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Original Research Article

Influence of body mass, sociality, and movement behavior on improved detection probabilities when using a second camera trap

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A B S T R A C T

Maximizing detection probability is a common goal for occupancy studies using camera traps for data collection. Placing additional cameras at a survey station may improve precision of occupancy and detection estimates. However, these benefits are situational and potentially influenced by species' physical characteristics and behavior. We estimated null occupancy and detection probabilities for 20 mammalian species with >10 detections at multiple sites from one- and two-camera data sets from 63 stations set in a commercial forest reserve in Sabah, Malaysian Borneo during October–December 2015. We used a cross-validated absolute shrinkage and selection operator approach to model the effects of species' body mass, social behavior, dietary niche, and foot posture on detection probability using one- and two-camera designs. The number of species detections, sites where species were detected, detection probability estimates, and precision of model parameter estimates for all species improved using two cameras. Our results showed that unguligrade species were associated with both high detection probability estimates with one camera and also the greatest improvements using the two-camera design in detection probability compared to all other species. Greater improvements in precision of model parameter estimates from two-camera designs were observed in species detected less frequently. Our data suggests that camera designs need to be adapted based on the focal species and we suggest that future occupancy studies collect preliminary information to maximize effectiveness of camera effort and ensure that data collection is efficient and meets project needs.

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1. Introduction

Understanding species distributions and habitat use are necessary for effective conservation and management (Kanagaraj et al., 2013). Modeling species distributions can predict areas where species may occur and help identify areas with potential for human-wildlife conflict (e.g. Kanagaraj et al., 2011; Ngoprasert et al., 2011). Distribution models are based on occurrence data, but many wildlife species are rare and elusive, making studies employing direct observation difficult (Mathai et al., 2010; Sunarto et al., 2013). Consequently, many studies have based their findings on indirect surveys for scat and tracks (Smith et al., 2005; Mortelliti and Boitani, 2008). Specifically, camera traps have emerged as a common tool for collecting reliable data on elusive species without the need for direct observation (Cutler and Swann, 1999; Sunarto et al., 2013).

Camera traps are useful for collecting species records across large areas for longer periods of time with less effort compared to traditional survey methods (O'Connell et al., 2011; Meek and Fleming, 2014; Rovero and Zimmerman, 2016). One issue with cameras is that they represent a highly directional and point-based sampling method; even species in the immediate vicinity of cameras will not be detected if they do not pass the camera's sensor field. This causes false-negative errors which can result in incorrect conclusions about species occurrence and habitat associations (Tyre et al., 2003). Deploying additional cameras at a sampling station can increase the number of species detected, number of sites where a species is detected, improve detection probability, and reveal habitat associations that would otherwise be missed with fewer detectors (Pease et al., 2016; O'Connor et al., 2017). Adding a second camera, however, increases equipment cost, or reduces the number of locations that can be sampled. Moreover, the effectiveness of an additional detector may vary depending on species physical characteristics and behaviors.

A positive association has been observed between species detection and body size (Lyra-Jorge et al., 2008; Tobler et al., 2008; Burton et al., 2015). Also, sociality may influence species detectability, with social species that travel or forage in groups more likely to be detected (Treves et al., 2010). Movement speed can affect detectability (Rowcliffe et al., 2011), where animals that move quickly past a camera's detection zone are less likely to be detected (Burton et al., 2015). Deploying an additional camera at sample sites may therefore be particularly useful for smaller-bodied, solitary, and faster-moving species.

We evaluated species characteristics that may influence detection probability estimates derived from one- or two-camera based occupancy models, using empirical data from a survey in Sabah, Malaysian Borneo. Given our working hypothesis that animal detections are influenced by physical characteristics and behavior, we assessed the effect of species body mass, social behavior, dietary niche, and foot posture (the latter 2 characteristics as indices of movement behavior and potential speed). We predicted that 1) larger bodied, social, and slower moving species would have high detection probability with one camera, 2) detection probability would be higher for species exhibiting multiple of these traits, and 3) detection probability for species with high one-camera detection rates would benefit less from a second camera (i.e., they would have a lower difference in detection probability between 2- and 1-camera designs). Understanding the effects of species physical characteristics and behavior associated with detection probability can aid in optimizing effort allocation in future camera surveys.

2. Methods

2.1. Study area

We conducted our survey in Deramakot Forest Reserve (DFR) located in the lowlands of central Sabah, Malaysian Borneo. Since 1995, DFR (550 km^2) has experienced reduced-impact logging strategies whereby placement of logging roads and skid trails and harvesting methods are designed to reduce forest disturbance. In 1997, it received certification from the Forest Stewardship Council, 1996 (Lagan et al., 2007). Currently, DFR is managed by the Sabah Forestry Department and is designated as Class II Production Forests (primarily intended for commercial timber production) under the Sabah Forest Enactment (Forest Enactment, 1968; Kitayama, 2013). Mean annual rainfall during 2008–2010 was about 309 cm and was evenly distributed throughout the year (Kitayama, 2013). The mean annual temperature of DFR is 27.0 °C, with a mean daily temperature of 25.2 °C (mean daily minimum of 19.8 °C and mean daily maximum of 35.5 °C).

2.2. Camera survey

We surveyed the terrestrial mammal community within DFR during October–December 2015, establishing 63 stations in a grid with 2.2-km spacing (Fig. 1). At each station, we set two infrared motion detection cameras about 5 m apart (Reconyx PC850 Hyperfire Whiteflash LED, Reconyx, Wisconsin, USA) and 30–45 cm above ground, each oriented towards either different sections of the same or two separate logging roads or animal trails. We programed cameras to take 3 consecutive images during each detection, with camera options set to “no delay” between detections. We cleared vegetation to reduce false triggering of cameras. We checked cameras after 30 days to download images and replace batteries, then retrieved cameras after ≥60 days of operation.

2.3. Data preparation

We identified mammals in images to species, with muntjacs (Bornean yellow muntjac (*Muntiacus antherodes*) or red muntjac (*M. muntjac*)), mongooses (collared mongoose (*Herpestes semitorquatus*) or short-tailed mongoose (*H. brachyurus*)),

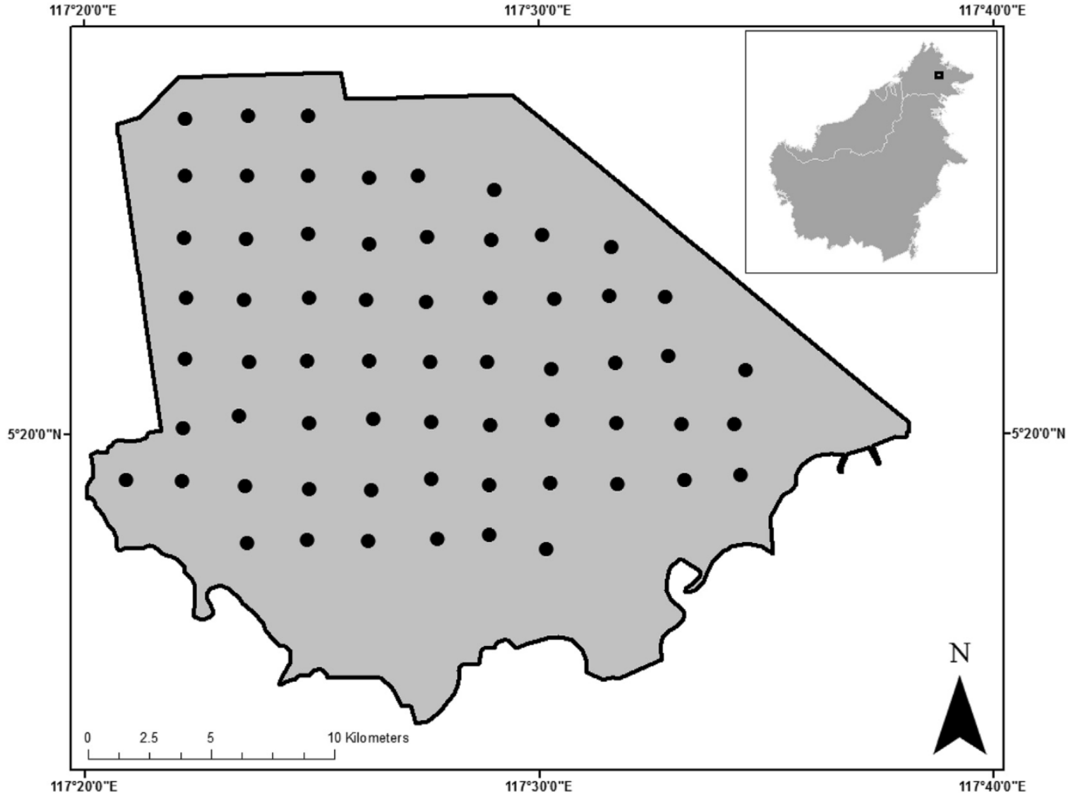

Fig. 1. Location of Deramakot Forest Reserve, central Sabah, Malaysian Borneo (black square: inset). Black dots represent 63 camera-stations surveyed during October–December 2015.

and mousedeer (greater mousedeer (*Tragulus napu*) or lesser mousedeer (*T. kanchil*)) identified only to genus due to similarities in body mass, sociality, dietary niche, and foot posture between sister species. We used the package "camtrapR" version 0.99.5 (Niedballa et al., 2016) in program R version 3.2.2 (R Core Team 2015) to organize and build a record database from all cameras. We recorded the percent of independent detections (>30 min apart) that were recorded on both cameras at a station (±standard deviation, SD). For each mammalian species or pair with >10 detections at multiple stations, we conducted a literature search to determine average body mass, sociality (social or solitary), dietary niche (herbivore, omnivore, or carnivore), and foot posture (plantigrade, digitigrade, or unguligrade; Table 1). We considered dietary niche as an indicator for how a species moves while foraging and passing camera detection zones. Particularly, all species which primarily consume motile prey were considered carnivorous. We used foot posture classification as an alternate indicator for the manner and potential speed at which a species moves.

2.4. Occupancy modeling

Since the number of detections varied among cameras within a station, we bootstrapped the random selection of a single camera from each station for 150 iterations to generate datasets based on a one-camera design. For each iteration, we used the package "camptrapR" (Niedballa et al., 2016) to generate detection/non-detection matrices for each mammal species with more than 10 detections across all stations. We considered 5 days as a sample occasion and used only full 5-day occasions in detection matrices. We implemented single-species, single-season occupancy models (MacKenzie et al., 2006) in program R using the package "unmarked" version 0.11–0 (Fiske and Chandler, 2011). We estimated the null (i.e., no covariates) occupancy and detection probabilities for each species in each iteration. Due to sparse single-camera data sets, models did not always converge. Therefore, from these 150 iterations, we took the first 50 models which converged and extracted standard errors and confidence intervals for both occupancy and detection probability estimates across iterations. For each parameter estimate, we also calculated the coefficient of variation (CV, standard error divided by estimate) to represent precision of estimates. We then calculated the average occupancy and detection probability (±SD) and average CV (±SD) for estimates across all species from the subset of 50 model iterations. Using the full record database, which included all records taken by both cameras at each station, we estimated null occupancy and detection probability for each mammalian species with >10 detections and calculated a CV for these parameters.

Table 1
Characteristics for 20 mammalian species with >10 detections during a camera-trap survey conducted between October–December 2015 in Deramakot Forest Reserve, Sabah, Malaysian Borneo.

Foot posture	Species common name	Species scientific name	Body mass (kg)	Social behavior	Dietary niche	References
Digitigrade	Asian elephant	*Elephus maximus*	3000.0	Social	Herbivore	Payne and Francis (1985), Shil et al., (2013)
	Sunda clouded leopard	*Neofelis diardi*	20.0	Solitary	Carnivore	Payne and Francis (1985), Kimura, 1996, Gordon and Stewart (2007), Hearn et al., (2016)
	Sunda pangolin	*Manis javanica*	7.0	Solitary	Carnivore	Payne and Francis (1985), Nowak (1999)
	Malay civet	*Viverra tangalunga*	5.0	Solitary	Omnivore	Medway (1983), Payne and Francis (1985), Taylor (1988), Ross et al., (2016b)
	Mongoose	*Herpestes sp.*	2.6	Solitary	Carnivore	Taylor (1970), Payne and Francis (1985), Taylor (1988), Jennings et al., (2010)
	Leopard cat	*Prionailurus bengalensis*	2.1	Solitary	Carnivore	Payne and Francis (1985), Rabinowitz (1990), Kimura, 1996, Mohamed et al., 2016
Plantigrade	Bornean orangutan	*Pongo pygmaeus*	67.5	Solitary	Omnivore	Payne and Francis (1985), Kimura, 1996
	Sun bear	*Helarctos malayanus*	55.5	Solitary	Omnivore	Payne and Francis (1985), Kimura, 1996, Normua et al. 2004, Servheen et al., 1998
	Malayan porcupine	*Hystrix brachyura*	8.5	Solitary	Herbivore	van Weers, 1979, Payne and Francis (1985), Nowak (1999)
	Pig-tailed macaque	*Macaca nemestrina*	6.5	Social	Omnivore	Payne and Francis (1985), Kimura, 1996
	Thick-spined porcupine	*Hystrix crassispinis*	4.6	Solitary	Herbivore	Payne and Francis (1985), Nowak (1999)
	Banded civet	*Hemigalus derbyanus*	2.3	Solitary	Omnivore	Payne and Francis (1985), Taylor (1988), Jennings et al., 2013, Ross et al., 2016a
	Sunda stink-badger	*Mydaus javanensis*	1.7	Solitary	Omnivore	Payne and Francis (1985), Hwang and Lariviere, 2003, Samejima et al., (2016)
	Long-tailed porcupine	*Trichys fasciculata*	1.7	Solitary	Herbivore	Payne and Francis (1985), Kimura, 1996, Nowak (1999)
	Moonrat	*Echinosorex gymmura*	1.0	Solitary	Carnivore	Payne and Francis (1985), Nowak (1999), Dunn and Rasmussen (2009)
Unguligrade	Banteng	*Bos javanicus*	500.0	Social	Herbivore	Payne and Francis (1985), Kimura, 1996, Hedges and Meijaard (1999)
	Sambar deer	*Rusa unicolor*	115.0	Solitary	Herbivore	Payne and Francis (1985), Kimura, 1996, Heydon and Arberdeen, 1994
	Bearded pig	*Sus barbatus*	70.0	Social	Omnivore	Payne and Francis (1985), Kimura, 1996, Oliver (1993)
	Muntjac	*Muntiacus sp.*	15.6	Solitary	Herbivore	Payne and Francis (1985), Kimura, 1996
	Mousedeer	*Tragulus sp.*	3.2	Solitary	Herbivore	Payne and Francis (1985), Kimura, 1996

To evaluate the effect of using a single-camera design, we compared parameter CVs between one-camera and two-camera detection estimates for each species. We also calculated the confidence interval (CI) coverage, which is the proportion of 95% CIs for estimates of detection probability from the one-camera design which included the corresponding two-camera estimate for each species.

2.5. Influence of species traits

We fitted linear models describing the influence of body mass, social behavior, dietary niche, foot posture, and two-way interactions between each of these traits on detection probability for each species. To avoid model overfitting and improve interpretability, we used the least absolute shrinkage and selection operator (LASSO), a regularization technique which penalizes the magnitude of coefficients through a tuning parameter λ (Tibshirani, 1996). We performed logit transformation of the detection probability response variable before implementing LASSO regression in program R using the package “glmnet” version 2.0–10 (Friedman et al., 2010). We performed 5-fold cross validation (due to sample size, default 10-fold cross validation was not appropriate for our data; Kohavi, 1995) to determine the optimal value of λ and assessed the resulting model coefficient values. We replicated this process with the difference between two-camera and one-camera detection estimates for each species as the response variable. Difference in detection values were cube root transformed (transformation method accounting for both positive and negative values) to fit normal distribution assumptions for linear modeling. We assessed resulting model coefficients for traits associated with an increase in detection probability.

3. Results

We collected 4198 records of 35 mammal species over 4390 trap nights. An average of 18.82% of detections (±10.34%) occurred on both cameras across all stations. We collected >10 detections for 20 species for which we compiled information on average body mass, sociality, dietary niche, and foot posture (Table 1). Of these 20 species, sambar deer (*Rusa unicolor*), muntjac, mousedeer, bearded pig (*Sus barbatus*), pig-tailed macaque (*Macaca nemestrina*), and Malay civet (*Viverra *tangalunga*) were detected frequently with at least an average of 110 detections from a single camera. Total number of detections for each species (with >10 detections) in the two-camera design was about twice the average number of records from individual cameras (Table 2). Species were recorded on average at 7.0 (±3.6) more stations in the two-camera design.

Estimates of occupancy probability increased from a one-camera to two-camera design by 1.3–28.8% (with an average increase of 11.5% ± 8.1%) across all species excluding Asian elephant (*Elephas maximus*) and Sunda pangolin (*Manis javanica*) where the occupancy probability estimate decreased by 0.2% and 18.3% respectively. Coefficients of variation for occupancy probability estimates decreased from a one-camera to two-camera design by 1.12–21.88 (average decrease of 12.47 ± 9.22) for all species excluding Sunda pangolin where the CV increased by 1.55. Confidence interval coverage for occupancy probability estimates was <25% for three species: 0% for sambar deer and pig-tailed macaque, with both species having a 2-camera probability of occupancy estimate of 100%, and 10% for Malay civet. For all other species, CI coverage ranged from 46% to 100% (mean = 81% ± 16.9%).

Estimates of detection probability increased from the one-camera to the two-camera design by 0.1–19.2% across all species (Table 3), with an average increase of 5.2% (±5.1%). The CVs of two-camera detection probability estimates decreased by 1.3–29.7 for all species compared to one-camera estimates, with an average decrease of 23.1 (±8.3). Confidence interval coverage from one-camera detection probability estimates of the corresponding two-camera detection estimate was <25% for five species: 0% coverage for muntjac, mousedeer, and bearded pig; 16% coverage for sambar deer; and 8% coverage for Malay civet. For all other species, CI coverage ranged from 42 to 100% (mean = 81% ± 19.2%).

Only foot posture was influential on the single-camera detection probability. An unguligrade foot posture had a positive influence on detection probability ($\beta = 0.902$), while digitigrade and plantigrade foot postures had coefficients = 0. The cross-validated LASSO procedure suggested no other variables were associated with detection probability as all coefficient values were 0. Foot posture was also the single influential predictor for difference between 2-camera and 1-camera detection probabilities. An unguligrade foot posture had a positive influence on the difference in detection probability with $\beta = 0.128$. All other coefficient values were zero.

4. Discussion

Our results of null occupancy and detection estimates for 20 mammal species from one- and two-camera stations support previous suggestions that multiple cameras improve species detection probabilities (Pease et al., 2016, O'Connor et al., 2017). Addition of a second camera increased the number of detections and sites detected for all species as animals present at a sample site were likely missed less often. Increasing the number of cameras can therefore benefit camera studies where detection rates for species are low (e.g. Ahumada et al., 2011). Occupancy estimates generally increased along with precision of estimates; occupancy estimates for both sambar deer and pig-tailed macaque increased to 100% with two cameras likely due to the high proportion of presence in detection histories. For Asian elephant and Sunda pangolin, a decrease in occupancy probability from a one-camera to two-camera design could be attributed to the low detection probability in the one-camera dataset. With sparse data, detection probability is likely underestimated and occupancy probability overestimated. Additional

Table 2
Average number of records (±standard deviation [SD]) and sites (±SD) detected for 20 mammal species across 63 stations during a camera-trap survey conducted between October–December 2015 in Deramakot Forest Reserve, Sabah, Malaysian Borneo. Number of records and sites for one-camera were derived from 150 simulated record databases where a single random camera was selected from each survey station. Two-cameras included all records from both cameras at each station.

Species		One-camera		Two-cameras	
Common name	Scientific name	Records	Sites	Records	Sites
Asian elephant	*Elephus maximus*	16.8 ± 4.7	6.8 ± 1.4	37	11
Sunda clouded leopard	*Neofelis diardi*	17.7 ± 4.0	10.3 ± 2.0	36	19
Sunda pangolin	*Manis javanica*	5.9 ± 1.5	5.3 ± 1.3	12	9
Malay civet	*Viverra tangalunga*	**139.2 ± 14.2**	34.9 ± 2.2	277	46
Mongoose	*Herpestes sp.*	10.4 ± 3.5	6.5 ± 1.8	21	13
Leopard cat	*Prionailurus bengalensis*	15.2 ± 8.2	3.4 ± 1.2	26	6
Bornean orangutan	*Pongo pygmaeus*	17.5 ± 3.6	14.5 ± 2.7	35	27
Sun bear	*Helarctos malayanus*	**58.5 ± 9.9**	22.3 ± 2.2	116	33
Malayan porcupine	*Hystrix brachyura*	49.2 ± 10.6	16.7 ± 2.1	101	25
Pig-tailed macaque	*Macaca nemestrina*	**110.0 ± 11.2**	40.2 ± 2.9	223	54
Thick-spined porcupine	*Hystrix crassispinis*	20.3 ± 4.4	10.9 ± 1.6	41	16
Banded civet	*Hemigalus derbyanus*	17.1 ± 4.9	10.3 ± 2.2	35	20
Sunda stink-badger	*Mydaus javanensis*	16.9 ± 4.4	8.0 ± 1.9	34	15
Long-tailed porcupine	*Trichys fasciculata*	8.4 ± 1.5	6.4 ± 1.4	17	11
Moonrat	*Echinosorex gymmura*	31.7 ± 7.1	11.5 ± 1.6	65	17
Banteng	*Bos javanicus*	15.2 ± 4.0	4.9 ± 1.0	31	7
Sambar deer	*Rusa unicolor*	**215.7 ± 40.5**	42.8 ± 2.5	434	55
Bearded pig	*Sus barbatus*	**247.1 ± 21.1**	48.8 ± 1.8	496	55
Muntjac	*Muntiacus sp.*	**256.4 ± 28.7**	52.1 ± 1.5	519	56
Mousedeer	*Tragulus sp.*	**691.0 ± 42.6**	54.0 ± 1.1	1403	57

Table 3
Null occupancy and detection probability estimates and corresponding coefficient of variation (CV) values for 20 mammalian species detected across 63 stations during a camera-trap survey conducted between October–December 2015 in Deramakot Forest Reserve, Sabah, Malaysian Borneo. Two-camera estimates were derived from a record database with all species detections during the survey, while one-camera estimates represent mean values derived from a subset of 50 simulated database including only records from a single, randomly selected camera at each survey station. The difference in detection probability (ΔDet) and CV (ΔCV) were calculated by subtracting one-camera estimates from two-camera estimates. Species which were detected frequently (>50 detections from one camera) are in bold.

Species		One-Camera		Two-Cameras			
Common name	Scientific name	Occu	Det	Occu	Det	dDet	dCV
Asian elephant	*Elephus maximus*	0.229 (43.0)	0.076 (44.8)	0.227 (30.5)	0.101 (28.8)	0.026	−16.0
Sunda clouded leopard	*Neofelis diardi*	0.269 (39.3)	0.070 (40.4)	0.418 (22.7)	0.090 (23.5)	0.019	−16.9
Sunda pangolin	*Manis javanica*	0.571 (60.3)	0.019 (77.1)	0.388 (61.8)	0.033 (66.9)	0.014	−10.2
Malay civet	***Viverra tangalunga***	**0.568 (11.9)**	**0.193 (10.2)**	**0.744 (7.7)**	**0.256 (7.0)**	**0.064**	**−3.3**
Mongoose	*Herpestes sp.*	0.274 (48.6)	0.066 (51.9)	0.331 (32.3)	0.069 (34.1)	0.003	−17.8
Leopard cat	*Prionailurus bengalensis*	0.087 (57.9)	0.171 (41.2)	0.099 (39.0)	0.207 (22.1)	0.037	−19.1
Bornean orangutan	*Pongo pygmaeus*	0.787 (37.7)	0.027 (46.8)	1.000 (0.4)	0.038 (17.1)	0.011	−29.7
Sun bear	*Helarctos malayanus*	0.412 (18.0)	0.143 (16.2)	0.551 (12.1)	0.196 (10.2)	0.053	−6.0
Malayan porcupine	*Hystrix brachyura*	0.309 (23.0)	0.128 (20.3)	0.411 (16.3)	0.175 (13.0)	0.047	−7.3
Pig-tailed macaque	***Macaca nemestrina***	**0.711 (10.5)**	**0.144 (11.9)**	**1.000 (NA)**	**0.183 (7.2)**	**0.040**	**−4.8**
Thick-spined porcupine	*Hystrix crassispinis*	0.281 (37.4)	0.073 (39.0)	0.294 (22.6)	0.134 (19.7)	0.061	−19.3
Banded civet	*Hemigalus derbyanus*	0.394 (47.3)	0.052 (51.8)	0.512(25.4)	0.068 (28.5)	0.016	−23.4
Sunda stink-badger	*Mydaus javanensis*	0.164 (39.3)	0.102 (36.3)	0.295 (24.4)	0.113 (22.8)	0.012	−13.5
Long-tailed porcupine	*Trichys fasciculata*	0.283 (72.7)	0.038 (77.6)	0.412 (49.6)	0.039 (54.1)	0.001	−23.5
Moonrat	*Echinosorex gymmura*	0.202 (28.9)	0.148 (22.8)	0.286 (20.9)	0.191 (14.6)	0.043	−8.2
Banteng	*Bos javanicus*	0.091 (46.0)	0.141 (34.5)	0.117 (35.8)	0.201 (21.3)	0.060	−13.2
Sambar deer	***Rusa unicolor***	**0.734 (9.0)**	**0.178 (9.7)**	**1.000 (0.0)**	**0.231 (6.2)**	**0.053**	**−3.5**
Bearded pig	***Sus barbatus***	**0.786 (7.0)**	**0.246 (7.1)**	**0.858 (5.1)**	**0.389 (4.6)**	**0.143**	**−2.5**
Muntjac	***Muntiacus sp.***	**0.838 (6.0)**	**0.242 (6.9)**	**0.890 (4.5)**	**0.389 (4.5)**	**0.147**	**−2.4**
Mousedeer	***Tragulus sp.***	**0.854 (5.2)**	**0.477 (3.9)**	**0.905 (4.1)**	**0.668 (2.5)**	**0.192**	**−1.3**

detections or recaptures of both species in the two-camera dataset led to a higher estimates of detection probability, resulting in lower estimates of occupancy probability.

Precision of parameter estimates is important in avoiding misguided inference about habitat associations which can be used to determine further research and management decisions (Tyre et al., 2003). As investigating habitat associations is a primary question addressed by occupancy studies, additional sampling can reveal relationships otherwise missed with less effort (Pease et al., 2016). Lower coefficients of variation for parameter estimates in two-camera models demonstrated that deploying a second camera at a station can improve precision of parameter estimates (i.e. Mackenzie and Royle, 2005). However, our null-model parameter estimates showed relatively high (>25%) confidence interval coverage for many species, where the 95% confidence intervals of one-camera model estimates included the two-camera estimates. Occupancy probability estimates for sambar deer, pig-tailed macaque, and Malay civet had relatively low (<25%) confidence interval coverage, and detection probability estimates for muntjac, mousedeer, bearded pig, and Malay civet also had relatively low to no confidence interval coverage. This suggests that a second camera in occupancy studies can be beneficial for occupancy estimates and detectability of species, but it is not clear what determines the kind of species which would benefit most from a second camera.

We found that foot posture influenced one-camera detection probability and precision of parameter estimates. Unguligrade species had higher detection probabilities compared to digitigrade and plantigrade species. Though unguligrade species are capable of high speeds (Halfpenny and Biesiot, 1986) and faster moving species are less likely to be detected (Rowcliffe et al., 2011), unguligrade species are potentially slower moving due to foraging and vigilance behaviors (e.g. Little et al., 2014, 2016). Contrasting with initial predictions, when data from a second camera was incorporated, unguligrade species were also associated with higher differences in detection probability between one- and two-camera designs compared to all other species. Our results suggest that though one camera is likely sufficient for detecting ungulates, an additional camera at sites would further increase their detectability. Improving detectability and precision of parameter estimates for ungulates are important because they are often the primary target for hunters and therefore susceptible to over-exploitation (Brodie et al. 2015; Hoffman et al., 2015).

Though sociality was suggested to increase detectability of species (Treves et al., 2010), we did not find associations between social behavior and single-camera detection probability or differences in detection probability estimates. Our results suggest that detection probability for social and solitary species are equally variable, and the improvement in detectability for social species was lower than improvements associated with foot posture. Also, we did not find any effect of species' dietary niche on detection probability estimates. Previous studies have highlighted that carnivores have higher detectability due to a tendency toward traveling and foraging along well-defined trails and roads in contrast to the movement and foraging strategies of omnivores and browsing ungulates (Rowcliffe et al., 2011; Cusack et al., 2015). Though we did not investigate the specific influence of camera placement along animal trails and logging roads on detection probability, our results showed that both detection probability estimates with one camera and improvements in detection between one and two cameras were equally variable across carnivores, omnivores, and herbivores. Social behavior and dietary niche did not have strong associations with detection probability when one camera was used and likely are not associated with improvements in detection probability with a second camera.

Beyond our analysis of ecological traits, we observed higher improvements in detection probability with a second camera for species which were detected frequently (>50 detections from one camera), though changes in precision of parameter estimates based on CVs were low (Fig. 2). Conversely, species that were detected less frequently (<50 detection using one camera) had greater improvements in precision of parameter estimates with the two-camera design but smaller changes in detection probability. An increase in precision of parameter estimates for less frequently detected species is likely due to an increase in the number of sites detected while detection probability is less improved with the few additional detections from two cameras. The increase in detection probability for frequently detected species is due to the larger number of additional detections from a second camera, while the number of sites detected from one camera is already sufficient for precise parameter estimates. Therefore, our results provide further support for suggestions that increasing the number of cameras at a station to improve detection and precision of parameter estimates is situational and species-dependent (Pease et al., 2016; O'Connor et al., 2017). For occupancy studies where the modeling process accounts for imperfect detection, a second camera may only benefit species that are detected less frequently by improving precision of parameter estimates.

Investing in a second camera at a sample station may sometimes be beneficial, but incurs additional costs and reduces the survey area (Mackenzie and Royle, 2005). As an alternative to surveying a larger area with a 1-camera design, budget- and equipment-limited projects could consider relocating or rotating paired-camera stations during the course of a survey to increase spatial coverage while maximizing detection probability. Though our study and previous work (Mackenzie and Royle, 2005; Pease et al., 2016; O'Connor et al., 2017) have suggested that additional camera effort produces additional detections, increases the number of sites where species are detected, and improves detection probability, we stress that the magnitude of these effects is influenced by species behavior. A two-camera study design benefits the detectability of unguligrade species, whereas one camera may be sufficient for the detection of all other non-ungulate species. Additionally, a second camera may only benefit less frequently detected species by improving precision of model estimates. We advise that occupancy studies first conduct a pilot study to gather preliminary information on species detection rates, to improve study efficiency and help ensure that reliable information is obtained to meet project objectives.

Declaration of interests

All authors have participated in the conception and design, or analysis and interpretation of the data; drafting the article or revising it critically for important intellectual content; and approval of the final version.

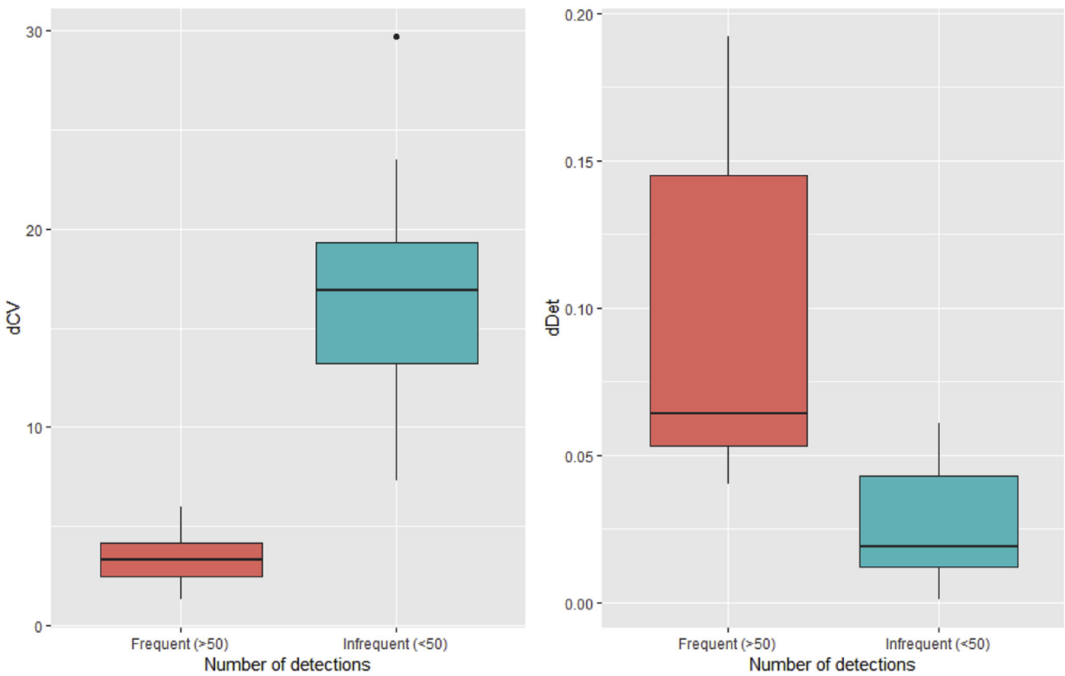

Fig. 2. Distribution of the difference in coefficients of variation (dCV) and difference in detection probability estimates (dDet) for frequently detected species (>50 detections, red) and infrequently detected species (<50 detections, blue) with the inclusion of a second camera. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. The authors have no affiliation with any organization with a direct or indirect financial interest in the subject matter discussed in the manuscript.

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