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Estimating animal density using camera traps without the need for individual recognition

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Summary

1. Density estimation is of fundamental importance in wildlife management. The use of camera traps to estimate animal density has so far been restricted to capture–recapture analysis of species with individually identifiable markings. This study developed a method that eliminates the requirement for individual recognition of animals by modelling the underlying process of contact between animals and cameras.
2. The model provides a factor that linearly scales trapping rate with density, depending on two key biological variables (average animal group size and day range) and two characteristics of the camera sensor (distance and angle within which it detects animals).
3. We tested the approach in an enclosed animal park with known abundances of four species, obtaining accurate estimates in three out of four cases. Inaccuracy in the fourth species was because of biased placement of cameras with respect to the distribution of this species.
4. *Synthesis and applications.* Subject to unbiased camera placement and accurate measurement of model parameters, this method opens the possibility of reduced labour costs for estimating wildlife density and may make estimation possible where it has not been previously. We provide guidelines on the trapping effort required to obtain reasonably precise estimates.

Key-words: abundance estimation, animal movement, camera traps, day range, density estimation, detection probability, trapping rate

Introduction

Camera trapping uses fixed cameras, triggered by infra-red sensors, to ‘trap’ images of passing animals. It is a quantitative technique that has relatively low labour costs, is non-invasive, incurs minimal environmental disturbance (Henschel & Ray 2003; Silveira, Jacomo & Diniz-Filho 2003), is robust to variation in ground conditions and climate and, most importantly, can be used to gain information on highly cryptic species and in difficult terrain where other field methods are likely to fail (Karanth & Nichols 1998; O’Brien, Kinnaird & Wibisono 2003; Silveira, Jacomo & Diniz-Filho 2003). Furthermore, camera traps are equally efficient at collecting data by day and night and provide the opportunity to collect additional information on species distribution and habitat use (Henschel & Ray 2003; Silveira, Jacomo & Diniz-Filho 2003), population structure and behaviour (Silveira, Jacomo & Diniz-Filho 2003; Wegge, Pokheral & Jnawali 2004).

In principle, the number of photographs taken per unit time (trapping rate) contains information about the density of a species. Supporting this expectation, a significant correlation

between trapping rates and independent estimates of density has been demonstrated across species in Sumatra (O’Brien, Kinnaird & Wibisono 2003). However, the application of trapping rate as an index of abundance (Carbone *et al.* 2001; Silveira, Jacomo & Diniz-Filho 2003) is controversial, both on theoretical and practical grounds (Jennelle, Runge & MacKenzie 2002; Karanth *et al.* 2003). This is primarily because it does not estimate the probability of detection and might therefore be confounded by variation in this factor (MacKenzie *et al.* 2002; Pollock *et al.* 2002). In an extreme interpretation, this would mean that correlations between trapping rate and density are only reliable if they are recalibrated for every location and time period to which they are applied, thus negating the need for the index.

A well-established and effective way to get around this problem is to use capture–recapture models to estimate abundance, based on the retrapping of recognizable individuals by cameras (Karanth 1995; Karanth & Nichols 1998; Maffei *et al.* 2005). This method is preferable to trapping rate indices as it is capable of providing robust, unbiased density estimates that are comparable across sites (Jennelle, Runge & MacKenzie 2002; Wilson & Delahay 2001; Srbek-Araujo & Chiarello 2005). However, the method is restricted to species with

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individually unique natural markings or, in principle, to those for which a sample can be individually marked prior to camera trapping (Trolle & Kery 2003). Relatively few species have natural markings sufficiently variable to be individually recognizable, most camera trap studies focusing on spotted and striped felids (Karanth & Nichols 1998; Henschel & Ray 2003; Maffei *et al.* 2005). Furthermore, although a robust method to measure the area effectively sampled in capture-recapture studies has recently become available (Borchers & Efford, *in press*), most camera trapping studies have so far used *ad hoc* approaches to handle this problem, such as average distances moved between captures and independent measures of home range size (Soisalo & Cavalcanti 2006). These methods have no basis in theory and their reliability is questionable (Williams, Nichols & Conroy 2002).

Species without individual markings have been under-represented in recent camera trapping research, consideration being restricted largely to presence in mammal inventories (Trolle 2003; Srbek-Araujo & Chiarello 2005) or as a supplement to the study of an individually identifiable target species (O'Brien, Kinnaird & Wibisono 2003). Models of occupancy (MacKenzie *et al.* 2002) and population size (Royle & Nichols 2003; Stanley & Royle 2005) that can estimate underlying detection probabilities from camera trapping data provide an important advance in this respect. However, currently these methods do not provide estimates of density and the extension of camera trapping methods to do this for species not individually identifiable would greatly extend the value of the technique.

Jennelle, Runge & MacKenzie (2002) suggest that a robust way to derive density estimates from camera trapping rates would be to model the underlying observation process. We present such a model, and provide field evidence of its reliability by comparing density estimates derived from camera trapping with known densities of several species in a large, enclosed animal park. Using simulations, we also explore how the precision of estimation is influenced by changing the amount and spatial allocation of sampling effort.

Methods

ESTIMATING DENSITY FROM TRAPPING RATES

Physicists have used mechanistic models to describe rates of collision between gas molecules for almost 150 years, and biologists have more recently adapted these models to describe rates of contact, for example between animal groups, between animals and observers and between sperm and eggs (for a comprehensive guide to gas models in biology see Hutchinson & Waser 2007). Classic two-dimensional models assume a circular zone around objects within which a contact occurs. In contrast, the contact zone of a camera trap is a segment-shaped area within which the infra-red detector can be triggered. We derive a model that describes rates of contact between animals and camera traps from which an estimator for animal density can be derived.

To envisage the basis of the two-dimensional ideal gas model, imagine a particle moving in space, covering an area that is the product of the width of the particle and the total distance moved in a given time. The expected number of contacts between particles in a given period is simply the ratio of the area covered by all particles present to the total area within which they are contained (Hutchinson & Waser 2007). For a stationary object with a circular detection zone within which contact occurs, the area covered by moving animals is very easily defined as the product of animal speed (v), time (t), twice the radius of the detection zone (r) and the number of particles present, given by the product of density and area (DA). Dividing this covered area by A , the number of contacts, y , is independent of the area notionally sampled:

$$y = 2rvD \quad \text{eqn 1}$$

(Hutchinson & Waser 2007). For camera traps, the detection zone is segment-shaped with radius r and angle θ (Fig. 1), rather than circular, and the width of an animal's covered path is no longer simply $2r$ but a variable dependent on the angle of approach. The width of the covered path in this case can be defined as the width of the profile presented to animals by the detection zone, averaged across all possible angles of approach. Figure 1 defines these profiles for π approach angles and, since the case is symmetrical, the average profile across all possible angles of approach is given by:

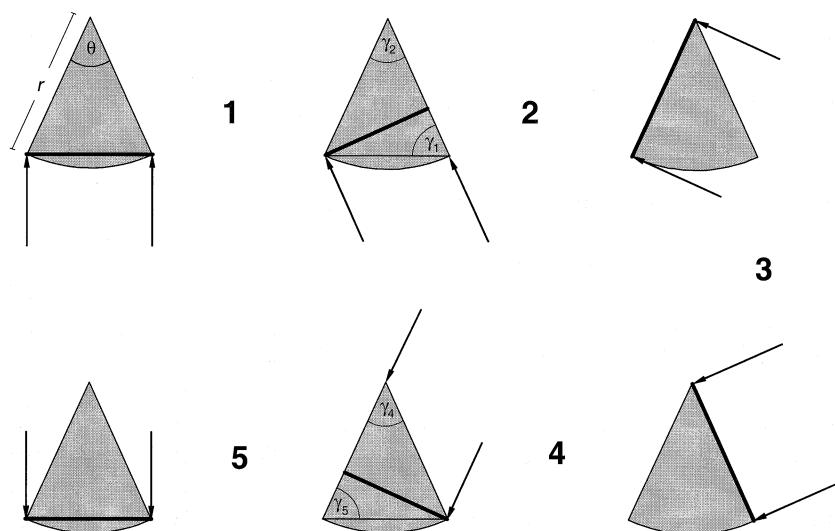


Fig. 1. Diagram illustrating the variation in profile presented to animals approaching from different angles by a segment-shaped camera trap detection zone. Approach directions are indicated by arrows, the detection zone is the shaded segment, defined by radial distance r and angle θ , and the profiles presented are indicated by heavy lines. Six limiting cases are shown for π approach angles, with five resulting transitions. The angles opposite the profiles, γ , are indicated for transitions 1, 2, 4 and 5 (the profile for transition 3 is constant so no such angle is required). The widths of profiles and ranges of γ for each transition are given by: transitions 1 and 5, $2r \sin(\theta/2) \sin(\gamma)$, $(\pi - \theta)/2 \leq \gamma \leq \pi/2$; transitions 2 and 4, $r \sin(\gamma)$, $0 \leq \gamma \leq \pi/2$; transition 3, r for θ approach angles.

$$\frac{2 \int_{(\pi-\theta)/2}^{\pi/2} 2r \sin\left(\frac{\theta}{2}\right) \sin(\gamma) d\gamma + 2 \int_{\theta}^{\pi/2} r \sin(\gamma) d\gamma + r\theta}{\pi} = \frac{4\sin\left(\frac{\theta}{2}\right)\cos\left(\frac{\pi-\theta}{2}\right) + 2\cos(\theta) + \theta}{\pi} = r \frac{2+\theta}{\pi} \quad \text{eqn 2}$$

where γ is the angle opposite the profile to be measured. The expected number of contacts between animals and camera traps (each contact giving rise to one photograph) is therefore given by:

$$y = \frac{2+\theta}{\pi} r t v D \quad \text{eqn 3}$$

Re-arranging gives density as a function of trapping rate (the number of photographs per unit time, y/t), animal speed of movement (v) and the dimensions of the camera detection zone (r and θ):

$$D = \frac{y}{t} \frac{\pi}{v r (2+\theta)} \quad \text{eqn 4}$$

This enables density to be estimated from trapping rate data, in combination with unbiased independent estimates of the other parameters. A modification of the formula is required when animals move in cohesive groups, in which case the independent unit recorded by the camera is the group rather than the individual. In this case, D in equation 4 is group density and must be multiplied by an unbiased independent estimate of average group size, g , to give the density of individual animals. It is also worth noting that setting $\theta = 0$ in equation 4 gives the FMP formula described by Stephens *et al.* (2006) for estimating animal density from the rate of contact between animal tracks and linear transects.

ESTIMATING VARIANCE

We estimated variance by non-parametric bootstrapping (Efron & Tibshirani 1993), resampling camera locations with replacement and taking the variance of a large number of resampled density estimates. Variances of independently estimated parameters (v , g , r and θ) can be incorporated using the delta method (Seber 1982), adding the squared coefficients of variation to that derived from bootstrapping to give an overall squared coefficient of variation for the density estimate. In the field study presented below, camera-related parameters r and θ were measured without sampling variance and we therefore assumed zero variances for these. None the less, because of small sample sizes in the field study, precision was generally low (particularly for the speed of movement estimates) and log-normal confidence intervals are therefore presented for density estimates.

Precision of estimates can often be improved by stratifying estimation. In this study, overall density is calculated as the average of the density estimates in different zones weighted by the areas of those zones. Confidence intervals for stratified estimates are given by resampling, with replacement within zones but without replacement between them, thus holding the numbers of camera placements per zone the same as the numbers in the original data.

FIELD TEST

Field work was carried out over 6 weeks from the 13 June to the 24 July 2005 at Whipsnade Wild Animal Park, located in Bedfordshire, south England. The park houses several free-ranging species, which

are enclosed within an area of 226 ha by an outer perimeter fence but which otherwise move freely throughout the park. For the purposes of this analysis, attention focused on four of these species: red-necked wallaby *Macropus rufogriseus* Desmarest, Chinese water deer *Hydropotes inermis* Swinhoe, Reeve's muntjac *Muntiacus reevesi* Ogilby and mara *Dolichotis patagonum* Zimmermann.

The park can be divided readily into four areas of contrasting habitat: two areas of open grassland with scattered scrub (the Institute Paddock with gentle slopes and the Downs with a steep scarp slope), one area of rough grassland and thicket on largely level but highly broken ground (the Old Farm) and one area of mixed lawns, roads, buildings and enclosures housing large animals with scattered trees (Central Park). Each free-ranging species uses these areas differentially in a predictable way, giving rise to contrasting densities of each across the park.

CAMERA SETTINGS AND PARAMETERS

Six DeerCam DC300 camera traps (Non Typical Inc., Wisconsin, USA; www.deercam.com) were used. These are passive infrared heat and motion detectors (Henschel & Ray 2003) linked to a 35-mm camera that records the date and time of every picture taken, imprinting it on the resulting photograph. Cameras were loaded with 36-exposure 200ASA colour films. Traps were moved to new locations approximately every 10 days, giving three trapping periods; however, one camera malfunctioned after its first placement and had to be withdrawn, leaving a total of 16 unique camera placements. Six of these were on the Downs, four on the Old Farm, three on the Institute Paddock and three in the Central Park. Subject to access constraints and the availability of suitable attachment points facing adequate open ground, the traps were placed semi-systematically, selecting locations in order to give good coverage of each area of the park.

The traps were placed at a height of approximately 0.75 m above ground to target the medium-sized mammals that were the focus of this study, and were not baited. The delay period between photographs was set at 2 min. This waiting period provides a balance between maintaining continuous sampling and avoiding film wastage through multiple records from a single effective contact caused by a single animal or group repeatedly triggering the trap while crossing the detection zone (Henschel & Ray 2003). The traps were checked near-daily and the film was usually removed and replaced before it was fully exposed. On occasions where the film ran out before it could be replaced, the time of the last exposure was determined from the developed photographs and the gap in sampling period removed before analysis.

The sensor detection zone parameters r and θ were estimated by a series of trials in which the camera was approached by a person at varying speeds and from varying directions, recording whether and at what point the sensor was triggered. In order to estimate the detection distance, r , the zone was crossed perpendicular to the sensor beam, while the detection arc, θ , was estimated by passing the camera parallel to the beam.

ESTIMATING ANIMAL PARAMETERS

In order to estimate density from camera trapping rate, independent estimates of speed of movement, v , and group size, g , are required for each of the focal species. An appropriate estimator of speed for our purposes was day range, and this was derived from focal watches of arbitrarily selected individuals, following each focal for 30 min and recording the total distance covered during that time as

the sum of all straight-line movements. The focal species were sufficiently habituated to the presence of people that a discretely positioned observer had no discernible influence on their behaviour. A total of 10 watches was carried out for each species, distributed evenly between 08:00 and 18:00 in order to control for any variation in movement patterns over the day. Day range for each species was then calculated as the mean across all focal watches for that species. Average group sizes were estimated by systematically recording the numbers of individuals in groups encountered along transects through the study area.

ANIMAL CENSUS

A complete census was carried out at the end of the camera trapping period between 09:30 and 14:00 by a team of 12 counters. In three peripheral open areas, a co-ordinated line of counters spaced approximately 20–40 m apart walked systematically through the area counting all animals breaking back through the line as it moved forward. Each of these three areas was covered in a single sweep and none of them adjoined each other, precluding any possibility of double counting. In Central Park, large animal enclosures prevented the use of this approach and small teams therefore systematically counted central areas, co-ordinating movements to ensure complete coverage without double counting. This counting technique has been used annually in the park for 6 years, and has been refined to ensure a high degree of confidence in the final counts, thus making a sampling approach unnecessary.

SIMULATING PRECISION

In order to explore the influence of varying amounts and spatial allocation of trapping effort on the precision of estimation, we simulated data by fixing overall average density, sampling time and animal and camera detection zone parameters and using equation 3 to calculate the expected average number of photographs per camera. Trapping data were then generated by drawing random numbers of photographs from a negative binomial distribution, with the mean defined by the expected number of photographs and variance defined by either the maximum observed in the field data or much lower, near-Poisson, variance, as would be expected if animal density was fairly uniform and the trapping process was well approximated by the ideal gas model (negative binomial dispersion parameters 0.4 and 20 for high and low variance, respectively). Densities were then estimated from these trapping rates, resampling 10 000 times for each case and calculating the coefficient of variation across density estimates as a measure of precision.

Simulations initially held deployment time constant at 10 days per camera, while varying the number of cameras between 2 and 100. A second set of simulations held the total number of cameras constant at 20 while varying the deployment time between 1 and 50 days per camera. In both these cases, the total amount of camera time varied from 20 to 1000 camera days. However, in practice, both the number of cameras and the amount of time available for the survey will often be limited, necessitating a trade-off between number of locations and time per location. A final set of simulations therefore fixed the total amount of camera time at 500 camera days, while varying the number of unique locations sampled between 2 (250 days location⁻¹) and 100 (5 days location⁻¹). In all simulations, average density was set at 10 km⁻², speed of movement v at 1 km day⁻¹, group size g at 1, camera detection radius r at 12 m and detection angle θ at 0.175 radians. The conclusions were not sensitive to any of these variables.

Table 1. Summary of the census data and camera trapping rates, split by species and zone

	Downs	Institute Paddock	Old Farm	Central Park	Total
Area (km ²)	0.49	0.28	0.23	1.26	2.26
Camera hours (day time)	898	440	543	317	2198
Census count					
Mara	15	2	0	136	153
Muntjac	3	0	5	22	30
Wallaby	544	213	185	120	1062
Water deer	36	10	133	91	270
Density (animals km ⁻²)					
Mara	30	7	0	108	68
Muntjac	6	0	22	18	13
Wallaby	1101	760	803	96	468
Water deer	73	36	577	72	119
Day-time camera trap photographs					
Mara	3	1	2	3	9
Muntjac	10	1	4	23	38
Wallaby	225	195	78	38	536
Water deer	32	3	89	23	147
Trap rate (photographs 12 h s ⁻¹)					
Mara	0.04	0.03	0.04	0.11	0.05
Muntjac	0.13	0.03	0.09	0.87	0.21
Wallaby	3.01	5.32	1.72	1.44	2.93
Water deer	0.43	0.08	1.97	0.87	0.8

Results

FIELD RESULTS

Wallabies were the most abundant species in the census, followed by water deer, mara and finally muntjac (Table 1). Local densities ranged from more than 1000 km⁻² (wallabies on the Downs) to 0 km⁻² (mara on Old Farm and muntjac on Institute Paddock). Despite this, camera traps revealed all four species in all four areas, confirming the utility of this technique in picking up low levels of usage.

A total of 3277 h of camera trapping was accumulated over 16 trap stations in the four sites. However, because the calculation of density requires estimates of day range, and these could only be obtained during the day, only daytime photographs were used in the following analyses, giving a total of 2198 camera hours. Diurnal trapping rate was significantly correlated with census density (Fig. 2a), although the precision of the relationship was moderate ($R^2 = 0.69$).

Animals generally moved little, particularly wallabies, although muntjac were considerably more mobile than the other species (Table 2). Wallabies and water deer were not found in cohesive groups, and were therefore assigned a group size of 1. Mara, and to some extent muntjac, on the other hand, were frequently found in pairs or family groups, and effective group sizes were therefore larger for these species (Table 2).

Densities estimated from camera trapping rates were more strongly correlated with observed census densities than the raw trapping rates [$r^2 = 0.76$ using $\log_{10}(x + 1)$ transformations].

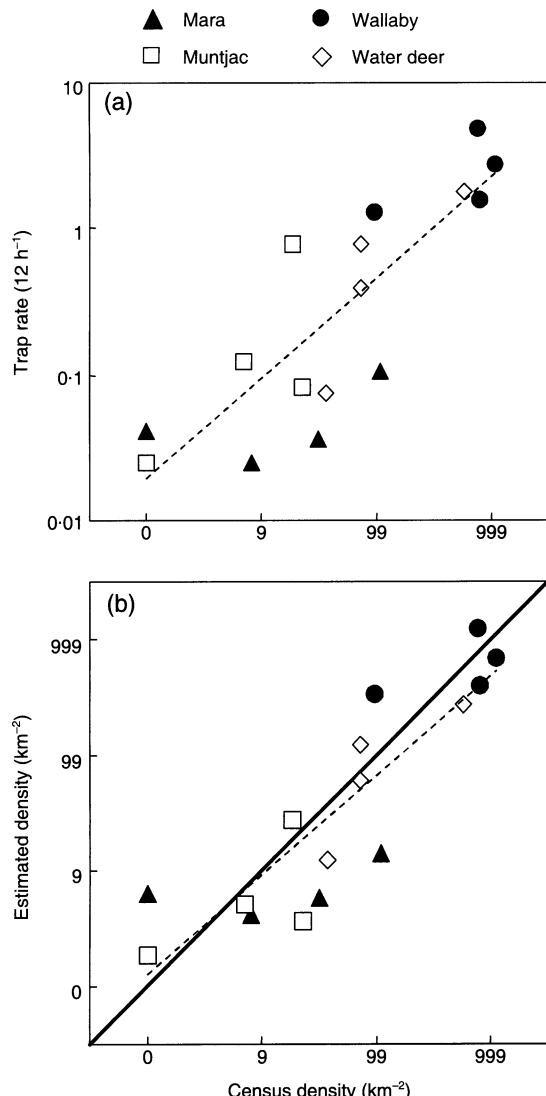


Fig. 2. (a) Camera trapping rates and (b) estimated densities of the four focal species plotted against census densities (note logarithmic scales). Dashed lines indicate linear regression lines; the solid line in (b) is the line of equality (estimated = census). Repeated points for each species represent the four discrete areas of the park.

Table 2. Summary of the independent variables required to calculate animal density from camera trapping rates (variance in parentheses)

	Mara	Muntjac	Wallaby	Water deer
Average day range (v, km day ⁻¹)	2.56 (11.57)	8.27 (36.87)	0.71 (1.27)	1.17 (2.22)
Average group size (g)	1.8 (0.4)	1.5 (0.28)	1 (0)	1 (0)
Detection arc (θ, radians)	0.175			
Detection distance (a, km)	0.012			

However, more importantly, absolute values of the estimated densities were scattered around the line of equality with census density (Fig. 2b). This indicates no strong bias in density estimates, suggesting that the method developed here for

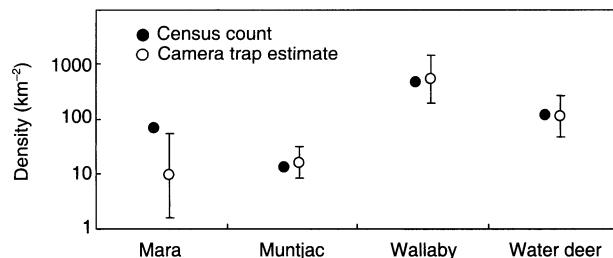


Fig. 3. Overall densities for the four focal species, compared between census densities and camera trap estimates stratified by region ($\pm 95\%$ bootstrap confidence intervals).

extracting absolute densities from trapping rate data performs well. The major exception to this appears to be at the lower end of the density range, where estimation is based on as few as one photo from only three camera locations. In addition, the census totals were extremely low in some cases, and represent a single count, which may not perfectly represent the longer term average densities picked up by the camera traps.

Given the issues raised above, a further test of prediction accuracy was made by estimating park-wide densities from camera trap data and comparing these with the census densities (Fig. 3). For muntjac, wallaby and water deer, estimated densities did not differ significantly from, and were within 22% of, the census results. However, the estimated number of mara was 86% lower than observed.

SIMULATION RESULTS

Obtaining a reasonable number of photographs from an adequate number of camera placements is clearly important for the success of this technique. We therefore explored the effect of increasing sampling effort on the precision of density estimates using simulations. We found that, for a fixed period of deployment per camera, precision increases rapidly up to around 20 camera placements, and continues improving much more slowly thereafter (Fig. 4a). If instead a fixed number of placements is available, but they are deployed for a variable period, precision is less sensitive to increasing effort, improving rapidly only up to around 10–20 photographs, with little change thereafter (Fig. 4b). When the total amount of camera time is fixed but the number of unique placements is varied, the influence of effort allocation on precision depends heavily on the variance in trapping rate (Fig. 4c). With high variance, precision improves rapidly up to around 20 placements, and more slowly thereafter, suggesting that, given fixed camera time, cameras should be moved often to maximize the number of placements. However, when variance in trapping rate is very low, precision is largely insensitive to the way in which the overall effort is allocated. The high variance case is usually likely to be closer to reality.

Taken together, these results suggest that an absolute minimum of 20 camera locations should be deployed, preferably at least 40 when the trapping rate is highly variable. In addition, cameras should be deployed for as long as necessary to obtain a minimum total of 10 photographs, preferably at least 20.

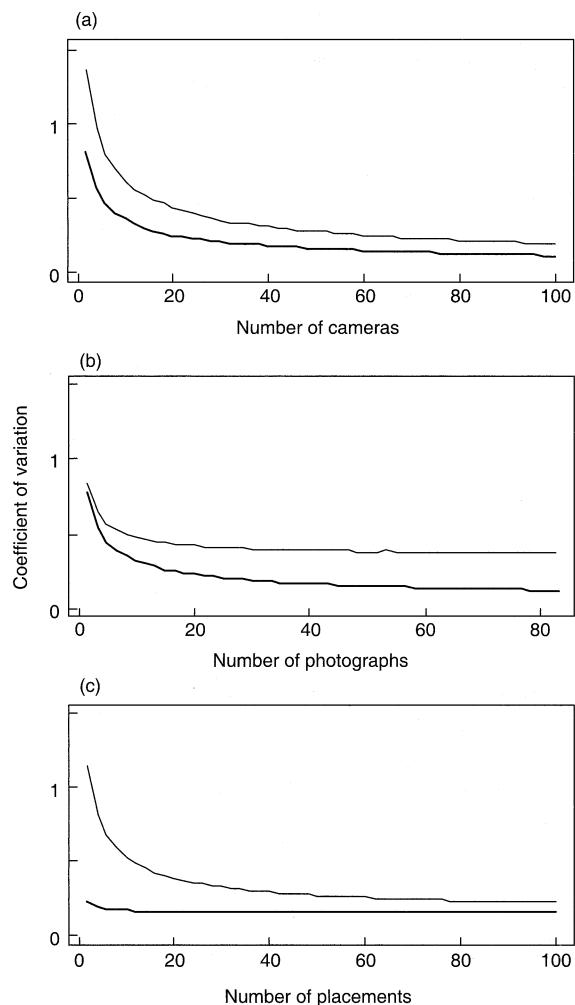


Fig. 4. The precision of estimated density from simulated data in relation to variation in sampling effort, assuming high or low variance in camera trapping rate (upper and lower curves, respectively, in each graph). Effort is varied as either (a) the number of cameras while holding time per camera constant; (b) the time per camera (indexed by the total number of photographs taken) while holding the number of cameras constant; and (c) the number of camera placements while holding the total amount of camera time constant.

The effort required to obtain an adequate sample will depend on the density and day range of the target species. Typical combinations of these biological parameters can be derived from comparative studies that provide allometric equations for day range and density in mammals (Silva & Downing 1994, 1995; Fa & Purvis 1997; Carbone & Gittleman 2002; Rowcliffe, Cowlishaw & Long 2003; Carbone *et al.* 2005). Figure 5 superimposes these typical combinations for three key mammal groups (carnivores, ungulates and rodents) on the expected trapping effort required to achieve 10 photographs. This indicates that for only the rarest populations of the large ungulates and carnivores would more than 1000 camera days be required. In most cases, considerably fewer than 1000 camera days are required, and sometimes fewer than 100 will be adequate, indicating that the method could yield robust results very rapidly in some circumstances.

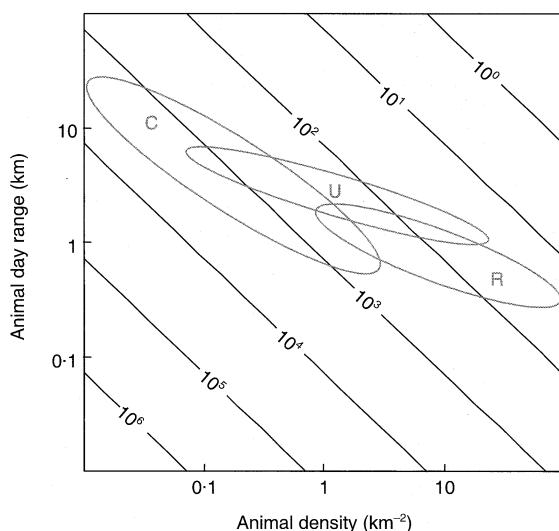


Fig. 5. Expected trapping effort (camera days, indicated by contours) required to achieve 10 photographs given varying density and day range, assuming a group size of 1. Typical combinations of day range and density are indicated for carnivores (C), ungulates (U) and rodents (R), calculated using allometric equations for day range and density at carrying capacity (see text) and illustrating densities between 10% and 100% of carrying capacity.

Discussion

In this paper, we have developed a technique for calculating animal densities from camera trapping rates by modelling the underlying detection process. By field-testing this novel approach, we have shown that it can provide reliable density estimates. By calculating the expected trapping rates for typical mammalian densities and day ranges (based on allometry), we have also shown that, in the majority of cases, the rate of return of records is likely to be sufficiently high to make the method efficient within realistic time frames under natural conditions. However, appropriate application of the technique requires a clear understanding of its constraints. First, there are three key assumptions, that: (i) animals conform adequately to the model used to describe the detection process; (ii) photographs represent independent contacts between animal and camera; and (iii) the population is closed. A second important consideration is the derivation of independent parameter estimates for modelling detection. These issues are discussed below, highlighting the implications for practical application of the method and considering possibilities for future statistical development.

A key underlying assumption is that animals behave like ideal gas particles, moving randomly and independently of one another. This is clearly unrealistic for animals in a natural setting, where individuals respond to one another and their physical environment. However, the purpose of the field test in this paper was to provide a preliminary assessment of whether the model can nevertheless provide an adequate approximation of the detection process. The fact that there was no apparent bias in density estimates for three out of the four species was encouraging, and it is also worth noting that

an equivalent method used to model rates of capture by snares has proved successful across a wide range of species in natural settings (Rowcliffe, Cowlishaw & Long 2003). This suggests that the method is reasonably robust to typical behaviour patterns that may violate underlying model assumptions.

A second important assumption of the detection model is that animals move independently of the cameras, and this assumption will clearly be violated if camera placement strategies either avoid or target focal species. Indeed, inappropriate camera placement explains the dramatic underestimation of mara abundance in this study. During census counts, around 90% of this population was observed in the Central Park area, where they typically graze open lawns. These areas are also heavily frequented by visitors to the park and, in order to avoid clogging the cameras with photographs of people, and possible interference with cameras, cameras were placed in less crowded areas away from the open lawns. These areas were also less frequented by mara, hence the underestimation of abundance.

The mara example represents the opposite extreme to placement strategies typically used in camera trapping studies, which often attempt to maximize trapping rates of rare species by placing cameras near to signs of the animal, on trails, ridge tops and water holes known to be used by them, or by using baits and lures. These approaches violate the underlying observation model developed here and cannot be used to obtain unbiased density estimates. However, rigidly random placement is unlikely to be viable in many situations. A balanced approach is needed, in which the random ideal is followed as closely as possible, while giving each camera enough clear view to provide a reasonable chance of detecting animals. We anticipate that further experience with the method will yield more concrete practical guidelines on placement strategies.

Another possible way in which the assumption that animals move independently of cameras might be violated is trap shyness, caused by the avoidance of either the camera units themselves or of their flash (Séquin *et al.* 2003; Wegge, Pokheral & Jnawali 2004). The problem could in principle be detected by looking for signs of decline in trap rate over time, although such a trend could also be the result of a decline in abundance over time, or to a general decline in trapping probability caused, for example, by declining speed of movement. If suspected, trap shyness might be solved by using infra-red imaging instead of flash photography or, if the animal of interest is at least partly diurnal, by disabling the flash and relying on natural light and day-time photographs only. However, in some more extreme cases where animals detect and avoid any unusual objects associated with humans (Séquin *et al.* 2003), further work might be required to identify and eliminate the cue on which avoidance is based.

While the method described here does not allow camera placements to target focal species, a degree of directed sampling is possible through appropriate stratification. For example, if some areas of a study site are difficult to reach, so long as these areas can be defined and measured and at least

some, albeit reduced, trapping effort takes place there, stratification of the kind described in this study can be used to obtain unbiased density estimates. Furthermore, whenever spatial variation in density is influenced by recognizable zonation on the ground, such as habitat type, stratification by these zones will be desirable in order to improve the precision of estimates.

The data for the method described must be in the form of numbers of independent contacts between animal (individual or group) and camera. This requires that an animal leaves the camera detection zone after a contact, and that the same or a different animal later re-enters in order to give a second, independent contact. If an animal remains within the detection zone for a long time, or a large group passes through over an extended period, several photographs may result from a single effective contact. In the field study presented here, we attempted to avoid this problem while limiting the amount of film used by setting the cameras to become inactive for 2 min after each photograph. However, using a long latency period runs the risk of missing independent contacts occurring in quick succession. Further work would be useful to refine advice on sensible latency periods but, in the meantime, it may be preferable to use little or no camera latency and assess which groups of photographs represent independent contacts based on their timing and content. This is obviously more feasible with digital cameras, for which picture storage is not generally a limiting factor.

A final assumption of the method is that the population surveyed is closed. In the field study presented here, there was no possibility of migration, and the trapping period was both relatively brief and outside the main breeding and mortality seasons, effectively giving a closed population. Ideally, trapping period should be targeted in this way to meet the closure assumption as far as possible. However, if abundance does change during a survey, the method will provide an estimate that simply averages across the trend.

Turning to the estimation of independent parameters, accurate measurement of trap-related parameters (radius and angle of detection) is relatively straightforward. These values vary to some degree with different cameras and environmental conditions (particularly temperature), and may be sensitive to animal size (Swann *et al.* 2004). Trials should therefore be carried out to define detection zones specific to each survey.

However, variation in detection zone dimensions is probably less important, and certainly easier to measure, than the animal-related parameters (group size and speed of movement). These are more problematic because they are generally difficult to measure without bias. For example, animal surveys frequently suffer from the fact that smaller groups are harder to detect, leading to overestimation of group size. Furthermore, both group size and speed of movement may be highly variable within species, for example changing with habitat, season, lunar cycle, levels of disturbance and population density. Ideally, group size and speeds of movement should therefore be estimated at the same time and place as the camera trap survey, using appropriate survey methods to avoid bias. In some circumstances it may be reasonable to use

estimates from studies on the same or related species under similar conditions, and it is even possible to use allometric estimates of day range (Carbone *et al.* 2005). However, these indirect measures are likely to introduce a large degree of bias and should be used cautiously only in cases where rough approximations of density are fit for purpose. In order to understand the likely extent of errors inherent in using comparative species parameters, and to move towards an ability to control for these errors, we strongly encourage further empirical work on the determinants of spatial and temporal variation in group sizes and day range, both within and between species.

At this stage in the development of the method we have used bootstrapping to estimate variance in density. However, ideally variance would be estimated using a maximum likelihood approach. This would have the benefit of formally describing both observation error (variance in the number of photographs for a given local density) and process error (variance in local density between camera trap placements), and allowing classical hypothesis tests to be used when comparing densities. However, preliminary explorations suggest that trapping rate data may be unable to separate reliably the relative contributions of observation and process errors to overall variance. A possible solution would be to estimate independently the degree of skew in trapping rates expected given known patterns of animal movement, and to allow variance in local density to be estimated by the data. The ideal gas model on which the underlying trap rate is based assumes that particles move in straight lines, in which case the number of contacts is theoretically Poisson distributed (Hutchinson & Waser 2007). Animals clearly do not follow this pattern and Hutchinson & Waser (2007) show that, while this has no effect on the expected number of contacts, it leads to a more variable distribution of contacts. Despite this useful observation, the theoretical underpinning needed to support a maximum likelihood estimator is not yet sufficiently advanced and we therefore leave this development to a future publication.

Summing up the advantages and disadvantages, the method developed here represents an advance in circumventing two limitations of mark–recapture analyses of camera trap data. First, and most importantly, it does not require the study species to have individually recognizable markings, allowing the technique to be used for a far wider range of species. Secondly, the method is not sensitive to the spacing of cameras relative to the size of animal home ranges, and can therefore be applied more flexibly across a wide range of species. However, the method has a significant disadvantage in comparison with mark–recapture analyses in that the placement of camera traps must be carefully randomized relative to the distribution of animals. As a result, directed placement of traps in order to maximize trapping rates cannot be used, and records of extremely scarce species may therefore accumulate too slowly to be of use. Finally, we emphasize that the need for unbiased, independent estimates of group size and day range are the most significant constraints on the use of this approach.

In conclusion, we feel that careful application of this method, taking full account of its limitations, has the potential to provide a useful contribution to the animal survey tool box, either as a less labour-intensive alternative to existing methods or, for some highly cryptic species, perhaps the only practical way to estimate density. The underlying principles may also be applicable to other static methods such as acoustic monitoring. Priorities for further work are, on the theoretical side, to develop a maximum likelihood estimator and to quantify the degree and determinants of variation in the model parameters across space, time and animal taxa. On the practical side, further testing of the approach is needed on a larger scale, and with a wider range of species. For example, camera trapping while simultaneously monitoring individuals by intensive radio-telemetry would help greatly to show how variation in movement patterns might influence results.

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