

# Monitoring the ungulate prey of komodo dragons (*Varanus komodoensis*) using faecal counts

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Suggested RH: Monitoring ungulates in Komodo National Park

**Abstract**

The endangered Komodo dragon (*Varanus komodoensis*) persists on five islands in Indonesia and there is concern about its long-term persistence on some of these islands. A possible threat is a decline in the abundance of the three ungulate species that form the bulk of the diet of adult dragons: Timor deer (*Cervus timorensis*), wild pigs (*Sus scrofa*) and water buffalo (*Bubalis bubalis*). We tested the usefulness of faecal counts along 20–48 transects for monitoring the abundance of these three ungulate species at 11 sites on five islands within Komodo National Park. Transects consisted of 30 3.14-m<sup>2</sup> plots at 5-m intervals. Deer pellet groups were detected at all 11 sites, pig and buffalo dung was detected at 8 and 3 sites on the two largest islands, respectively. The coefficient of variation of the estimates of faecal density were  $\leq 16\%$  for deer pellet groups,  $\geq 19\%$  for pig dung and  $\geq 39\%$  for buffalo dung. We also tested distance sampling at one site each for pig and buffalo dung. Distance sampling took a similar amount of time but gave similar estimates with better precision. The density of deer, buffalo and pig faeces varied significantly among the five islands. The implications of these results for the management of ungulates in Komodo National Park are discussed.

## Introduction

The endangered Komodo dragon (*Varanus komodoensis*), the largest extant monitor lizard, is currently restricted to five islands in the Lesser Sundas region of Eastern Indonesia (Ciofi *et al.* 2004). Four of the five island populations are located within Komodo National Park (KNP) (Fig. 1), and there is concern about the long-term persistence of some of these populations. The major perceived long-term threat to these populations is the availability of large ungulate prey. Anthropogenic and natural effects including illegal hunting of large prey species, human-caused fires, forest clearance, and stochastic factors could influence prey density and hence the viability of dragon populations.

Historically, the prey of large dragons included pygmy elephant (Diamond 1987), but now the diet of adults is now almost entirely composed of Timor deer (*Cervus timorensis*) (present on all five islands in KNP), wild pigs (*Sus scrofa*) and in some valleys water buffalo (*Bubalis bubalis*) (Auffenberg 1981). Timor deer are commonly hunted on nearby Flores Island and in the past have been illegally harvested on all of the islands within KNP (H. Rudiharto, Komodo National Park, personal communication). Dragons on Padar, the third largest island in KNP, became locally extinct in the 1980s, possibly as a result of reduced deer abundance caused by illegal harvesting (Sastrawan and Ciofi 2002). Although patrols by KNP rangers have now greatly reduced illegal harvesting, there remains the potential for illegal harvesting of deer, pigs and buffalo. These ungulate species could also decline for other reasons (e.g., disease, drought or fire).

The four islands in KNP with extant dragon populations differ considerably in area (10 km<sup>2</sup>–343 km<sup>2</sup>), reciprocal proximity, biogeography (Monk *et al.* 1997), and habitat diversity. These factors may also influence both the abundance and distribution of ungulates. Quantifying island differences in the abundance of ungulates, and their temporal dynamics, is thus important for understanding the ecological interactions between komodo dragons and their prey.

The primary objective of this study was to develop a method for quantifying spatial and temporal changes in the abundance of deer, pigs and buffalo in KNP. The method(s) must be able to be implemented with existing resources at KNP, and be of reasonable accuracy and precision (Thompson *et al.* 1998).

## **Methods**

### *Study areas*

Field work was conducted at 11 sites on five islands within KNP (Fig. 1): Komodo (330 km<sup>2</sup>; four sites), Rinca (232 km<sup>2</sup>; four sites), Padar (20.4 km<sup>2</sup>; one site), Gili Motang (13.4 km<sup>2</sup>; one site), and Gili Dasami (11.0 km<sup>2</sup>; one site) located in south eastern Indonesia (8° 39' 20" S; 119° 42' 57"E). The sites were not selected randomly but were centered on valleys where annual mark-recapture trapping of komodo dragons has been undertaken since 2002 (T. Jessop *et al.*, unpublished data). Valley sites varied in size from 8.99 to 1.83 km<sup>2</sup> (mean ± SEM: 4.06 ± 0.87 km<sup>2</sup>).

Auffenberg (1981) described three habitat types within our study areas. Deciduous monsoon forest was restricted to coastal valley floors abutting significantly elevated hills that received precipitation and thus provided adequate run-off to the valley. Monsoon forest consists of deciduous fire-resistant trees, primarily *Tamarindus indicus*, *Sterculia foetida*, *Jatropha curcas*, and *Cladogynos orientalis*. The canopy of monsoon forest is partially closed and the understorey is either open or dominated by a perennial shrub. Monsoon forest is abruptly displaced by savannah woodland and/or savannah grassland, in areas that receive little run-off or precipitation. The canopy of savannah woodland is sparse and very open and the dominant trees are *Borassus flabellifer*, *Zizyphus jujube*, and *T. indicus*. Savanna grassland and the understorey of savannah woodland are both composed of medium and tall grasses.

#### *Survey methodology*

Direct counts (Mayle *et al.* 1999) of deer, pigs and buffalo from vantage points were not possible in most of these study sites due to the forest and woodland habitats (see above). Other direct survey methods (e.g., distance sampling) were inappropriate because all three species avoid people and would likely generate severely negatively biased estimates of abundance. We therefore chose to use indirect survey techniques (review in Thompson *et al.* 1998) based on faecal counts: estimates from these techniques should be less influenced by the tendencies of deer, pigs and buffalo to avoid people.

Counts of the standing crop of faecal pellets or faecal pellet groups have been widely used to estimate the relative or absolute abundance of many deer species (e.g., Marques *et al.* 2001). Hone (2002) used counts of pig dung on plots in Namadgi National Park

(south-eastern Australia) as an index of relative abundance. To our knowledge, faecal counts have not previously been used as an index of abundance of water buffalo.

Faeces may be counted in quadrats of fixed area and, assuming that all faeces are counted, converted to a density of faeces per unit area. Distance sampling has been used to estimate the density of faeces for sika deer (*Cervus nippon*) in Scotland (Marques *et al.* 2001), and has the advantage that only groups falling on the transect line (i.e.,  $g_0$ ) cannot be missed. Preliminary observations indicated that the deep leaf litter in the forest habitats and the tall grassland in some savannah areas hid many deer pellet groups. Since a substantial proportion of pellet groups would not be observed at  $g_0$ , estimates of deer pellet group density would likely be severely negatively biased (see Buckland *et al.* 2001). We therefore decided to use total counts of pellets in plots that were sufficiently small ( $3.14\text{m}^2$ ) such that the entire plot could be searched in all habitats.

We used a table of random numbers to randomly locate start points across grid referenced digital maps for between 20 and 48 transects in each of the 11 sites. Each transect was also allocated a random compass bearing. The 150 m transects consisted of 30  $3.14\text{m}^2$  circular plots (i.e., a radius of 1 m) at 5 m intervals. The plots were thoroughly searched and the total number of deer pellets and deer pellet groups recorded on each plot. We only counted 'intact' pellets (Fraser 1998), and those groups with  $\geq 50\%$  of pellets inside the plot. Previous work in New Zealand and Australia using this method gave estimates of deer faecal pellet group abundance with coefficients of variation (CV) of  $\leq 20\%$  (Forsyth *et al.* 2003; D.M. Forsyth *et al.*, unpublished data). We also counted the number of intact feral pig and buffalo faeces in each plot.

All field work was conducted during September and October (i.e., the late dry season) of 2004. We navigated to the start point of each transect using a Global Positioning System (GPS; Garmin Etrex, USA). A 150-m nylon cord with flagging tape at 5m intervals delineated each transect. A plastic peg was pushed into the ground at the plot centre and a 1-m string was used to delineate the perimeter of the plot. Leaf litter and grass was removed and parted, respectively, to enable all faeces to be counted. For each transect we also recorded the predominant habitat type and the time taken to complete the counts.

The much larger pellets of pigs and buffalo will be more likely to be observed than deer pellets. Hence, we undertook a pilot study of distance sampling methods for buffalo at one site (Loh Buaya, Rinca Island) and wild pig at one site (Loh Liang, Komodo Island). We chose a subset of transects at both sites (14 at Loh Buaya and 10 at Loh Liang) and after completing the plot count DMF walked back along the 150-m transect at ca. 1 km hr<sup>-1</sup> and searched left and right for buffalo or pig faeces. The perpendicular distance from the transect to the centre of each faeces was measured to within  $\pm 5$  cm. The time taken to complete each transect was also recorded.

### *Statistical analyses*

We used bootstrapping (Manly 1997) to calculate means, 95% confidence intervals ('CI') and CVs for the plot-based estimates of faeces abundance (per ha) for each species at each site. Bootstrap estimates were based on 10 000 samples. The CV was:

$$CV = \frac{\hat{\sigma}}{\hat{x}} \times 100\% .$$

We used conventional distance sampling methods to estimate the density of buffalo and pig dung at Loh Buaya and Loh Liang, respectively. In this method the number of pellet groups located within the survey area are modelled as a function of perpendicular distance of the detected pellet groups from the line (Buckland *et al.* 2001). Data were analysed using the program DISTANCE 4.2 release 1 (Buckland *et al.* 2001). DISTANCE is freeware available at <http://www.ruwpa.st-and.ac.uk/distance/>, and is widely used for the analysis of line transect data. Initially, histograms of the data were examined for evidence of heaping (i.e., clumping of data at particular distances), outliers and measurement error. Five models were considered in the analysis, with each model comprising a key function that may be adjusted with a series expansion containing up to five parameters (which, by default, were added sequentially). The models were a uniform or hazard-rate key function with either a cosine or a polynomial series expansion, and a half-normal key function with a Hermite polynomial. Following the recommendations of Buckland *et al.* (2001) and Marques *et al.* (2001), the choice of a final model was based on corrected Akaike's Information Criterion ( $AIC_c$ ), low CV, and shape criteria. Data were analysed ungrouped and DISTANCE's default data groupings were used to examine the goodness of fit of the model with the raw data.

Density ( $\hat{D}$ ) was estimated using DISTANCE as:

$$\hat{D} = \frac{nf(0)}{2L},$$

where,  $n$  is the number of sightings,  $f(0)$  is the probability density function of the perpendicular density data at zero distance from the transect line and  $L$  is the total length of the survey transect (Buckland *et al.* 2001). The variance (var) of  $\hat{D}$  was estimated as:



$$\text{var}(\hat{D}) = \hat{D}^2 \{ (CV(n))^2 + (CV(f(0)))^2 \},$$

where,  $CV(n)$  is the coefficient of variation of the number of sightings across transect lines and  $CV(f(0))$  is the coefficient of variation of the probability density function of the perpendicular density data at zero distance (Buckland *et al.* 2001). We used a paired  $t$ -test to determine whether the time taken to complete the plot-based counts and distance estimates were significantly different for the same transects (i.e.,  $P < 0.05$ ).

To assess differences in ungulate faecal density among the five islands we used the plot estimates. The four sites on both Komodo and Rinca islands were pooled and used to infer a total island sample. Comparison of island means for each of the three species was analysed by parametric and non-parametric analysis of variance depending on data meeting the assumptions of normality and homogeneity of sample variance. To discriminate significant differences among islands appropriate post- hoc methods (Tukey's test and Dunn's method) was used to identify subgroups.

## Results

### *Timor Deer*

Timor Deer pellet groups were recorded at all sites on all five islands. Densities ranged from  $323.07 \pm 50.35$  (SEM) pellet groups  $\text{ha}^{-1}$  on Gili Motang Island to  $4376.61 \pm 243.42$  groups  $\text{ha}^{-1}$  on Liang on Komodo Island (Table 1). The CVs ranged from 5.6% (Liang) to 15.6% (Gili Motang Island). The mean time to complete a transect was  $11.28 \pm 0.63$  minutes ( $n = 347$ ).

### *Wild Pig*

Pig dung was found on all eight sites on the two largest islands (Komodo and Rinca), but not on the other islands. Pig dung densities ranged from  $5.52 \pm 2.30$  dung groups  $\text{ha}^{-1}$  in Tongkir Valley (Rinca Island) to  $134.83 \pm 33.52$  groups  $\text{ha}^{-1}$  in Liang Valley (Komodo Island; Table 2). The CVs for the eight sites at which pig dung was recorded ranged from 19.2% in Wau Valley (Komodo Island) to 64.7% in Tongkir Valley (Rinca Island).

Distance sampling was conducted along 10 transects at Los Liang. These transects took a mean time of  $6.60 \text{ min} \pm 0.87 \text{ min}$ , giving a total time of 66.00 min to record 118 sightings of dung. Examination of the perpendicular distance data did not reveal any rounding problems or outliers (Fig. 2a). The final model selected was a half-normal with a two-order cosine adjustment, with  $f(0)$  ( $\pm\text{SE}$ ) estimated as  $1.05 \pm 0.10$  (Fig. 2a). The density of pig dung was thus estimated to be  $41.35 \text{ ha}^{-1}$  (95% CI: 18.30, 93.45; CV, 38.0%).

### *Water Buffalo*

Water buffalo dung was recorded at only one site on Komodo Island and two sites on Rinca Island (Table 3). The density of buffalo dung was greatest at Buaya Valley (Rinca Island;  $98.48 \pm 37.20$  dung groups  $\text{ha}^{-1}$ ) and lowest at Sebita Valley (Komodo Island;  $11.45 \pm 6.22$  dung groups  $\text{ha}^{-1}$ ). The CVs for these estimates ranged from 38.84 – 49.23%.

Distance sampling was conducted along 16 transects at Los Buaya. These transects took a total of 186.00 min to complete (mean, 12.40 min; SE, 2.2 min) to record 446 sightings of dung. Examination of the perpendicular distance data did not reveal any rounding

problems or outliers (Fig. 2b). As for feral pig dung at Liang, the final model selected was a half-normal with a two-order cosine adjustment (Fig. 2b).  $f(0)$  ( $\pm$ SE) was estimated as  $0.1273 \pm 0.10066$ . The density of dung was thus estimated to be  $11.83 \text{ ha}^{-1}$  (95% CI, 56.22 to 24.88; CV, 36.2%).

#### *Plot counts and distance sampling for water buffalo and wild pigs*

The densities of water buffalo dung at Loh Buaya (Rinca Island) estimated by the plot and distance methods were similar (Table 4). However, the CV for the bootstrapped plot estimates was more than five times that for the distance estimate. Although the times taken to complete the two methods were not significantly different (Paired  $t$ -test;  $t_{1,14} = 0.107$ ,  $P = 0.9$ ), it took a total of 24 min longer (13%) to complete the distance transects compared to the plot transects, and we note that deer pellet groups were also counted in plots (see Methods).

The densities of pig dung at Loh Liang (Komodo Island) estimated by the plot and distance methods were similar (Table 4). However, the CV for the bootstrapped plot estimates was more than five times that for the distance estimate. Although the times taken to complete the two methods were not significantly different (Paired  $t$ -test;  $t_{1,9} = 1.07$ ,  $P = 0.3$ ), it took 13 more minutes (20%) to complete the plot counts at Liang compared to the distance plots, although again we note that deer pellet groups were also counted in plots.

### *Island differences in faeces density*

Timor deer pellet group densities were significantly different between islands (ANOVA:  $F_{4, 331} = 50.52, P < 0.001$ ). Post-hoc analysis (Tukey's method) indicated that islands could be separated into three groups, with estimated pellet group density higher on Komodo than Rinca and Padar, which were in turn higher than Nusa Kode and Gili Motang (Fig. 3a).

Wild pig dung densities were significantly different between islands (Kruskal-Wallis ANOVA:  $H_{4, 331} = 21.82, P < 0.001$ ). Post-hoc analysis (Dunn's method) indicated that estimated pig dung density was greater on Komodo and Rinca, with pig dung not detected on Padar, Nusa Kode and Gili Motang (Fig. 3b).

Water buffalo dung densities differed significantly between islands (Kruskal-Wallis ANOVA:  $H_{4, 331} = 17.29, P < 0.001$ ). Post-hoc analysis (Dunn's method) indicated that estimated buffalo dung densities on Rinca were greater than Komodo, with buffalo dung not detected on Padar, Nusa Kode and Gili Motang Islands (Fig. 3c).

## **Discussion**

### *Timor deer pellet group density*

Estimates of Timor deer pellet group densities at all 11 sites had CV's  $\leq 16\%$ . Although the relationship between the true abundance of Timor deer and the index of pellet group abundance used here has not been investigated, the relationship between this index and known densities of deer has been evaluated at 20 sites in New Zealand by D. M. Forsyth *et al.* (unpublished manuscript). It was shown that pellet group density was positively

correlated with deer density, but the relationship was non-linear (concave-down; D. M. Forsyth *et al.* unpublished manuscript). Hence, although the index does not relate to deer density in a 1:1 linear relationship, it is likely to be suitable for detecting large changes in the abundance of deer.

Marques *et al.* (2001) used distance sampling to estimate the standing crop of sika deer in south Scotland. We did not distance sampling to estimate deer pellet group density because the tall savannah grass and leaf litter would have meant that all groups on the transect line would not have been detected, thus violating an important assumption of distance sampling (Buckland *et al.* 2001). Marques *et al.* (2001) noted that the best method to estimate deer abundance depends upon the question and the circumstances. Although our method is assumed to be an index of relative deer abundance, we note that the number of deer present could be estimated if both the deposition and decay rates of pellet groups were estimated. Marques *et al.* (2001) outline methods for estimating decay rates of deer pellet groups.

#### *Water buffalo and wild pig dung densities*

Whereas Timor deer pellet groups were present at all 11 sites, wild pigs were detected only on Komodo and Rinca Islands and water buffalo were detected on one site on Komodo Island and two sites on Rinca Island. There are no records of buffalo and pigs being observed on the three smaller islands (i.e., Padar, Gili Motang and Nusa Kode), and buffalo - or their signs - have not been sighted at any sites on the larger islands where they were not detected in this study (T. S. Jessop, personal observation).

Our results, albeit based on a small number of transects, suggest that distance sampling is a more useful method for estimating the density of water buffalo and wild pig dung than plot counts. For the same transects, distance sampling gave estimates with much smaller CVs than plot sampling for a similar amount of time (Table 4). The dung of buffalo and feral pigs is far larger than that of Timor deer, and it is unlikely that buffalo or pig dung along the transect line would be missed (c.f. Timor deer). We also note that in the three sites where buffalo were detected the savannah grassland was much shorter than in the sites where they were absent, presumably because of grazing: this would also reduce the likelihood of buffalo dung on line being missed. The observed distribution of water buffalo and wild pig dung (Fig. 2) suggests (but does not confirm) that few, if any, dung groups along the line were missed. It is encouraging that both plot and distance sampling along the same transects produced similar estimates of wild buffalo dung at Loh Buaya. However, one advantage of using plot sampling is that Timor deer pellet groups and buffalo/pig dung can be counted at the same time.

Both wild pigs and water buffalo are common in parts of Australia (Choquenot 1996; Corbett 1995). Hone (2002) has used dung counts on permanent plots as an index of abundance of pigs in Namadgi National Park (south east Australia), but to our knowledge dung counts have not previously been examined for water buffalo. Our results indicate that plot counts or distance sampling may be useful ways of monitoring these species in some circumstances in Australia and elsewhere.

The methods reported here could be repeated such that temporal changes in the relative abundance of the three ungulate species could be estimated. KNP rangers conducted plot

counts at some sites after one day of instruction, under supervision from one or more of the authors. We are thus optimistic that KNP staff could conduct future monitoring using the plot counts outlined here. However, distance sampling is a more difficult methodology to apply and thus may be less suitable for widespread use in the field. The plot count method is advantageous because it is well suited to the funding and technical resources available in Komodo National Park and thus we hope will be implemented within a long-term monitoring program. Continued monitoring of this kind could provide valuable data from which to plan the long-term management of Komodo dragon populations both inside and outside of Komodo National Park

We observed significant differences in the density of ungulate faeces among the five major islands within Komodo National Park. Could such differences underpin ecological interactions between ungulate and Komodo dragon populations? Ungulates, particularly Timor deer, are the primary prey of large Komodo dragons (Auffenberg 1981). We do not know how these apparently large differences in the abundance of Timor Deer influences the ecology and population dynamics of Komodo dragons. Ungulate density has been shown to influence the population dynamics of other apex predators (e.g., wolves [*Canis lupus*] and deer spp. in Poland; Jedrzejewski *et al.*, 2002). Conversely, the top down effects of predation on ungulate populations appear to be more variable (Mduma *et al.* 1999; Jedrzejewski *et al.* 2002). However the relationship between predator and ungulate prey dynamics is often complex and other factors such as forage quality and quantity appear to be important in driving ungulate population dynamics (Peterson 1999). Further studies are required to understand the ecological interactions between Komodo dragons and their ungulate prey.

## **Conclusions**

We investigated the utility of faecal counts in plots for estimating the relative abundance of the large ungulate prey of Komodo dragons. Plot counts along randomly located transects provided estimates of Timor deer pellet group densities with good precision (CVs <16%), but were less precise for wild pig dung (CVs>19%) and water buffalo (CVs>38%). A pilot study suggested that distance sampling may provide estimates with greater precision for wild pig and water buffalo dung. There were large differences in the density of ungulate faeces among the five islands, and these differences are likely to have effects on the ecology of the Komodo dragons.

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## References

- Auffenberg, W. (1981). *The Behavioral Ecology of the Komodo Monitor*. (University of Florida Press: Gainesville.).
- Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., and Thomas, L. (2001.). *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. (Oxford University Press: Oxford.)
- Fraser, K. W. (1998). *Assessment of Wild Mammal Populations*. Landcare Research Contract Report LC9798/79 (unpublished). 102 p.
- Choquenot, D., McIlroy, J., Korn, T. (1996). *Managing Vertebrate Pests: Feral Pigs*. (Australian Government Publishing Service: Canberra.).
- Ciofi, C. (1999). The Komodo dragon. *Scientific American* **280**, 92–99.
- Ciofi, C., Beaumont, M. A., Swingland, I. R., and Bruford, M. W. (1999). Genetic divergence and units for conservation in the Komodo dragon *Varanus komodoensis*. *Proceedings of the Royal Society of London B* **266**, 2269–2274.
- Ciofi, C., and de Boer, M. E. (2004) Distribution and conservation of the Komodo monitor (*Varanus komodoensis*). *Herpetological Journal* **14**, 99–107.
- Corbett, L. K. (1995). Swamp buffalo. In ‘The Mammals of Australia’. (Ed. R. Strachan.) pp. 713–725. (Reed New Holland: Sydney.).
- Daimond, J. M. (1987). Did Komodo dragons evolve to eat pygmy elephants? *Nature* **326**, 832.
- Forsyth, D. M., Scroggie, M. P., and Reddiex, B. (2003). A review of methods to estimate the density of deer. Landcare Research Contract Report: LC0304/015 (unpublished). 55 pp.

- Forsyth, D. M., Link, W. A., Webster, R., Nugent, G., and Warburton, B. In Press.  
 Nonlinearity and seasonal bias in an index of brushtail possum abundance.  
*Journal of Wildlife Management*
- Hone, J. (2002). Feral pigs in Namadgi National Park, Australia: dynamics, impacts and management. *Biological Conservation* **105**, 231–242
- Jedrzejewski, W., Schmidt, K., Theuerkauf, J., Jedrzejewska, B., Selva N., Zub, K., and Szymura, L. (2002) Kill rates and predation by wolves on ungulate populations in ialowieza primeval forest (Poland). *Ecology* **83**, 1341–1356.
- Manly, B. F. J. (1997). Randomization, Bootstrap and Monte Carlo Methods in Biology. (Chapman & Hall: London.).
- Marques, F. F. C., Buckland, S. T., Goffin, D., Dixon, C. E., Borchers, D. L., Mayle, B. A., and Peace, A. J. (2001). Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. *Journal of Applied Ecology* **38**, 349–363.
- Mayle, B. A., Peace, A. J., Gill, R. M. A. (1999). How Many Deer? A field Guide to Estimating Deer Population Size. (Forestry Commission: Edinburgh.).
- Mduma, S. A. R., Sinclair, A. R. E., and Hilborn, R. (1999). Food Regulates the Serengeti wildebeest: a 40-year record. *Journal of Animal Ecology* **68**, 1101–1122.
- Monk, K. A., Y. de Fretes, and G. Reksodiharjo-Lilley (1997). The Ecology of Nusa Tenggara and Maluku. Oxford University Press, Oxford, UK.

Peterson, R. O. (1999). Wolf-moose interaction on Isle Royale: The end of natural regulation? *Ecological Applications* **9**, 10–16.

Thompson, W. L., White, G. C., and Gowan, G. V. (1998). *Monitoring Vertebrate Populations*. (Academic Press: San Diego.).

**Table 1. Estimates of the density of Timor deer pellet groups (per ha) at 11 sites on five islands in Komodo National Park**

*N* is the number of transects

Site	<i>N</i>	Mean $\pm$ SD	95% CI	CV%
Komodo Island				
Liang	41	4375.61 $\pm$ 243.42	3871.33, 4859.24	5.56
Sebita	48	3265.21 $\pm$ 211.72	3726.01, 2872.61	6.48
Lawi	33	2954.14 $\pm$ 358.31	2286.62, 3805.73	12.13
Wau	30	4019.09 $\pm$ 305.06	3391.72, 4627.39	7.59
Rinca Island				
Buaya	31	1698.06 $\pm$ 133.67	1432.06, 1986.20	7.87
Baru	28	2346.54 $\pm$ 227.17	1908.92, 2875.48	9.68
Tongkir	20	2751.26 $\pm$ 362.25	2020.28, 3592.78	13.17
Dasami	30	2486.12 $\pm$ 208.37	2080.89, 2965.92	8.38
Padar Island	30	1736.75 $\pm$ 213.43	1400.21, 2356.05	12.29
Gili Motang Island	28	323.07 $\pm$ 50.35	229.83, 441.16	15.59
Nusa Kode Island	20	751.37 $\pm$ 99.91	549.15, 976.43	13.30

**Table 2. Estimates of the density of wild pig dung (per ha) at 11 sites on five islands  
in Komodo National Park**

*N* is the number of transects

<b>Site</b>	<b><i>N</i></b>	<b>Mean <math>\pm</math> SD</b>	<b>95% CI</b>	<b>CV%</b>
Komodo Island				
Liang	41	134.83 $\pm$ 33.52	72.18, 217.62	24.86
Sebita	48	88.11 $\pm$ 23.34	33.12, 159.23	36.34
Lawi	33	86.52 $\pm$ 22.18	32.17, 147.56	36.54
Wau	30	113.2 $\pm$ 21.71	70.80, 166.66	19.18
Rinca Island				
Buaya	31	15.39 $\pm$ 5.34	0.00, 32.90	51.45
Baru	28	31.55 $\pm$ 9.03	11.35, 56.89	34.99
Tongkir	20	5.52 $\pm$ 2.30	0.00, 26.52	64.72
Dasami	30	14.65 $\pm$ 5.12	0.00, 45.99	62.34
Padar Island	30	0	0	0
Gili Motang Island	28	0	0	0
Nusa Kode Island	20	0	0	0

**Table 3. Estimates of the density of water buffalo dung (per ha) at 11 sites on five islands in Komodo National Park**

*N* is the number of transects

<b>Site</b>	<b><i>N</i></b>	<b>Mean <math>\pm</math> SD</b>	<b>95% CI</b>	<b>CV%</b>
Komodo Island				
Liang	41	0	0	0
Sebita	48	11.45 $\pm$ 6.22	0.00, 33.22	49.23
Lawi	33	0	0	0
Wau	30	0	0	0
Rinca Island				
Buaya	31	98.48 $\pm$ 37.20	32.91, 185.77	38.84
Baru	28	15.81 $\pm$ 7.13	0, 34.11	47.23
Tongkir	20	0	0	0
Dasami	30	0	0	0
Padar Island	30	0	0	0
Gili Motang Island	28	0	0	0
Nusa Kode Island	20	0	0	0

**Table 4. Comparison of estimates of dung density ( $\hat{D}$ ) from plot and distance methods at two sites in Komodo National Park**

There were 16 150-m transects for water buffalo at Buaya and 10 150-m transects for wild pigs at Liang (see Methods)

Animal, site	Plot				Distance			
	$\hat{D}$	95% CI	CV (%)	Time (min)	$\hat{D}$	95% CI	CV (%)	Time (min)
Water buffalo, Buaya	106.16	87.22, 122.03	236.64	162.00	118.28	56.22, 248.81	36.18	186.00
Wild pig, Liang	31.84	0, 64.75	316.00	79.00	38.44	0, 72.23	37.99	66.00

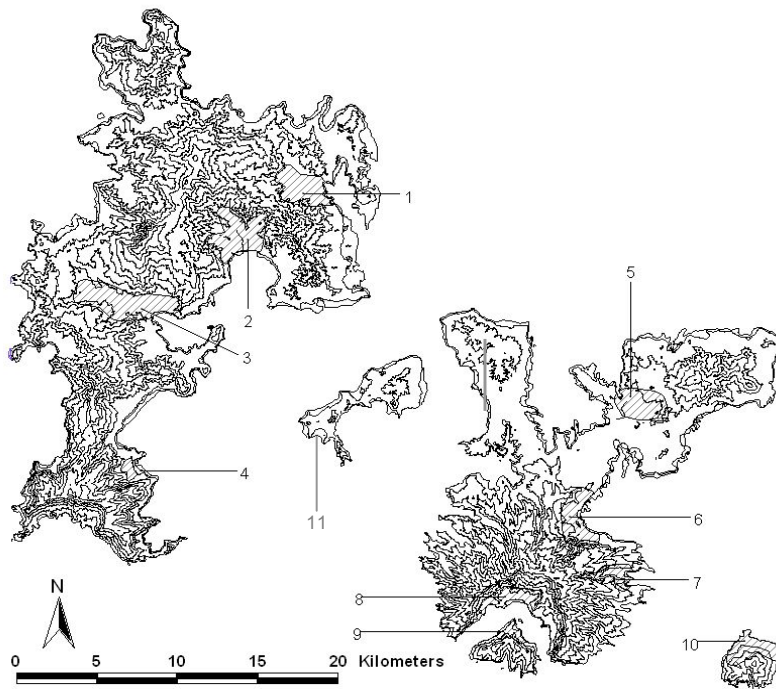
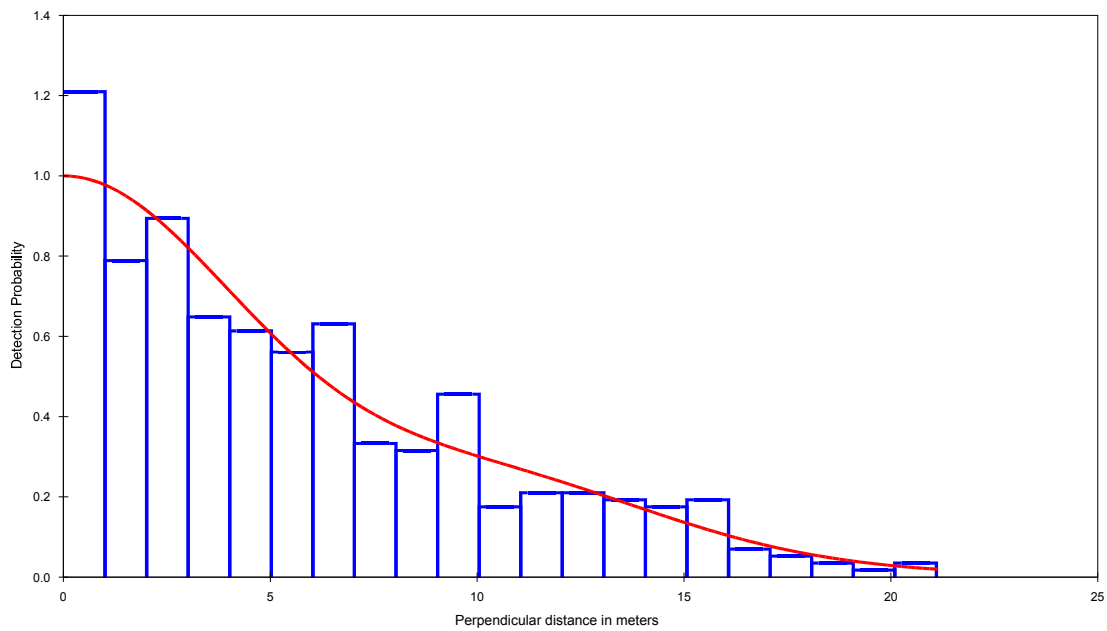


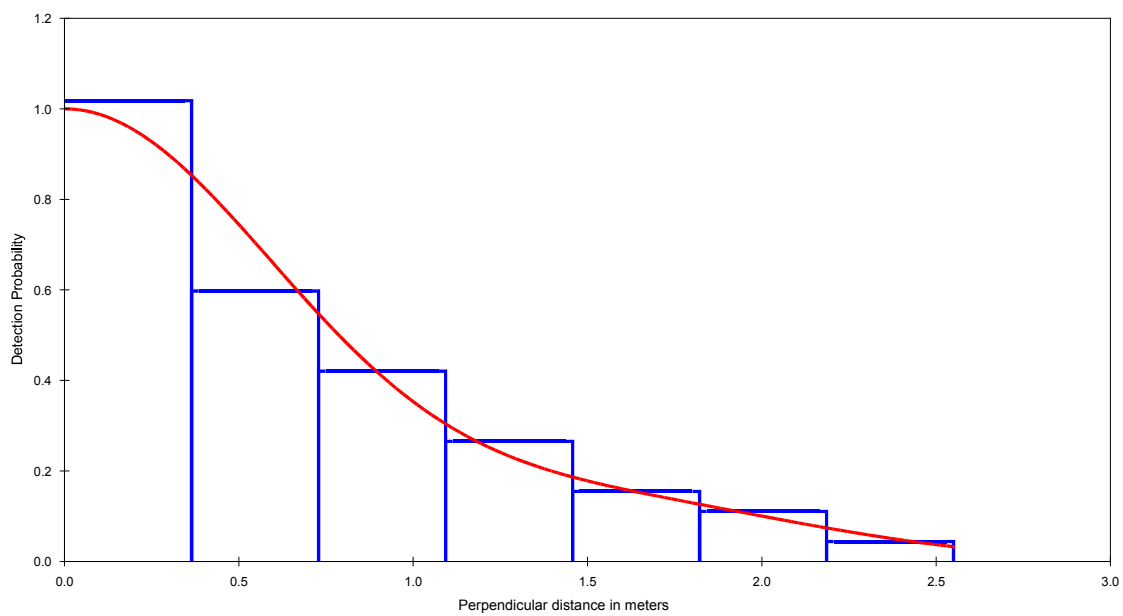
Fig 1. Location of study sites across Komodo National Park in South Eastern Indonesia. Sampling sites are marked numerically and were situated across 5 islands and include Komodo Island sites: 1) Loh Sebita 2) Loh Liang, 3) Loh Lawi, 4), Loh Wau,5); Rinca Island sites: Loh Buaya, 6) Loh Baru, 7) Loh Tonker, 8) Loh Dasami, and the three small islands of 9) Nusa Kode,10) Gili Motang and 11) Padar. Stippling indicates the area of study utilised at each site.



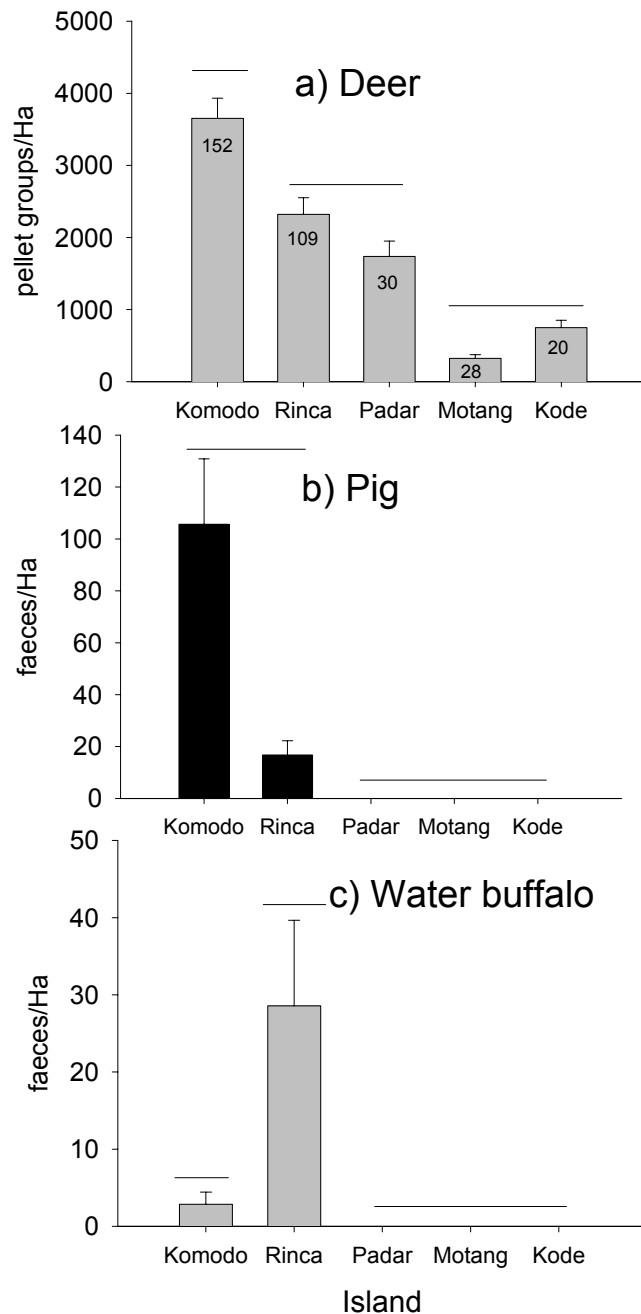
a).



b).



**Fig. 2.** Histograms of perpendicular distances and fitted detection functions for (a) water buffalo dung at Loh Buaya (Rinca Island) and (b) wild pig dung at Loh Liang (Komodo Island). These figures are routine output from the DISTANCE software.



**Fig. 3.** Density of faeces of the three species of ungulate prey utilised by adult komodo dragons on five islands in Komodo National Park, Indonesia. (a) Timor deer; (b) wild pigs; (c) water buffalo. Post-hoc differences among islands are denoted by horizontal lines demarking homogenous subsets that have significantly different faecal densities ( $P < 0.001$ ). Numbers within bars indicate the total numbers of transects performed at each island.