect on *D. lumholtzi* detectability. The effect of soil type may be clearer if a wider environmental range is surveyed.

Due to the homogeneity of our study sites in terms of vegetation type, soil type, altitude and base layer, we may be missing an influence of these factors on detectability. It is reasonable to expect that detectability would increase in more open vegetation as long as abundance remained constant. With surveys covering a greater environmental range other covariates may have shown to be important, based on studies showing increased *D. lumholtzi* abundances 600m in altitude and in habitat on basalts (Kanowski *et al.* 2001). To better understand the role of vegetation type and density on detectability, future surveys should be undertaken across a wider region than reported here.

The limited time period in each year that data was collected means that any potential seasonal variation will not be accounted for. Heise-Pavlov and Gillanders (2016) reported higher than expected sightings in dry season months and lower than expected in the wet season, although the reasons behind these differences are unclear, as data is based on reported sightings from members of the public. In northern Queensland, temperatures are generally lower in the dry season, and *D. lumholtzi* may simply be more likely to move between patches during daylight hours in lower temperatures, increasing their likelihood of being seen. Detectability differences may also be driven by resource changes, encouraging movement of individuals, or alternatively simply the result of people spending more time outdoors in dry weather than wet. (Heise-Pavlov and Gillanders 2016). Foliar nutrient concentrations can vary between seasons, and this may lead *D. lumholtzi* to move in search of high-quality food more frequently when there are less suitable food sources within their home range (Townsend *et al.* 2007; Heise-Pavlov and Gillanders 2016). This could increase detectability of individuals in dry periods, although when quality of resources decreases, the carrying capacity of *D. lumholtzi* may decrease and it is possible that the population fluctuates between season. Systematic surveys in both wet and dry seasons will assist in identifying any seasonal differences in *D. lumholtzi* occupancy or detectability.

Weather was another potential limitation, with some surveys being delayed or abandoned due to both rain and fog. Despite surveys being scheduled for the dry season in both study years, rain was the most prevalent limiting factor to the completion of surveys. Surveys were not carried out when rain was heavy enough that maintaining a view into the canopy was difficult or tracks became unsafe to walk on. There were also occasions when extremely thick fog meant that surveys were abandoned. Where fog was present but not so extreme to prevent detection of animals, surveys were carried out and the presence of fog noted. Fog showed no significant impact on detectability and would not be expected to be an issue in future surveys unless carried out in extreme fog, as the impact on detection is likely to follow a gradient. This study could not assess any effect of rain on detectability of *D. lumholtzi*, because of the small number of surveys performed under light rain, but some impact would be expected due to sub-optimal survey conditions.

Detectability estimates can be used to predict the likelihood of species presence at sites where the species hasn’t been surveyed (conditional on presence; Mackenzie *et al*. 2002) and, if applied in a systematic regional monitoring effort, can provide a clearer picture of the total *D. lumholtzi* distribution and detect any changes in that distribution through time.

Our results hold relevance to other large-bodied arboreal marsupials such as *D. bennettianus* (Bennett’s tree-kangaroo), which is typically monitored using spotlighting (Newell 1999a). *D. bennettianus* individuals have significantly larger home ranges than *D. lumholtzi*, another factor that would encourage the use of any method to increase detectability (R. Martin, pers. comm.). For some species and circumstances, it may be desirable to compare the effectiveness of this technology to indirect methods such as camera trapping. Camera traps have advantages over traditional methods for monitoring a range of species, although their application for arboreal species is relatively new (Harley *et al.* 2014; Whitworth *et al.* 2016). This method is ideally used when cameras can be positioned in an area that is central to the range of a target species or close to a resource that most indivuduals must use (e.g. watering point), or if baits can be used (Harley *et al.* 2014; Whitworth *et al.* 2016). However, for a wide-ranging canopy folivore such as tree-kangaroos, this seems unlikely to be an economical method of monitoring. Knowledge of the species' ecology and the strengths of various survey techniques may guide researchers as to whether to compare thermal imaging to other methods or potentially utilise it for monitoring surveys without requiring further assessment. In this study we show how such comparisons can be conducted and the potential insights gained through doing so, illustrating clear advantages of a novel survey technique.

Conflicts of interest

The authors declare no conflicts of interest

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