Monitoring the ungulate prey of the Komodo dragon Varanus komodoensis: distance sampling or faecal counts?

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Monitoring the abundances of prey is important for informing the management of threatened and endangered predators. We evaluated the usefulness of faecal counts and distance sampling for monitoring the abundances of rusa deer *Rusa timorensis*, feral pig *Sus scrofa* and water buffalo *Bubalus bubalis*, the three key prey of the Komodo dragon *Varanus komodoensis*, at 11 sites on five islands in and around Komodo National Park, eastern Indonesia. We used species-specific global detection functions and cluster sizes (i.e. multiple covariates distance sampling) to estimate densities of rusa deer and feral pig, but there were too few observations to estimate densities of water buffalo. Rusa deer densities varied from from 2.5 to 165.5 deer/km^2 with coefficients of variation (CVs) of 15-105%. Feral pig densities varied from 0.0 to 25.2 pigs/km^2 with CVs of 25-106%. There was a positive relationship between estimated faecal densities and estimated population densities for both rusa deer and feral pig: the form of the relationship was non-linear for rusa deer, but there was similar support for linear and non-linear relationships for feral pig. We found that faecal counts were more useful when ungulate densities were too low to estimate densities with distance sampling. Faecal count methods were also easier for field staff to conduct than distance sampling. Because spatial and temporal variation in ungulate density is likely to influence the population dynamics of the Komodo dragon, we recommend that annual monitoring of ungulates in and around Komodo National Park be undertaken using distance sampling and faecal counts. The relationships reported here will also be useful for managers establishing monitoring programmes for feral pig, rusa deer and water buffalo elsewhere in their native and exotic ranges.

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Spatial and temporal variation in the abundances of primary prey can have major demographic effects on predators (Dale et al. 1994, O'Donoghue et al. 1997, Ramakrishnan et al. 1999, Karanth et al. 2004). Large declines in prey abundances may reduce the viability of endangered predator populations (Karanth & Stith 1999), and predators on islands may be especially vulnerable to declines in prey abundances (Frankham 1998). A key feature of many predator-prey systems is the large prey base required to sustain the predator (Karanth et al. 2002a, 2004). Hence, apex predators typically occur at low densities, making robust inference about changes in the abundance of the predator difficult because of the impracticality of obtaining even modest sample sizes. In such systems, monitoring prey abundances may be

particularly useful for providing an early warning of changes in predator populations (Karanth et al. 2002b, Lovari et al. 2009).

The Komodo dragon *Varanus komodoensis* is the world's largest lizard. Adult male dragons can reach 3 m in length and weigh up to 87 kg (Jessop et al. 2006). Currently, the Komodo dragon is listed in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and is classified by the International Union for the Conservation of Nature (IUCN) as 'vulnerable' due to its demographic decline and limited distribution (World Conservation Monitoring Centre 1996, CITES 2011). The Komodo dragon is endemic to five small islands in eastern Indonesia, with four island populations in Komodo National Park (KNP) and several fragmented populations on Flores (Ciofi & De Boer 2004). The Komodo dragon is an apex predator, with three ungulate species dominating the diet of adults: rusa deer *Rusa timorensis*, feral pig *Sus scrofa* and water buffalo *Bubalus bubalis* (Auffenberg 1981, Jessop et al. 2006; Fig. 1). Previous work has shown the distributions and abundances of these three species to be important determinants of the demography of Komodo dragon populations (Jessop et al. 2006; but see Laver et al. 2012).

Anthropogenic threats such as habitat loss (from illegal logging and agriculture) and illegal hunting could reduce the densities of ungulates (Groom 2006, Steinmetz et al. 2010), and hence Komodo dragon populations, inside and outside KNP (Ciofi et al. 2007). For example, a reduction in the density of deer caused by illegal hunting was considered the major cause of the extinction of the Komodo dragon on the island of Padar within KNP during the early 1980s (Ciofi & De Boer 2004). Regular patrols by rangers since 2000 are thought to have reduced illegal hunting of deer and feral pigs within KNP. However, outside KNP, especially on the island of Flores, illegal hunting of deer still occurs and may be affecting the local distribution and abundance of the Komodo dragon (Ciofi & De Boer 2004). Despite these concerns, no attempt has been made to implement monitoring of the distribution and abundance of the ungulate prey species of the Komodo dragon.

A wide variety of methods have been used to estimate the abundance of ungulates (reviews in Thompson et al. 1998, Mayle et al. 1999). Faecal counts are a commonly used indirect sampling method for estimating the relative abundance of ungulates, particularly in wooded habitats where animals are difficult to observe directly (Mayle et al. 1999). The faecal count method is a relatively inexpensive method that is easy for park rangers to use and can be implemented in a wide range of habitats (Forsyth et al. 2003, Månsson et al. 2011). However, as for any index of animal abundance, it is desirable that the relationship between faecal density and animal density be validated for the species and area of interest: the relationship should be positive and linear (e.g. Forsyth et al. 2007). Distance sampling is a direct sampling method used to estimate the abundance of animals (Buckland et al. 2001, Thomas et al. 2010). Distance sampling can

Figure 1. Komodo dragon killing an adult male rusa deer, Komodo National Park, Indonesia (Photo: Aganto Seno).

provide robust estimates of abundance at less cost than methods based on mark-recapture (Buckland et al. 2001, Wingard et al. 2011). Density is estimated using the perpendicular distances to detected animals from line transects (Thomas et al. 2010).

Our study had two aims. First, to estimate the densities of rusa deer, feral pigs and water buffalo using faecal counts and distance sampling at 11 sites in and around KNP. Second, to evaluate the relationship between faecal densities and ungulate densities at the 11 sites.

Material and methods

Study area

Our study was conducted at 11 sites on five islands; four islands in KNP and the Wae Wuul Nature Reserve (WW) on Flores (Fig. 2). KNP and WW have highly seasonal climates dominated by long dry seasons (April-November) and short wet seasons (December-March). The annual rainfall is < 1,000 mm (Auffenberg 1981, Ciofi et al. 2007).

KNP (1,817 km^2; 603 km^2 land and 1,214 km^2 sea) consists of the two large islands of Komodo and Rinca (311.5 km^2 and 204.8 km^2, respectively) and three smaller islands (Padar covering 14.1 km^2, Gili Motang 9.5 km^2 and Nusa Kode 7.3 km^2). There are four main habitat types in KNP (Auffenberg 1981, Monk et al. 1997). Tropical monsoon forest dominates the landscape above 500-700 m a.s.l. and deciduous monsoon forest (primarily tamarind

Tamarindus indica) occurs in valley floors and along water courses. Savanna woodland and savanna grassland dominate the drier areas.

Of our 11 study sites, 10 were on four islands within KNP; Komodo island sites: 1) Loh Liang (K1), 2) Loh Lawi (K2), 3) Loh Sebita (K3) and 4) Loh Wau (K4); Rinca island sites: 5) Loh Buaya (R1), 6) Loh Baru (R2), 7) Loh Tongker (R3) and 8) Loh Dasami (R4); and the two small islands 9) Gili Motang (GM) and 10) Nusa Kode (NK). Hunting of ungulates is prohibited in KNP and park rangers regularly patrol these 10 areas selected as sites. For further details on these 10 sites, see Jessop et al. (2006). Site 11 was located in WW (14.84 km^2, 8°35'50''N, 119°50'05''E) on the west coast of Flores (13,540 km^2). The habitat in WW is mostly savanna woodland and savanna grassland, with patches of bamboo forest and deciduous monsoon forest along seasonally inundated water courses (Ciofi & De Boer 2004). WW is less well protected than KNP due to the absence of permanent rangers, and illegal harvesting of ungulates is thought to be common there (M. Bona, WW, pers. comm.).

Faecal counts

Faecal counts were conducted from July to November 2009 (i.e. in the late dry season) along 150-m transects. Between 20 and 48 transects were randomly positioned and orientated in each of the 11 study sites. A hand-held GPS unit (Garmin Summit, Kansas, USA) was used to locate the starting points of transects. A total of 350 transects were surveyed,

Figure 2. The 11 study sites located within Komodo National Park (KNP) and Wae Wuul Nature Reserve (WW). The KNP sites comprise four Komodo Island sites (K1 on Loh Liang, K2 on Loh Lawi, K3 on Loh Sebita, K4 on Loh Wau) and four Rinca Island sites (R1 on Loh Buaya, R2 on Loh Baru, R3 on Loh Tongker, R4 on Loh Dasami). Additionally, KNP sites were located on each of the two small islands of Nusa Kode (NK) and Gili Motang (GM). The single WW site was located on the island of Flores immediately east of KNP. Polygons denote the boundaries of KNP and WW, and the inset depicts field site location within Indonesia.
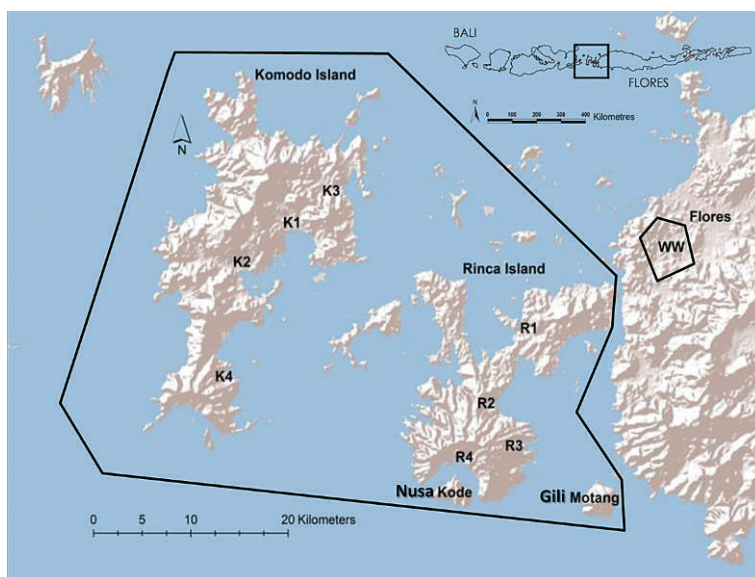
with a total length of 52.5 km. Preliminary observations indicated that leaf litter in deciduous monsoon forest and tall savanna grassland possibly hid some deer pellets. To minimise the possibility of pellets being missed by observers, we used 30 small plots ($3.14 m^2$) spaced at 5-m intervals along each transect (Jessop et al. 2006, Forsyth et al. 2007).

Each plot was thoroughly searched for faeces of rusa deer, feral pig and water buffalo, lifting grass and clearing leaf litter if present. Deer deposit numerous pellets in a single defecation ('pellet group') and the group may be spread over several metres: in these cases, the pellet group was counted if > 50% of its pellets lay inside the plot (Thompson et al. 1998). Faeces of feral pig and water buffalo were recorded as single defecations. The faeces of the three species were readily distinguished by size and morphology (Triggs 2005). Faecal counts were undertaken throughout the day in good light. No other wild or domestic ungulates were present in the 11 study sites except for feral horses *Equus caballus* at Loh Buaya.

For each species, the total number of faeces (pellet groups for deer) counted along each transect (which covered an area of $94.2 m^2$) was converted to an estimate of ungulate faecal density (UFD; faeces/ha). Mean faecal densities and their 95% confidence intervals (CI) were then estimated for each species-site combination using transect as the sampling unit (Forsyth et al. 2007).

Distance sampling

We conducted distance sampling surveys in the same months as the faecal counts. However, most distance surveys were conducted in the early morning (05:30-09:00) and late afternoon (16:00-18:30) when ungulates were most active, to increase the likelihood of sighting individuals of all three species (for deer, see Focardi et al. 2005; for feral pigs, see Choquenot et al. 1996 and for water buffalo, see Corbett 1995). Transects were located systematically in each of the 11 sites, with the distance between transects ≥ 500 m. The 111 transects were of variable length (0.5-6.15 km) and a total 163.65 km was surveyed.

The same observers (A. Ariefiandy and D. Purwandana) conducted all surveys. Observers first walked 13.5 km of transect together to standardise methodology. Thereafter, the two observers surveyed alternate transects at each site. Surveys were conducted at a slow walking speed of 2-3 km/hour. When one of the three ungulate species was observed, the radial distance from the observer to the animal(s) was estimated using a laser range finder (Bushnell Range Finder Elite 1500, Bushnell Corporation, Overland Park, Kansas, USA) and the bearing to the animal(s) determined with an electronic compass (Garmin Summit, Kansas, USA). The number of animals in the group ('cluster size') was also recorded. Perpendicular distances were calculated from the radial distances and sighting angles by trigonometry (Buckland et al. 2001).

We analysed data using the program DISTANCE 6.0 release 2 (Thomas et al. 2009; available at: http://www.ruwpa.st-and.ac.uk/distance/). Buckland et al. (2001) recommend having at least 60 observations for robust estimation of density using distance sampling. Since there were far fewer than 60 observations of each ungulate species at most sites, we used multiple covariates distance sampling to estimate a global detection function and cluster size for each species: densities were then estimated for each site from the species-specific encounter rate (Marques et al. 2007, Thomas et al. 2009). Cluster size was estimated using the size-bias regression method (Buckland et al. 2001).

Our exploratory data analyses revealed that detection data for rusa deer and feral pigs had long tails, so the 5% of detections with the greatest distances were discarded for both species (Buckland et al. 2001, Thomas et al. 2009). There was also evidence of both species moving small distances away from the transect line prior to detection, so we left-truncated observations of rusa deer and feral pigs by 5 m (Buckland et al. 2001).

Following Thomas et al. (2010), we evaluated the following detection functions, g(y), for each species, where y is the perpendicular distance (m) of an observation from the transect. The half-normal key,

$$g(y) = \exp\left(-y^2/2\sigma^2\right),$$

was evaluated with cosine adjustments, and the hazard rate,

$$g(y) = 1 - \exp\left(-(y/\sigma)^{-b}\right),$$

with simple polynomial adjustments. Further details on these keys and adjustments are given in Buckland et al. (2001). Histograms, quantile-quantile plots and Cramér-von Mises tests were used in conjunction with our biological understanding of each species in our study area to assess the fit of the keys and adjustments. We sought a detection function with a good shoulder and used Akaike's Information Criterion corrected for small sample sizes (AIC_c) and

Akaike weights (w_i) to assess the relative support for each model (Burnham & Anderson 2002). Following Buckland et al. (2001) and Thomas et al. (2010), site-specific estimates of ungulate density (UD) are presented with their 95% CI and coefficient of variation (CV).

Relationships between faecal and ungulate population densities

Following Forsyth et al. (2007), we evaluated the relationship between faecal and ungulate densities with three models. We first considered the linear model,

$$UFD_i = a + b \, UD_i,$$

where a is the intercept and b is the slope of the relationship between the UFD and UD at site i. Because the relationship between ungulate faecal counts and density could be non-linear, we next considered the power model,

$$UFD_i = a(UD_i)^b.$$

We also considered another non-linear model, i.e. the logistic model,

$$UFD_i = \frac{a}{(1 + b\exp^{-cUD_i})}$$

Model parameters were estimated by non-linear least squares regression using the NLS2 package in program R 2.11.1 (Grothendieck 2010). The data used in the models were the mean faecal count and distance sampling estimates obtained at each of the 11 sites. Since non-linear least squares regression assumes that the variation in X (i.e. distance sampling estimates) is substantially less than the variation in Y (i.e. faecal count estimates), we evaluated the variation in these estimates for each ungulate species. Since there was no evidence of overdispersion in the data (evaluated by comparing the degrees of freedom to the residual deviance for each model; Crawley 2007), we again used AIC_c and w_i to assess the relative support for each model.

Results

Faecal counts

The mean time to conduct faecal counts along each 150-m transect was 8.5 minutes, with 49 hours required to complete all faecal counts. Mean deer pellet group densities varied greatly among sites (Fig. 3). Mean deer pellet group densities at sites on the

two large islands in KNP were higher than at the sites on the small islands of Gili Motang and Nusa Kode. Loh Wau (K4) in KNP had the highest mean ($\pm$ SE) pellet group density (3,319.2 $\pm$ 308.1 pellet group/ ha). The lowest mean deer pellet group density was at WW in Flores (141.5 $\pm$ 36.0 pellet group/ha). Precision (CV) of the deer pellet group estimates at
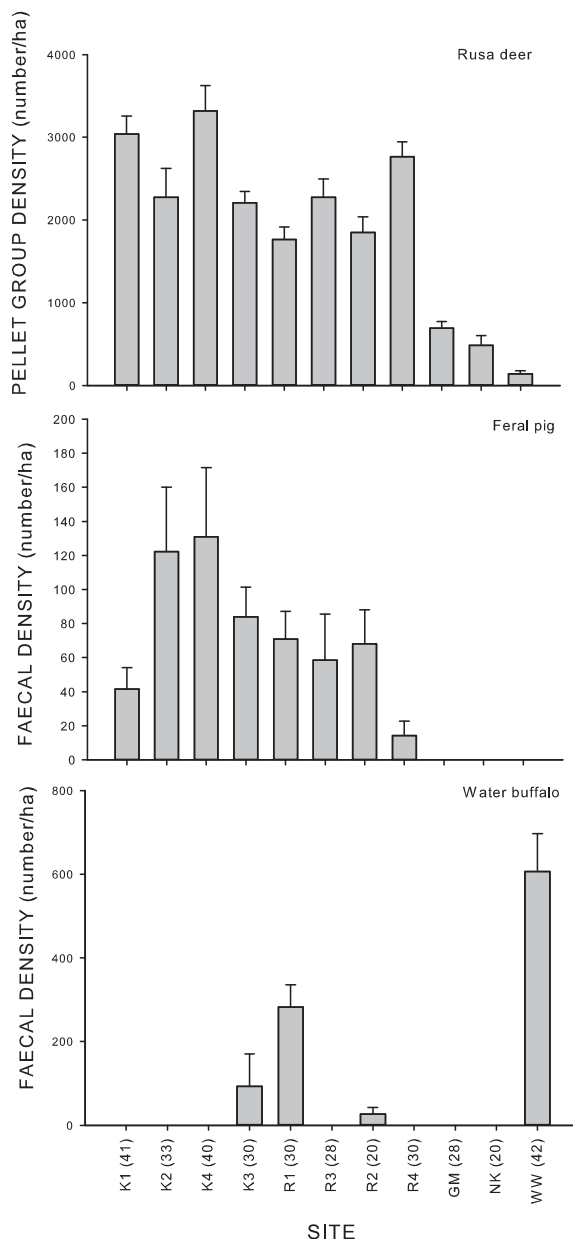

Figure 3. Mean ($\pm$ SE) ungulate faecal densities at 11 sites in Komodo National Park and Wae Wuul Nature Reserve, Indonesia, in 2009. For site abbreviations, see Figure 2. Numbers in parentheses are the total number of transects sampled at each site.

the 11 sites ranged from 6.4 to 25.4% (mean = 12.3%).

Feral pig faeces were found at eight sites on the two large islands in KNP, but were absent at the two sites on the small islands (Nusa Kode, Gili Motang) and at Flores. Feral pig faecal densities varied greatly among sites (see Fig. 3). Among the sites where feral pig faeces were present, the mean ($\pm$ SE) faecal densities ranged from 14.2 $\pm$ 8.4 faeces/ha in Loh Dasami (R4) to 131.0 $\pm$ 40.6 faeces/ha in Loh Wau (K4). Precision (CV) of the feral pig faecal density estimates at the 11 sites ranged from 20.6 to 46.6% (mean = 34.0%).

Water buffalo faeces were recorded at only four sites, all on the three largest islands. Water buffalo faecal densities (mean $\pm$ SE) were greatest at WW (606.6 $\pm$ 90.8 faeces/ha, CV = 15.0%) and lowest at Loh Baru (R2; 26.5 $\pm$ 16.0 faeces/ha, CV = 60.4%; see Fig. 3).

Distance sampling

The time required to conduct distance sampling along the 163.65 km of transects was 74 hours. A total of 807 deer in 431 clusters were observed at the 11 sites, with a minimum of two and a maximum of 116 clusters observed at a site (Table 1). Mean ($\pm$ SE) cluster size also varied among sites, ranging from 1.00 $\pm$ 0.00 at Nusa Kode to 2.77 $\pm$ 0.51 at Loh Dasami (see Table 1).

The best detection function model for rusa deer was the hazard rate key with no adjustments (AIC_c = 3,665.41, w_i = 0.89). The fitted detection function had a reasonable shoulder (Fig. 4A) and the q-q plot showed no substantial departures from expectation (see Fig. 4B). The Cramér-von Mises tests were also

non-significant (P > 0.2). The point estimates ($\pm$ SE) for the parameters in the best model were σ = 34.64 ($\pm$ 3.17) and b = 2.33 ($\pm$ 0.18), and the estimated effective half-strip width was 46.5 m. Deer densities estimated using distance sampling varied 60-fold among the 11 sites, ranging from 2.5 deer/km^2 at Nusa Kode (NK) to 165.5 deer/km^2 at Loh Wau (K4; Table 2). Precision of the estimates also varied greatly, with CVs ranging from 15.2 to 104.8% (see Table 2).

A total of 121 feral pigs were observed in 90 clusters (see Table 1). Feral pigs were not observed at the two sites on the smallest islands or at one site on the large island of Rinca (see Table 1). Feral pig cluster sizes varied among sites: Loh Dasami had the largest mean cluster size (1.80 $\pm$ 0.58), almost double that recorded at Loh Baru, Loh Tongker and WW (1.00 $\pm$ 0.00). As for rusa deer, the best detection function model for feral pig was the hazard rate key with no adjustments (AIC_c = 630.8, w_i = 0.77). The fitted detection function had a reasonable shoulder (see Fig. 4C) and the q-q plot showed no substantial departures from expectation (see Fig. 4D). The Cramér-von Mises tests were also non-significant (P > 0.8). The point estimates ($\pm$ SE) for the parameters in the best model were σ = 21.44 ($\pm$ 5.90) and b = 1.94 ($\pm$ 0.48), and the estimated effective half-strip width was 27.7 m. Among all the sites where feral pigs were present in KNP, the mean estimated densities ranged from 8.1 pigs/km^2 at Loh Baru (R2) to 25.2 pigs/km^2 in Sebita (K3). Interestingly, the mean feral pig density was more than 10 times lower at WW on Flores compared to the lowest density site in KNP. As for rusa deer, precision of the feral pig

Table 1. Transect length, number of clusters and mean ($\pm$ SE) cluster sizes observed during distance sampling of three ungulate species at 11 sites in Komodo National Park and Wae Wuul Nature Reserve, Indonesia, in 2009.

Site	Transect length (km)	Rusa deer		Feral pig		Water buffalo	
		No. clusters	Cluster size	No. clusters	Cluster size	No. clusters	Cluster size
Loh Liang (K1)	26.50	116	2.04 $\pm$ 0.16	11	1.36 $\pm$ 0.15	0	NA
Loh Lawi (K2)	30.00	60	1.63 $\pm$ 0.15	32	1.44 $\pm$ 0.17	0	NA
Loh Sebita (K3)	21.00	77	1.71 $\pm$ 0.11	24	1.12 $\pm$ 0.09	1	1.00 $\pm$ 0.00
Loh Wau (K4)	9.00	83	1.83 $\pm$ 0.19	11	1.55 $\pm$ 0.28	0	NA
Loh Buaya (R1)	12.00	25	1.60 $\pm$ 0.18	0	NA	13	1.31 $\pm$ 0.17
Loh Baru (R2)	6.00	17	1.76 $\pm$ 0.34	2	1.00 $\pm$ 0.00	1	1.00 $\pm$ 0.00
Loh Tongker (R3)	7.70	22	2.73 $\pm$ 0.56	4	1.00 $\pm$ 0.00	0	NA
Loh Dasami (R4)	6.00	13	2.77 $\pm$ 0.51	5	1.80 $\pm$ 0.58	0	NA
Gili Motang (GM)	9.00	3	1.67 $\pm$ 0.33	0	NA	0	NA
Nusa Kode (NK)	7.60	2	1.00 $\pm$ 0.00	0	NA	0	NA
Wae Wuul (WW)	28.85	13	1.23 $\pm$ 0.17	1	1.00 $\pm$ 0.00	29	2.48 $\pm$ 0.32
Total	163.65	431	1.87 $\pm$ 0.07	90	1.34 $\pm$ 0.08	44	2.07 $\pm$ 0.23

Figure 4. Detection functions (A and C) and q-q goodness-of-fit plots (B and D) for rusa deer and feral pig distance sampling data collected in Komodo National Park and Wae Wuul Nature Reserve, Indonesia, in 2009. The detection function (solid line in A and C) for both species is hazard rate key, and the histograms are the frequencies of observations.
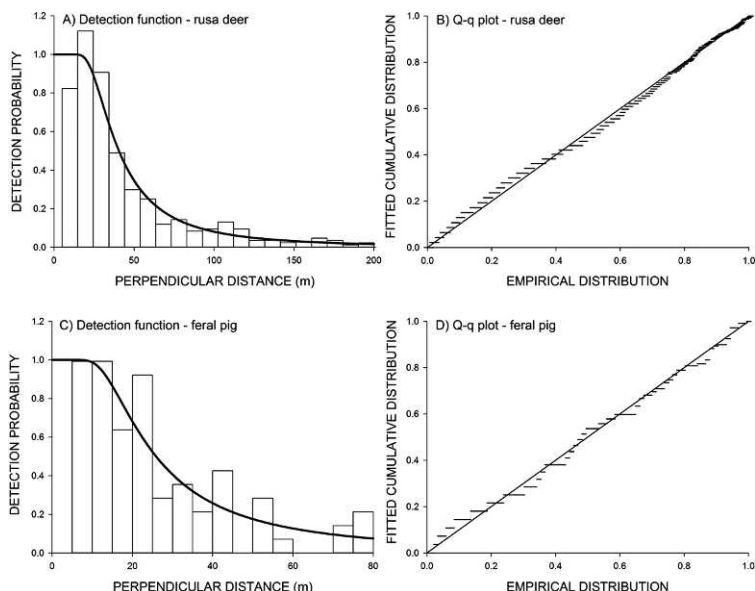
density estimates varied greatly, with CVs ranging from 24.8 to 105.8% (see Table 2).

Water buffaloes were observed at the same four sites on the large islands (see Table 1) where faeces were detected (see Fig. 3). However, too few clusters (N = 44) were observed to estimate densities using distance sampling at any site, and this species was not considered further in our analyses.

Relationships between faecal densities and ungulate population densities
There was a positive relationship between estimated faecal densities and estimated population densities for both rusa deer and feral pig (Fig. 5). However, no one model overwhelmingly explained the form of the relationship between faecal density and population

density for either species (Table 3). For rusa deer, the power model ($w_i = 0.82$) had substantial support and the logistic model ($w_i = 0.17$) had some support. The linear and null models had little support ($w_i \leq 0.01$). The point estimates ($\pm$ SE) for the parameters in the rusa deer power model were a = 391.66 ($\pm$ 137.60) and b = 0.44 ($\pm$ 0.08), and for the logistic model, the parameters were a = 2,890 ($\pm$ 276), b = 6.99 ($\pm$ 4.57) and c = 0.08 ($\pm$ 0.02).

For feral pig, the linear ($w_i = 0.58$) and power ($w_i = 0.38$) models of the relationship between faecal densities and abundances estimated by line-transect sampling had moderate support, but the logistic and null models had little support ($w_i \leq 0.04$). The point estimates ($\pm$ SE) for the parameters in the feral pig linear model were a = 23.13 ($\pm$ 17.24) and b = 2.99 ($\pm$

Table 2. Estimated densities (number/km²) of rusa deer and feral pig using distance sampling at 11 sites in Komodo National Park and Wae Wuul Nature Reserve, Indonesia, in 2009.

| Island (area; km²)	Site	Rusa deer density			Feral pig density		
		Mean	95% CI	CV (%)	Mean	95% CI	CV (%)
Komodo (311.5)	Loh Liang (K1)	81.0	59.1-115.2	15.2	9.1	4.7-17.7	35.5
	Loh Lawi (K2)	37.4	23.9-58.4	20.1	22.6	13.1-39.0	27.3
	Loh Sebita (K3)	70.7	50.8-98.4	15.9	25.2	15.5-41.1	24.8
	Loh Wau (K4)	165.5	105.7-259.2	21.0	18.8	8.5-41.7	39.4
Rinca (204.8)	Loh Buaya (R1)	32.3	13.5-77.3	38.9	0.0	NA	NA
	Loh Baru (R2)	48.4	16.9-138.3	50.9	8.1	2.1-31.7	70.4
	Loh Tongker (R3)	43.6	24.6-77.4	24.8	9.4	2.8-31.4	57.3
	Loh Dasami (R4)	41.9	22.3-79.0	29.9	20.2	7.3-55.6	50.6
Gili Motang (9.5)	Gili Motang (GM)	6.5	1.8-23.7	59.9	0.0	NA	NA
Nusa Kode (7.3)	Nusa Kode (NK)	2.5	0.3-23.1	104.8	0.0	NA	NA
Flores (13,540.0)	Wae Wuul (WW)	6.0	2.6-14.2	42.4	0.8	0.14-5.2	105.8
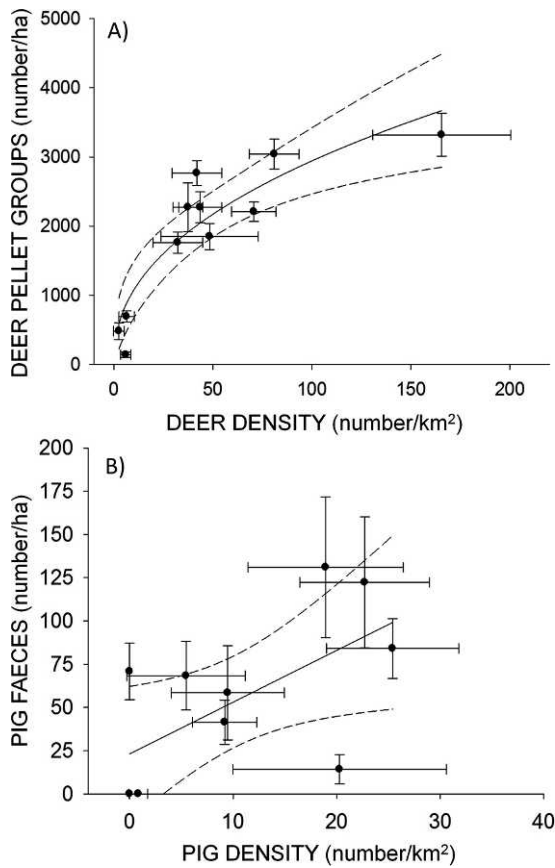
Figure 5. Observed (solid circles) and modelled (solid lines) relationships between faecal densities (number of faeces/ha) and densities estimated by distance sampling for rusa deer (A) and feral pig (B) at 11 sites in Komodo National Park and Wae Wuul Nature Reserve, Indonesia, in 2009. Error bars and dashed lines indicate ± 1 SE.

1.24), and for the power model they were a = 18.60 (± 21.99) and b = 0.50 (± 0.41).

Discussion

The primary objective of our study was to evaluate the usefulness of faecal counts and distance sampling for monitoring the abundances of the ungulate prey of the Komodo dragon in and around KNP. The importance of estimating changes in the abundances of rusa deer, feral pig and water buffalo populations will depend on their relative importance as prey for Komodo dragons. Demographic and diet studies suggest that rusa deer are the most important ungulate prey species for Komodo dragons (Auffenberg 1981, Jessop et al. 2006, 2007). Our results indicate that distance sampling is a useful technique

Table 3. Model selection summary for analyses of the relationship between ungulate densities estimated using distance sampling and ungulate faecal densities at 11 sites in Komodo National Park and Wae Wuul Nature Reserve, Indonesia, in 2009. AIC_c = Akaike's Information Criterion corrected for small sample size, w_i = Akaike weight and K = number of estimated parameters.

Model	Rank	AIC_c	ΔAIC_c	w_i	K
Rusa deer					
Power	1	172.42	0.00	0.82	3
Logistic	2	175.50	3.08	0.17	4
Linear	3	181.09	8.67	0.01	3
Null	4	188.69	16.27	0.00	2
Feral pig					
Linear	1	118.98	0.00	0.58	3
Power	2	119.82	0.84	0.38	3
Logistic	3	124.05	5.06	0.04	4
Null	4	188.69	69.71	0.00	2

for estimating rusa deer density on large island sites, especially on Komodo Island where CVs were ≤ 21%. However, estimated rusa deer densities were much less precise at sites with few observations (i.e. CVs ≥ 42%).

There were two major limitations to the use of distance sampling in our study. First, the target species was not always observed during distance sampling despite being detected during faecal counts, resulting in underestimates of density at those sites (e.g. feral pig at Loh Buaya). Second, far fewer observations than the minimum 60 required for robust distance sampling estimation (Buckland et al. 2001) were recorded for the three ungulate species at some sites. Although using global detection functions and cluster sizes (i.e. multiple covariates distance sampling; Marques et al. 2007, Thomas et al. 2009) overcame that limitation for rusa deer and feral pig, there were still too few observations to robustly estimate the density of water buffalo at any site. Increasing the distance sampling effort (e.g. by walking more transects and/or by walking transects twice; Wingard et al. 2011) would require substantially more resources than were available for our study. However, our inability to estimate water buffalo densities using distance sampling is unlikely to be a major limitation for a Komodo dragon prey monitoring programme because this species is a less important prey species compared to rusa deer and feral pig (Auffenberg 1981).

We found positive relationships between estimated faecal and population densities for both rusa deer and feral pig at the 11 sites (see Fig. 5). Although there was a positive relationship between

rusa deer pellet group and population densities, the form of the relationship was non-linear and contrasts with the linear relationship observed in 20 enclosures with known densities of deer in New Zealand (Forsyth et al. 2007). It is desirable to have a positively linear relationship between an index of abundance and true abundance (Thompson et al. 1998, Gibbs 2000, Månsson et al. 2011), and the non-linearity observed for rusa deer in our study is likely due to observers undercounting pellets at sites with very high deer densities. Further work is needed to determine if the linearity of the relationship between rusa deer population density and faecal counts can be improved by better training of observers and/or modifying the sampling protocol. One possibility is to use distance sampling to estimate the abundance of deer pellet groups along transects (Marques et al. 2001), although tall grass and thick leaf litter may obscure some pellet groups, potentially violating the assumption that all objects on the transect are observed. Estimating the rates at which faeces are deposited and decay would enable population densities to be estimated, as done for sika deer *Cervus nippon* in Scotland by Marques et al. (2001). However, estimating faecal deposition and decay rates is a major task that would require substantial resources (Forsyth et al. 2003). In contrast to rusa deer, the relationship between feral pig population density and faecal density was best explained by the linear model, although there was some evidence that the relationship may have been non-linear. An assumption of non-linear least squares regression is that X is measured without error, but ungulate densities estimated with distance sampling were often subject to substantial uncertainty. It would, therefore, be desirable to have more precise estimates of ungulate densities but, as noted above, this would require an impractically large sampling effort. It would also be desirable to include a larger number of sites in these analyses, particularly for feral pig which were present at only eight of the 11 sites.

The time required to conduct faecal counts was half that required for distance sampling. Compared to distance sampling, faecal counts were also technically easier for rangers to conduct (requiring cheaper equipment). Another advantage of faecal counts is that the standing crop of faeces accumulated during the dry season, when decomposition is limited (A. Ariefiandy, unpubl. data), is counted. Faecal counts, therefore, capture a broader temporal window of ungulate activity within any site and may be more representative of ungulate density than the direct observations needed to estimate density using distance sampling.

The maximum rusa deer and feral pig densities estimated using distance sampling in our study (165.5 and 25.2 animals/km^2, respectively; see Table 2) are similar to the highest densities documented elsewhere. Densities of 75-160 rusa deer/km^2 were estimated in New Caledonia using 'nocturnal line-transect sight counts' (de Garine-Wichatitsky et al. 2005), and densities of 27.0 and 46.0 feral pigs/km^2 were estimated using distance sampling in a lowland Malaysian forest by Ickes (2001). Understanding the drivers of ungulate abundances was beyond the scope of our study, but the low densities of rusa deer and feral pig estimated at WW were likely a consequence of illegal hunting. Preventing illegal hunting may increase the densities of rusa deer and feral pig at WW.

Additional parameters could also be monitored in the context of Komodo dragon conservation. In particular, changes in the body condition of rusa deer, feral pigs and water buffalo (e.g. kidney fat (Riney 1955) or bone marrow (Sinclair & Arcese 1995)) may provide an 'early warning' of changes in the quality of prey populations due to density-dependent processes (Bonenfant et al. 2009). Monitoring the hunting efficiency (e.g. kill rate) of adult Komodo dragons (*sensu* Jędrzejewski et al. 2002, Smith et al. 2004) would also be useful; declines in the kill rate would be a cause for concern, perhaps indicating reduced prey abundances/vulnerability. Developing protocols for estimating these additional parameters in and around KNP is a priority area for further work.

Management implications

Monitoring of endangered predators and their prey is conducted for three main reasons (e.g. Karanth et al. 2002a). First, to evaluate the success or failure of management actions. Second, to establish benchmark data as a basis for future management. Third, to increase general knowledge of the system and hence increase the capacity of managers to deal with new situations. Because spatial and temporal variation in ungulate density is likely to influence the population dynamics of the Komodo dragon, we recommend that annual monitoring of ungulates in and around KNP be undertaken using distance sampling and faecal counts. Continued annual

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monitoring of ungulate prey would provide valuable information for the management of Komodo dragon populations both inside and outside of KNP. Ungulates, particularly rusa deer, are the primary prey of large Komodo dragons (Auffenberg 1981), and Jessop et al. (2006, 2007) showed that the maximum size of Komodo dragons increased with increasing ungulate prey density. Subsequent work will further investigate the relationships between Komodo dragon population dynamics and ungulate prey density, including annual and seasonal changes in hunting efficiency and kill rates.

Although site-specific factors such as vegetation composition and microclimatic conditions, and also season, may influence the deposition and decay rates of ungulate faeces (Van Etten & Bennett 1965, Neff 1968, Putman 1984), the relationships reported here will be useful for managers establishing monitoring programmes for feral pig, rusa deer and water buffalo elsewhere in their native and exotic ranges. The positive relationships between the abundances of dung and densities of rusa deer and feral pig observed in our study enable managers elsewhere to use these techniques confident that they can identify substantial differences in abundance (i.e. the relationships are positive and approximately linear). The feral pig has a particularly large and expanding global distribution (Oliver 1993, Long 2003) and causes significant economic and environmental impacts (reviews in Choquenot et al. 1996, Lowe et al. 2000) but, despite dung counts being a commonly used index of feral pig abundance (e.g. Choquenot et al. 1996, Hone 2002), this is the first study to investigate the form of the dung-density relationship for this species. Our results for rusa deer support previous work in New Zealand showing that the abundance of faecal pellets from other deer species (primarily red deer *Cervus elaphus scoticus*) increases with deer abundance. However, we encourage managers and researchers, whenever possible, to validate their indices of abundance in their study areas.

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