Quantifying levels of animal activity using camera trap data

J. Marcus Rowcliffe[1]*, Roland Kays[2,3], Bart Kranstauber[4,5], Chris Carbone[1] and Patrick A. Jansen[2,6]

[1]*Institute of Zoology, Zoological Society of London, Regent's Park, London, NW 1 4RY, UK;* [2]*Smithsonian Tropical Research Institute, Panamá City, Panamá;* [3]*North Carolina State University and Museum of Natural Sciences, Raleigh, NC, USA;* [4]*Department of Migration and Immuno-Ecology, Max Planck Institute for Ornithology, Radolfzell, Germany;* [5]*Department of Biology, University of Konstanz, Konstanz, Germany; and* [6]*Department of Environmental Sciences, Wageningen University, Wageningen, The Netherlands*

Summary

1. Activity level (the proportion of time that animals spend active) is a behavioural and ecological metric that can provide an indicator of energetics, foraging effort and exposure to risk. However, activity level is poorly known for free-living animals because it is difficult to quantify activity in the field in a consistent, cost-effective and non-invasive way.

2. This article presents a new method to estimate activity level with time-of-detection data from camera traps (or more generally any remote sensors), fitting a flexible circular distribution to these data to describe the underlying activity schedule, and calculating overall proportion of time active from this.

3. Using simulations and a case study for a range of small- to medium-sized mammal species, we find that activity level can reliably be estimated using the new method.

4. The method depends on the key assumption that all individuals in the sampled population are active at the peak of the daily activity cycle. We provide theoretical and empirical evidence suggesting that this assumption is likely to be met for many species, but may be less likely met in large predators, or in high-latitude winters. Further research is needed to establish stronger evidence on the validity of this assumption in specific cases; however, the approach has the potential to provide an effective, non-invasive alternative to existing methods for quantifying population activity levels.

Key-words: activity level, activity time, circular kernel, proportion active, remote sensors, Von Mises distribution, weighted kernel

Introduction

Animals must divide their time between various behaviours, among which there is a fundamental distinction between activity and rest (Halle & Stenseth 2000). Activity is essential to life, but is more energetically costly than resting. In addition, activity often involves elevated exposure to predation risk (Suselbeek *et al.* 2014) and thermal stress (Owen-smith 1998). Animals must therefore optimize the amount of time allocated to activity to meet basic needs while minimizing costs (Downes 2001).

The proportion of time spent active (hereafter activity level) is a key metric for understanding this fundamental behavioural trade-off, and is the focus of several strands of behavioural and ecological science. For example, there is a large and long-standing literature on the physiological constraints and mechanisms underpinning circadian rhythms, some of which touches on the implications for activity level (Daan & Aschoff 1975). There have also been efforts to understand the ecological context, for example focusing on environmental determinants of activity level (Owen-smith 1994; Pereira 2010), or using activity levels to construct energy budgets, from which ecological constraints can be understood (Ashkenazie & Safriel 1979; Houston, Prosser & Sans 2012). This area of research naturally extends to consideration of the population-level consequences of constraints on activity level, and the implications for population persistence (Gorman *et al.* 1999; Dunbar, Korstjens & Lehmann 2009).

Methods for measuring animal activity level have traditionally depended either on direct observation (Belovsky & Slade 1986), or on the use of laboratory apparatus such as running wheels (Sherwin 1998). Both methods are limited in the range of cases to which they can be applied. Furthermore, while activity measures in laboratory conditions have been a central tool for understanding mechanisms governing chronobiology and physiology, they are not helpful for understanding the behavioural ecology of activity in the field. However, technology has expanded the range of situations in which field measures of activity can be recorded, in particular through attaching telemetry devices to animals. Radio tracking has

*Correspondence author. E-mail: marcus.rowcliffe@ioz.ac.uk

been used to infer activity from speed of movement (Palomares & Delibes 1993), or from variance in signal strength (Kays *et al.* 2011a; Suselbeek *et al.* 2014). Tilt switches connected with telemetry devices have also been used to infer activity (Knowlton, Martin & Haug 1968), and more recently, multi-axial accelerometers have been used to provide detailed remote records of behavioural patterns (Shepard *et al.* 2008; Nathan *et al.* 2012).

An alternative to telemetry is to place remote sensors in the environment, rather than on animals. In particular, camera traps have a long history of use for providing information on patterns of activity (see Pearson 1960 for an early example; Bridges & Noss 2011 for a review), and new analytical methods are emerging that enable scientists to quantify aspects of behaviour from camera trap data (Ridout & Linkie 2009; Oliveira-Santos, Zucco & Agostinelli 2013). However, the potential for camera trap data to provide quantitative estimates of activity level has not yet been developed.

Here, we describe a method to estimate activity level from camera trap data collected at locations that are random with respect to the diel activity schedule. The method involves fitting a flexible circular distribution to time-of-detection data to describe the underlying activity pattern, and then calculating overall proportion of time active from this distribution. We assess the reliability of the method, first through simulations, second by applying the method to camera trap data from Panama and third by comparing the resulting activity-level estimates for 13 species of mammal with published estimates derived from other methods. Finally, we explore the precision of activity-level estimates as a function of sample size to determine sampling effort requirements.

The method

CONCEPTUAL DEVELOPMENT

As typically deployed, camera traps record animals only when they move outside refuges. For the purposes of this method, we therefore define animals as active whenever they move out of refuges that cannot be observed by cameras. Note that this definition may not map onto the finer categories of behaviour typically used by ethologists such as foraging, vigilant, sleeping or grooming, as any of these could potentially take place either within or outside refuges. However, as animals must fundamentally move to be recorded, and will be largely stationary within refuges, our definition captures the fundamental characteristic of activity as a more costly behavioural state than rest.

Assuming that activity level is the only determinant of the rate at which camera traps detect animals, the trap rate at a given time of day will be proportional to the level of activity in the population at that time, and the total amount of activity will be proportional to the area under the trap rate curve. In principle, if we have a point of reference linking trap rate to a known, nonzero amount of activity at one time in the daily cycle, we can calibrate the entire period and thereby estimate the overall absolute level of activity. Many populations of terrestrial mammals have highly predicable daily activity routines with distinct peaks when all individuals in the population are simultaneously active (Aschoff 1966). On this basis, we assume

that all animals in the population are active when camera trap rate reaches its maximum in the daily cycle.

The assumption of 100% activity at the peak rests on three lines of reasoning. First, we expect it to hold in many cases on theoretical grounds, in part because sensory adaptations tend to be specialized for particular light conditions (Peichl 2005), and also because the fundamental trade-off between the risks of starvation and predation are expected to generate an optimal time for activity to begin (Gerkema & Verhulst 1990; McNamara, Houston & Lima 1994). Second, empirical studies of synchrony support the assumption in some cases. Specifically, Suselbeek *et al.* (2014) demonstrated synchrony for one of the same species (agouti) at the same site as our study; Daan & Slopsema (1978) found synchrony of individual feeding times entrained by sunrise within common vole (*Microtus arvalis*) groups; Flowerdew (2000) showed that wood mice (*Apodemus sylvaticus*) are consistently active around midnight during the summer, although this study also showed that wood mice have no consistent activity scheduling during the winter. This last finding highlights a need to apply the method only in cases where synchrony can be demonstrated or reasonably assumed, a point we return to in the Discussion. Our third line of reasoning is that if the synchrony assumption is violated, we would expect this method to overestimate activity level relative to estimates made using other methods. However, under *Comparison with published activity levels* below, we show that camera trap activity-level estimates for a range of tropical forest species are exactly as expected on the basis of existing estimates made for similar species using other methods.

To evaluate the reliability of the second assumption made above, that the proportion of the population active is the only determinant of diel variation in trap rate, we need to determine whether other factors affecting trap rate vary in intensity over the daily cycle. In addition to activity level, trap rate is a function of speed while active, camera detection zone size and animal density (Rowcliffe *et al.* 2008). If there is no diel migration between observed and unobserved regions or habitats within the study site (which can be achieved by randomized camera placement), the surveyed population is closed over the daily cycle, and constant density can reasonably be assumed. By contrast, diel variation in animal travel speed and camera trap sensitivity is plausible. Using circular kernel regression (Xu, Nichols & Schoenberg 2011) to test whether animal travel speed while active varies significantly with time of day, we find no evidence for significant diel variation in speed among 12 Panamanian forest species (Appendix S1). However, using the covariate model for camera sensitivity described in Rowcliffe *et al.* (2011), we find that camera detection radius is 21% higher during the day than during the night (Appendix S2). During the development of the statistical model below, we therefore develop a method that allows us to correct for bias due to factors other than activity influencing diel variation in trap rate.

STATISTICAL DEVELOPMENT

Given a circular probability density function $f(x)$ fitted to a set of radian time of day observations, the area under the tangent to the maximum of the probability density function (f_{max}) between 0 and 2π is proportional to the maximum possible total activity level if the entire population was continually active (Fig. 1). The area under $f(x)$ (by definition 1) is proportional to total activity level, and the absolute overall activity level is therefore given by:
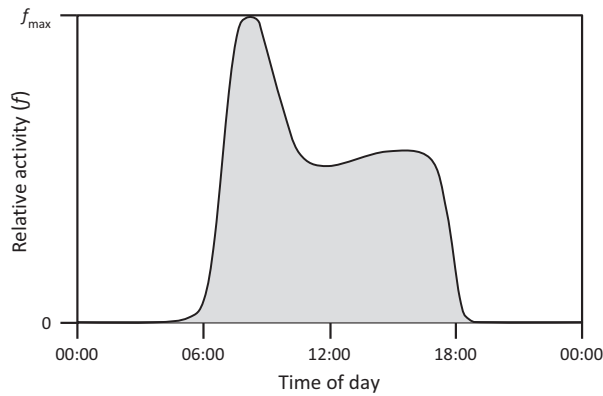
$$p = \frac{1}{2\pi f_{max}}$$

Fig. 1. The conceptual basis for estimating activity level from the diel distribution of animal detection events. The curve represents the pattern of relative activity over the day. The area under this curve (shaded) is proportional to the total amount of time allocated to activity. The area within the rectangle bounded by the maximum of the curve (f_{max}) and zero is proportional to the maximum possible amount of activity if the entire population remained 100% active throughout the day and night. Activity level, the proportion of time active, can be estimated as the ratio of these two areas.

we find f_{max} by solving numerically. The standard error of p can be estimated by nonparametric bootstrapping, sampling the data with replacement and refitting the model to yield a large number of estimates, the standard deviation of which provides an estimate of standard error. Bootstrap samples can also be used to estimate the standard error of relative activity at any given time of day. The significance of pairwise comparisons, either between relative activity levels at different times of day or between overall activity levels, can be estimated using a Wald test:

$$W = \frac{(E_1 - E_2)^2}{s_1^2 + s_2^2}$$

where E_i are the estimates to be compared, s_i their standard errors and the statistic W is χ^2 distributed on one degree of freedom.

The distribution of times of day at which animals are recorded is circular, and typically complex and multimodal, hence a flexible circular probability density function is needed to capture these patterns. We evaluated three such distributions for describing a sample of radian time of day observations, x_1, x_2, …, x_n. The first two of these are detailed in Ridout & Linkie (2009) and described only briefly here. First, given difference between radian time x and observation x_i:

$$d_i = \min(|x - x_i|, 2\pi - |x - x_i|)$$

the Von Mises kernel probability density is derived as the Von Mises probabilities (Mardia & Jupp 2000) of these differences with zero location parameter averaged across observations:

$$f(x) = \frac{1}{n}\sum_{i=1}^{n}\frac{e^{\kappa\cos(d_i)}}{2\pi I_0(\kappa)}$$

where the Von Mises concentration parameter κ defines the degree of smoothing (also known as bandwidth) and $I_0()$ is the modified Bessel function of order 0 (Bowman 1958). Second, the parametric non-negative trigonometric sums distribution proposed by Fernández-Durán (2004) is described by:

$$f(x) = 1 + 2\sum_{p=1}^{P} a_p \cos(x) + b_p \sin(x)$$

where the number of constituent parts P is optimized and parameters a_p and b_p estimated to fit the model. For both this and the kernel

model, we used the fitting procedures described in Ridout & Linkie (2009).

The third distribution that we explored was a Von Mises mixture distribution. This is a parametric approach that, as far as we know, has not been widely applied to complex circular distributions. In this case, the probability density with P constituent distributions is given by

$$f(x) = \sum_{p=1}^{P} w_p \frac{e^{\kappa_p \cos(x - \mu_p)}}{2\pi I_0(\kappa_p)}$$

where μ, κ and w are parameters defining the centre, concentration and weight, respectively, of each constituent distribution, and the weights have constraints $0 < w_p \leq 1$ and $\Sigma w_p = 1$. We fitted this model to data by maximizing the likelihood using package BBMLE (Bolker 2010) in R version 3·0·2 (R Core Team 2013). As in the non-negative trigonometric sums model, parameters were estimated for a given P, and P was optimized by sequentially adding component distributions until there was no further decrease in model AIC (Burnham & Anderson 2002).

A modified approach is needed where factors other than activity level are known to vary in intensity over the daily cycle. The random encounter model (REM, Rowcliffe *et al.* 2008) tells us that the key confounding factors considered above (animal speed and camera detection radius) have a linear relationship with trap rate. Therefore, given a confounding factor or product of factors q, our goal is to weight the distribution by the inverse of this value $v = 1/q$ to tune out the confounding effect, leaving only the activity signal in the distribution. In addition to being the best performing option in simulations (see following section), kernel distributions naturally lend themselves to weighting, as they are derived as the mean of a set of probabilities, and we can easily derive instead the weighted mean of these probabilities. The Von Mises kernel distribution weighted by v is a modification of the unweighted version above:

$$f(x) = \frac{1}{\sum_{i=1}^{n} v_i}\sum_{i=1}^{n} v_i \frac{e^{\kappa\cos(d_i)}}{2\pi I_0(\kappa)}.$$

Performance against simulations

To identify which of the three unweighted probability density functions described above provides the most robust estimator of activity level when activity alone determines the observed pattern of records, we carried out simulations to quantify bias for different underlying activity distributions and sample sizes. Simulated data were generated by taking random draws from complex Von Mises mixture distributions. Two different types of distribution were pre-defined, reflecting the two patterns most often seen in camera trap data: a diurnal (or equivalently nocturnal) pattern, with activity restricted to about half the daily cycle, and rapid onset, cessation and peaking of activity early and late; and a cathemeral pattern, with activity throughout the daily cycle, but with peaks of activity within that (Appendix S3a). For each of 500 datasets of varying sample size randomly drawn from these distributions, each of the three probability density functions was fitted to estimate activity level. For each estimate p, proportional bias was calculated as $p/p_{TRUE} - 1$, where p_{TRUE} is the true activity level defined by the underlying distribution used to generate the data. For the kernel model, the choice of bandwidth was initially made using the optimization procedure described in Ridout & Linkie

(2009), but this choice was additionally multiplied by a range of factors between 0·5 and 2 to explore the effect of varying function smoothness.

In most simulations, median bias was <20%. However, the outcome varied substantially between probability functions, sample sizes and underlying activity patterns. Increasing sample size reduced bias, and with a sample size of 500, bias was <10% in all cases. The worst performing case was the trigonometric sums model applied to the diurnal pattern with small sample size (Fig. 2, function TS). In this case, the best fit was almost always a single trigonometric component ($P = 1$), yielding an activity-level estimate of 0·5, which in this case is an overestimation of almost 100%. Although the trigonometric sums model performed better in other cases, it consistently overestimated proportion active as a result of oversmoothing. Ridout & Linkie (2009) point out that this model tends to have a very flat likelihood surface, with many local minima. Finding the global minimum is therefore problematic, requiring search

from many different starting parameter values, and making simulations slow. For practical reasons, the algorithm used to generate these tests used a limited number of starting positions for model fitting, which likely resulted in automatic selection of models that were not globally optimal in many cases, and which thus oversmoothed the distribution and overestimated proportion active.

The performance of Von Mises mixture models depended on the underlying activity pattern (Fig. 2, function VM). In the diurnal case, sudden onset and decay in activity tended to result in the selection of models with strongly spiked peaks that overshot the peak of the underlying data distribution, and so tended to underestimate proportion active, regardless of sample size. In contrast, the Von Mises mixture model was approximately unbiased for the smoother cathemeral activity pattern with large sample size, but at lower sample sizes tended to oversmooth, thus overestimating proportion active.
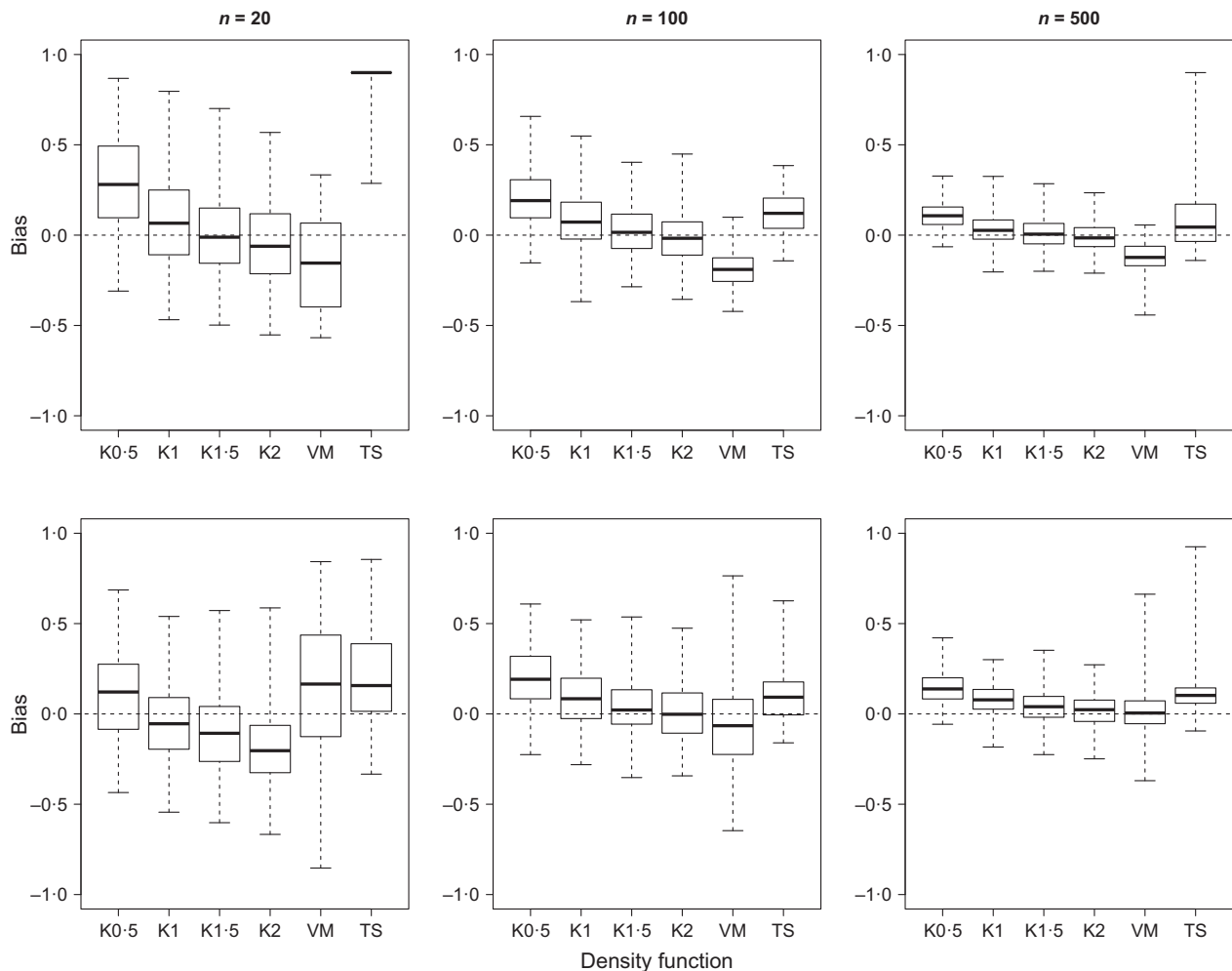

Fig. 2. Distributions of bias in estimated activity level *p* for alternative models fitted to data simulated with different underlying activity patterns and sample sizes. Given true proportion active p_{TRUE}, proportional bias is given by $p/p_{\text{TRUE}} - 1$. Sample size varies by column as indicated. Underlying activity patterns (Appendix S3a) vary by row: diurnal above, cathemeral below. Model codes are K, circular kernel, with following numbers indicating the multiplier used to adjust the bandwidth defining model flexibility; VM, Von Mises mixture; and TS, non-negative trigonometric sums. Bars are medians, boxes are interquartile ranges, and whiskers are ranges.

Finally, the performance of the kernel distribution depended primarily on the bandwidth adjustment used. The default bandwidth chosen using the algorithm described by Ridout & Linkie (2009) tended to oversmooth, giving activity-level estimates that were biased slightly upwards in most cases (Fig. 2, function K1). However, increasing the bandwidth by 50% (function K1·5) appeared to give an appropriate degree of flexibility, resulting in minimally biased activity-level estimates in all cases. These results indicate that a kernel distribution with bandwidth multiplier of around 1·5 is the most robust option for activity-level estimation.

To test the reliability of the weighted kernel function, we carried out a second set of simulations that used an underlying activity distribution with some degree of activity throughout the day (Appendix S3b), but used a plausible distribution of diel variation in other factors influencing trap rate to generate a confounded trap rate distribution from which to sample data (Appendix S3c). Activity-level estimates were then made by fitting the kernel model weighted by the inverse of the confounding factor distribution to sampled data, and bias explored for a range of sample sizes and kernel bandwidth adjustment multipliers, as above.

We found that bias of the weighted kernel model was minimal if bandwidth was adjusted upwards slightly, but that the amount of adjustment needed depended on sample size (Fig. 3). At very low sample size, bias was minimal without adjustment, but by $n = 500$, an adjustment multiplier of 2 was required to minimize bias. Overall, an adjustment multiplier of around 1·5 was the best compromise option across all sample sizes, consistent with the conclusion of the unweighted evaluation above.

Application to data

We applied the method to camera trapping data from Barro Colorado Island (BCI, 9°9′ N, 79°51′ W), Republic of Panama. Twenty camera traps were deployed at 764 random locations between February 2008 and February 2009, yielding 17 111 records of 25 species of mammal and bird. The study site and camera trapping methods are detailed fully in Kays *et al.* (2011b).

For the purpose of fitting activity functions to time-of-day data, activity records were defined as the times of day at which cameras were triggered by a given species. In cases where animals repeatedly triggered cameras without leaving the field of view, only the time of the initial trigger was used. The study additionally yielded data on animal travel speed and camera sensitivity used in the Appendices S1 and S2. We estimated activity levels for all mammal species for which we had a reasonable number of records, defined by inspecting the distribution of sample sizes. Several species had eight or fewer records, while the next most frequently captured had 42. We therefore considered the 13 species with at least this many records (Table 1). Because time of sunrise and sunset at this latitude varies little during the year, we fitted the models to clock time. Average body masses for BCI species were taken from BCI animal capture data (R. Kays unpublished data) where possible, otherwise from Emmons & Feer (1990) or Reid (1997).

Using fitted circular kernel distributions weighted to correct for shorter detection distances at night, estimated activity levels ranged from 0·21 to 0·56 (Table 1). The
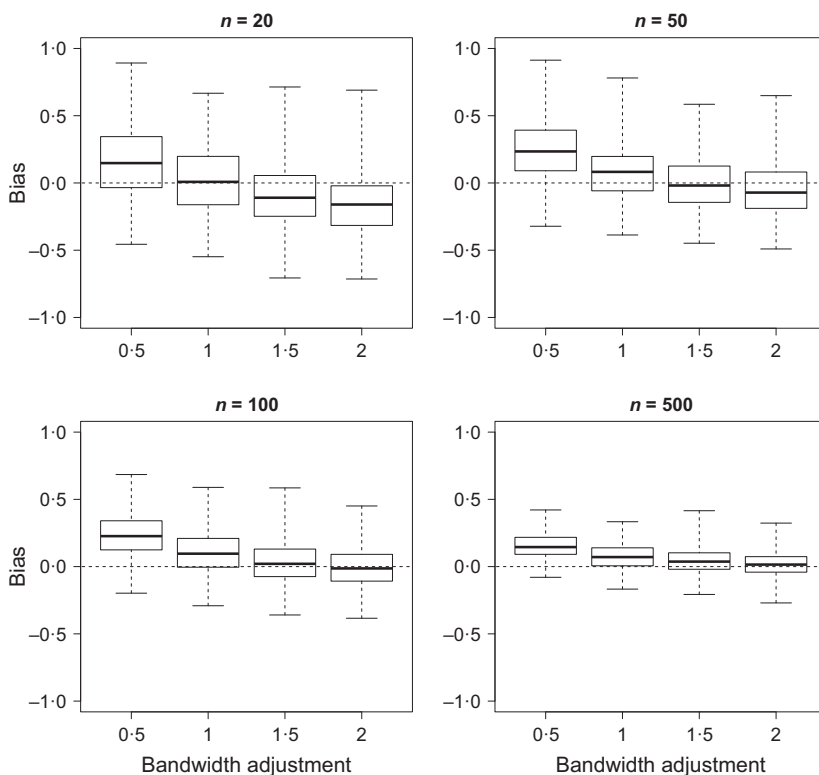

Fig. 3. Distributions of bias in activity level estimated using weighted circular kernels, as a function of sample size (n) and bandwidth. Definitions of bias and kernel bandwidth adjustment are as detailed in Fig. 2.

Table 1. Estimates of percentage of time active (activity level) for 13 species of mammal on Barro Colorado Island, Panama, estimated from the distribution of camera trapping photos over the daily cycle (Fig. 4)

Species	*n*	Mass (kg)	Estimate	SE	95% CI
			Activity level		
Mouse unknown species (mouse)	96	0·1	0·298	0·040	0·263–0·415
Tome's spiny rat (rat) *Proechimys semispinosus*	893	0·4	0·397	0·021	0·344–0·424
Red-tailed squirrel (squirrel) *Sciurus granatensis*	572	1·1	0·209	0·012	0·188–0·236
Common opossum (opossum) *Didelphis marsupialis*	120	3·5	0·373	0·033	0·326–0·454
Central American agouti (agouti) *Dasyprocta punctate*	10 292	3·6	0·286	0·006	0·274–0·298
White-nosed coati (coati) *Nasua narica*	459	4·0	0·409	0·022	0·345–0·431
Nine-banded armadillo (armadillo) *Dasypus novemcinctus*	121	4·2	0·366	0·027	0·311–0·417
Northern tamandua (tamandua) *Tamandua Mexicana*	128	4·2	0·563	0·066	0·450–0·707
Tayra *Eira Barbara*	42	5·0	0·359	0·074	0·146–0·445
Lowland paca (paca) *Cuniculus paca*	999	8·0	0·342	0·017	0·300–0·366
Ocelot *Leopardus pardalis*	317	11·9	0·353	0·038	0·283–0·427
Red brocket deer (brocket) *Mazama temama*	816	22·8	0·531	0·041	0·459–0·619
Collared peccary (peccary) *Tayassu tajacu*	2965	25·2	0·384	0·014	0·355–0·407

n, Number of camera trap records. Where given, the abbreviated common names in brackets are used in the text and Fig. 4.

coefficients of variation of these estimates lay between 2% and 21%, and were negatively related to sample size (Fig. 5). Confidence in the estimate was limited (CV = 21%) at the lowest sample size (42), but coefficients of variation declined rapidly to around 10% by the time sample size reached 100.

COMPARISON WITH INDEPENDENT ESTIMATES

Ideally, we would validate our activity-level estimates for Panamanian mammals against independent estimates for the same populations, but no such estimates exist for the mammal species on BCI. We therefore compared them with activity-level estimates from the literature, obtained for a range of terrestrial mammal species using other, well-established methods. The rationale of this analysis was to test whether camera trap activity-level estimates differed consistently from estimates made using other methods, controlling for other variables that potentially influence activity. We were particularly interested to discover whether the camera trap method tends to give estimates higher than those from other methods, as we would expect if the assumption that all individuals are active at the peak of the cycle is violated.

Fourteen activity-level estimates were initially obtained from Halle & Stenseth (2000). These data were augmented by literature search, using the search terms 'time budget*' and 'active' in the subject and keyword field of the ISI Web of Knowledge search engine to bring up potentially useful studies, yielding a further 27 estimates. Preliminary examination of these data indicated a few outlying points with extremely low activity levels, and these were found to be estimates for small species made in cold environments. Smaller mammals in cold environments typically spend much of their time torpid, and we might therefore expect activity levels for these cases to be categorically different from those in warmer environments. Six of the 41 activity-level estimates were excluded from the analysis for this reason.

We then used linear regression with information theoretic model selection to look for evidence that different methods yield consistently different activity-level estimates, while controlling for potentially confounding variables selected on the basis of previous studies of the determinants of activity, day range and home range. We took this broad view of metrics related to energy and space use because there are currently few substantial studies focusing specifically on activity level, and we conjectured that determinants of these other metrics might also be important for activity level. At a cross-species level, body mass is a pervasive influence (Belovsky & Slade 1986; Kelt & Vuren 2001; Carbone *et al*. 2005), while there is also evidence that social group size, diet category and taxonomic order can be important (Carbone *et al*. 2005). We therefore considered all of these variables, with body mass and group size log transformed, order categorized as carnivora, artiodactyla, rodentia or other, and diet categorized as herbivore or faunivore/omnivore. Activity might also be influenced by a wide range of more local factors that vary within species, including climate, photoperiod, habitat and the densities of food or competitors (Gittleman & Harvey 1982; Börger *et al*. 2006). We compared activity levels between rather than within species, and were therefore unable to consider all of these possible processes comprehensively; however, we controlled for local effects as far as possible by including latitude and average annual precipitation in the model. The activity-level estimation methods included were camera trapping (this article), direct observation, telemetry and telemetry with activity sensors. The data for this analysis are provided in Appendix S4.

We found that when controlling for body mass and diet, there was no evidence for consistent differences between activity-level estimates provided by different methods: the total AIC weight for method as a predictor of activity level was only 0·06, and the best model including method had a ΔAIC of 5·34 (Appendix S5). Activity level was strongly related to body mass, but there was no convincing evidence for any other confounding effects on activity level. Activity levels estimated from
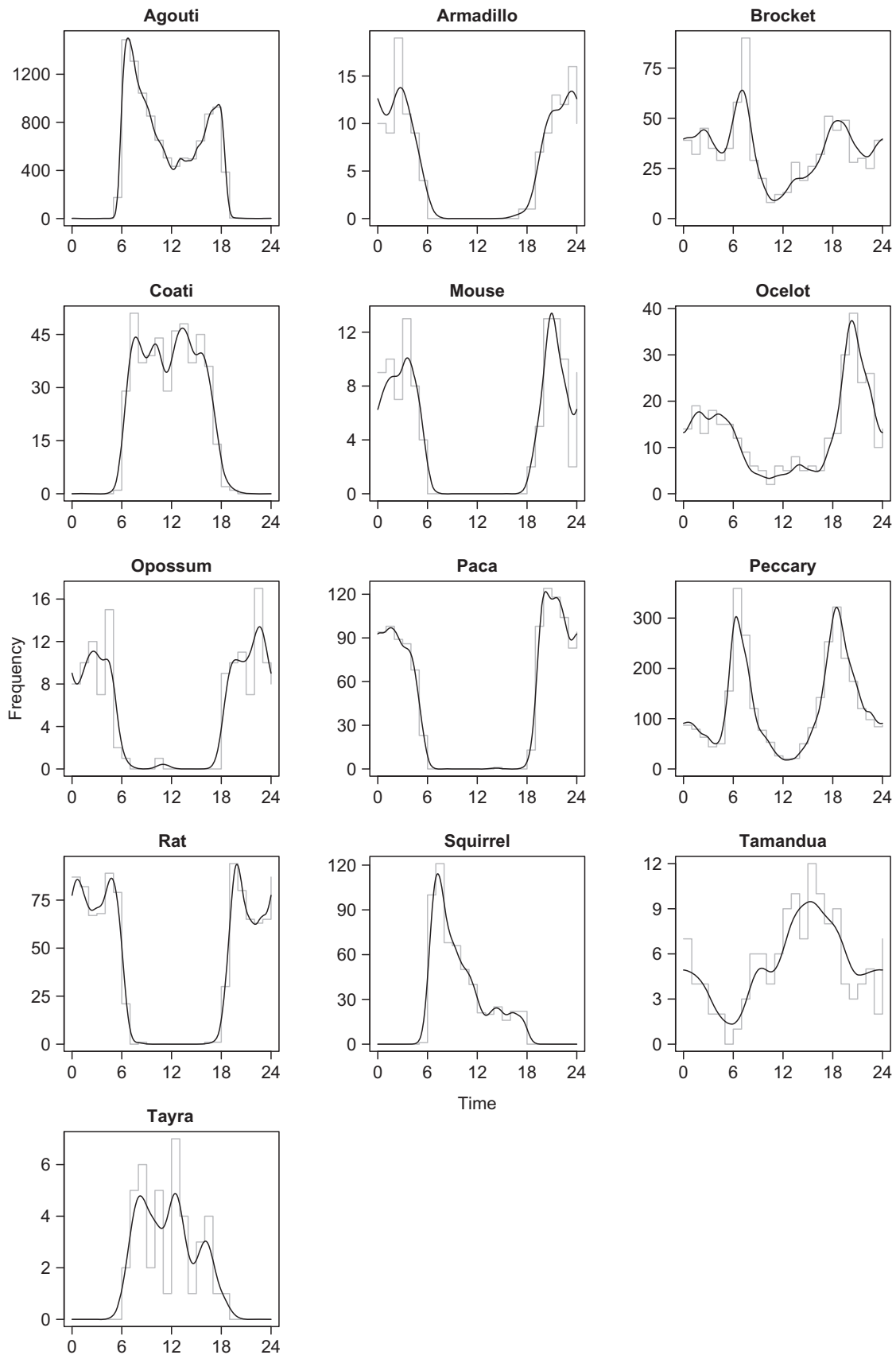
Fig. 4. Activity patterns of 13 species of mammal on Barro Colorado Island, Panama, as captured by distributions of camera trap records. Grey steps are observed frequencies, and black curves are fitted circular kernel distributions. Sample sizes and estimates of active level derived from the fitted distributions are given in Table 1.
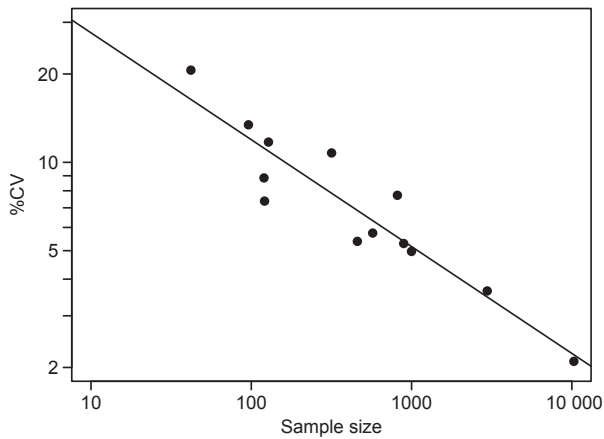
Fig. 5. Relationship between the percentage coefficient of variation of activity level, estimated from camera trap data for 13 mammal species, and sample size. The trend line is from a linear regression fitted to log–log data.
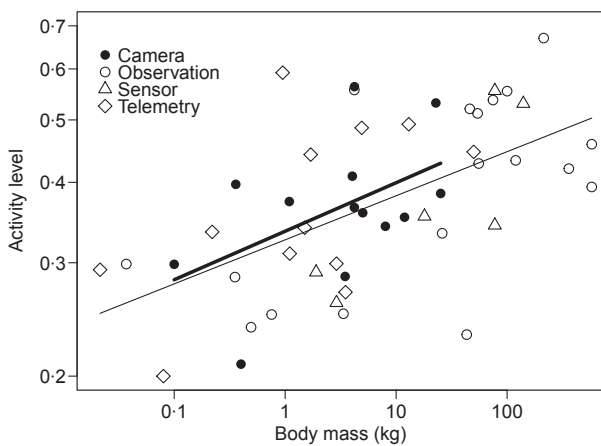

Fig. 6. Relationship between estimated activity level and body mass, separated by estimation method. Fitted lines are linear regression predictions for camera data [bold line, intercept: 0·347 (0·029 SE); slope: 0·026 (0·015 SE); Pearson correlation: 0·47] and other methods combined [fine line, intercept: 0·342 (0·023 SE); slope: 0·025 (0·007 SE); Pearson correlation: 0·56]. Method definitions are as follows: camera trapping using the analytical method developed in this paper (camera); direct observation of focal animals (observation); telemetry with activity sensors, including tilt switches or accelerometers (sensor); telemetry: inferring activity from telemetry-based movement patterns.

camera trap data were entirely within the range of estimates previously made for equivalently sized species using other methods, and the regression coefficients for the relationships between body mass and activity were almost identical for camera trapping and other methods (Fig. 6). This result indicates a lack of consistent bias in the camera trapping method relative to others.

Discussion

STRENGTHS

Activity level is a fundamental behavioural and ecological variable that has received relatively little attention in field settings

due to the difficulty in measurement. In this paper, we have shown that activity levels of terrestrial mammals can – under certain conditions – be reliably estimated at the population level from camera trap data, using an appropriately tuned probability density function. Furthermore, we show how the confounding effects of diel variation in animal movement speed or camera sensitivity can be controlled for by appropriately weighting the probability density function. Finally, we have shown that the precision of activity level estimated using these methods is reasonable for achievable sample sizes.

The key advantage of our method is the fact that camera trapping is non-invasive, involves relatively low labour costs, can be applied in a wide variety of field and captive settings, and yields data on a wide range of terrestrial species, including those that can neither be observed directly nor captured and tagged. The camera trap method is cost-effective compared with direct observations or tagging, which are generally extremely labour intensive and/or invasive. Furthermore, activity levels recorded by camera traps usually emerge from the records of many individual animals and so offer population-level measures that could readily be compared between different places or times. In contrast, tag-based approaches are typically applied to only a small sample of animals, and thus may not represent the wider population. Given these advantages, and enormous current growth in the use of camera traps (Rowcliffe & Carbone 2008), this new analytical method has the potential to improve our understanding of pattern and process in activity level. For example, we anticipate that new research avenues may open up on the effects of local animal density, human disturbance or seasonal food fluctuations on activity levels in free-ranging populations.

LIMITATIONS

A key limitation of our method is the need to assume that all individuals in the population are active at the peak of the activity cycle. This assumption could be dropped if it were possible to measure the proportion of the population active at any given point in the day; however, this is rarely likely to be practical. For our method to be widely useful, the assumption therefore needs to be predictably met in many situations. Under *Conceptual development* above, we reviewed the few empirical studies of synchrony in free-living animals that we were able to find, showing mixed support. However, rather than representing random outcomes, we suggest that the presence or absence of synchronized activity will be predictable on the basis of a few readily observed variables. For example, the unsynchronized example above was for wood mice in a northern winter under very short day lengths (Flowerdew 2000), and it seems generally likely that synchrony cannot be expected in these conditions, particularly for smaller species that rely on stored food reserves. We also expect that species such as large predators whose foraging cycles are longer than a day are unlikely to show a synchronous daily activity peak. For example, pumas (*Puma concolor*) go 2–5 days between large mammal kills, during which they spend much of their time static, either feeding or entirely inactive (Beier, Choate & Barrett 1995).While we do

not claim that this survey of activity synchrony is comprehensive, the published literature unfortunately appears to have little to say about the issue at present, highlighting a need for greater focus on this question.

A second potential limitation of our method is that the camera trap-based definition of activity underlying the approach may differ from definitions underlying other approaches, making estimates hard to compare across methods (see *Conceptual development*). Nevertheless, our comparative analysis demonstrated that different methods to estimate activity level give very similar results, suggesting that definitions of activity are reasonably consistent across methods. However, this conclusion is based on a test in which only one method was used for any given population, and it would be desirable to run a stronger test by applying multiple methods simultaneously to single populations. In the meantime, a degree of caution is warranted in comparing activity-level estimates derived using different methods.

Caution is also warranted when using datasets in which the time of sunrise and sunset varies. This problem is negligible in the tropics and in short studies, but variation can be dramatic over longer periods at higher latitudes. Peaks in activity are usually tuned to sunrise or sunset, and progression of these times therefore flattens peaks and overestimates activity level (Aschoff 1966). In these situations, probability density functions should be fitted to solar time (the deviation of clock time from sunrise and sunset). Nouvellet *et al.* (2012) offer equations and code to translate local clock time into solar time, based on latitude and date at which photographs were taken.

Finally, while we suggested under *Strengths* that achieving population-level estimates of activity level can be an advantage, for some purposes we may require individual-level activity estimates, which camera traps can provide only in exceptional cases. In contrast, tag-based studies readily allow for insight into individual strategies, for example comparing animals of different sexes or ages (Suselbeek *et al.* 2014).

PRACTICAL IMPLICATIONS

Under *Conceptual development*, we touched on the point that diel variation in animal density in the sampled area can lead to bias. Avoiding this bias requires that cameras are placed randomly with respect to diel patterns of movement, which could theoretically allow for placement strategies maximizing overall trap rate. For example, many camera trap studies currently place cameras on trails to maximize trap rate. This strategy is valid for activity-level estimation so long as animals use trails to the same extent across the daily cycle, which could be tested by comparing trap rate patterns on and off trail. In contrast, using bait to attract animals seems likely to introduce non-random diel patterns of space use that would preclude accurate estimation of activity level. In practice, it will probably be safer to use random camera placements in most cases, although this strategy may still not work in cases where some important habitat is entirely inaccessible. For example, in the case of

semi-arboreal species, it is not feasible to camera trap representatively in the canopy as well as on ground. In the absence of data from the canopy, diel variation in the proportion of the population using the ground will lead to bias in activity-level estimation.

Given that the assumption of a synchronized activity peak is central to the method but not always justifiable, the method clearly needs to be applied cautiously with this in mind. On the basis of the results and theoretical evidence discussed here, we expect that many of the terrestrial mammal species commonly captured by camera traps are likely to synchronize their activity peaks at some point in the daily cycle. However, a stronger research focus on the issue of synchrony is required to demonstrate this, given the paucity of evidence currently available. Users should seek the best possible evidence justifying the synchrony assumption on a case-by-case basis, and interpret results with a degree of confidence equivalent to the degree of confidence in this assumption being met.

Finally, we note that, although the method has been developed specifically for application to camera trap data, the idea could in principle be applied to data gathered using any sensor technology that records the temporal pattern of animal activity in the environment. For example, acoustic monitors might provide suitable records in some cases. We therefore encourage exploration of the method's application to other existing and emerging technologies. A new R package (activity) contains functions to fit and visualize circular kernel distributions with the option of weighting, calculate associated activity levels and their standard errors, statistically compare estimates, and perform circular kernel regression.

Data accessibility

The data used in this paper have been archived on figshare. (Rowcliffe *et al.* 2014).

References

Aschoff, J. (1966) Circadian activity patterns with two peaks. *Ecology*, **47**, 657–662.

Ashkenazie, S. & Safriel, U.N. (1979) Time-energy budget of the semipalmated sandpiper *Calidris pusilla* at Barrow, Alaska. *Ecology*, **60**, 783–799.

Beier, P., Choate, D. & Barrett, R.H. (1995) Movement patterns of mountain lions during different behaviours. *Journal of Mammalogy*, **76**, 1056–1070.

Belovsky, G.E. & Slade, J.B. (1986) Time budgets of grassland herbivores: body size similarities. *Oecologia*, **70**, 53–62.

Bolker, B.M. (2010) Tools for general maximum likelihood estimation. http://CRAN.R-project.org/package=bbmle.

Börger, L., Franconi, N., Ferretti, F., Meschi, F., De Michele, G., Gantz, A. & Coulson, T. (2006) An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *The American Naturalist*, **168**, 471–485.

Bowman, F. (1958) *Introduction to Bessel Functions*. Dover, New York.

Bridges, A.S. & Noss, A.J. (2011) Behavior and activity patterns. *Camera-Traps in Animal Ecology* (eds A.F. O'Connell, J.D. Nichols & K.U. Karanth), pp. 57–70. Springer, New York.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer, New York.

Carbone, C., Cowlishaw, G., Isaac, N.J.B. & Rowcliffe, J.M. (2005) How far do animals go? Determinants of day range in mammals. *The American Naturalist*, **165**, 290–297.

Daan, S. & Aschoff, J. (1975) Circadian rhythms of locomotor activity in captive birds and mammals: their variations with season and latitude. *Oecologia*, **18**, 269–316.

Daan, S. & Slopsema, S. (1978) Short-term rhythms in foraging behaviour of the common vole, *Microtus arvalis*. *Journal of Comparative Physiology*, **127**, 215–227.

Downes, S. (2001) Trading heat and food for safety: costs of predator avoidance in a lizard. *Ecology*, **82**, 2870–2881.

Dunbar, R.I.M., Korstjens, A.H. & Lehmann, J. (2009) Time as an ecological constraint. *Biological Reviews*, **84**, 413–429.

Emmons, L.H. & Feer, F. (1990) *Neotropical Rainforest Mammals: A Field Guide*. University of Chicago Press, Chicago, Illinois, USA.

Fernández-Durán, J.J. (2004) Circular distributions based on non-negative trigonometric sums. *Biometrics*, **60**, 499–503.

Flowerdew, J.R. (2000) Wood mice – small granivores/insectivores with seasonally variable patterns. *Activity Patterns in Small Mammals: An Ecological Approach* (eds S. Halle & N.C. Stenseth), pp. 177–190. Springer, Berlin.

Gerkema, M.P. & Verhulst, S. (1990) Warning against an unseen predator: a functional aspect of synchronous feeding in the common vole, *Microtus arvalis*. *Animal Behaviour*, **40**, 1169–1178.

Gittleman, J.L. & Harvey, P.H. (1982) Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, **10**, 57–63.

Gorman, M.L., Mills, M.G., Raath, J.P. & Speakman, J.R. (1999) High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature*, **391**, 479–481.

Halle, S. & Stenseth, N.C. (2000) *Activity Patterns in Small Mammals: An Ecological Approach*. Springer, Berlin.

Houston, A.I., Prosser, E. & Sans, E. (2012) The cost of disturbance: a waste of time and energy? *Oikos*, **121**, 597–604.

Kays, R., Tilak, S., Crofoot, M., Fountain, T., Obando, D., Ortega, A. *et al.* (2011a) Tracking animal location and activity with an automated radio telemetry system in a tropical rainforest. *The Computer Journal*, **54**, 1931–1948.

Kays, R., Tilak, S., Kranstauber, B., Jansen, P.A., Carbone, C., Rowcliffe, J.M., Fountain, T., Eggert, J. & He, Z. (2011b) Camera-traps as sensor networks for monitoring animal communities. *International Journal of Research and Reviews in Wireless Sensor Networks*, **1**, 19–29.

Kelt, D.A. & Vuren, D.H.V. (2001) The ecology and macroecology of mammalian home range area. *The American Naturalist*, **157**, 637–645.

Knowlton, F.F., Martin, P.E. & Haug, J.C. (1968) A telemetric monitor for determining animal activity. *The Journal of Wildlife Management*, **32**, 943–948.

Mardia, K.V. & Jupp, P.E. (2000) *Directional Statistics*. Wiley, Chichester.

McNamara, J.M., Houston, A.I. & Lima, S.L. (1994) Foraging routines of small birds in winter. *Journal of Avian Biology*, **25**, 287–302.

Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M. & Getz, W.M. (2012) Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *Journal of Experimental Biology*, **215**, 986–996.

Nouvellet, P., Rasmussen, G.S.A., Macdonald, D.W. & Courchamp, F. (2012) Noisy clocks and silent sunrises: measurement methods of daily activity pattern. *Journal of Zoology*, **286**, 179–184.

Oliveira-Santos, L.G.R., Zucco, C.A. & Agostinelli, C. (2013) Using conditional circular kernel density functions to test hypotheses on animal circadian activity. *Animal Behaviour*, **85**, 269–280.

Owen-smith, N. (1994) Foraging responses of kudus to seasonal changes in food resources: elasticity in constraints. *Ecology*, **75**, 1050–1062.

Owen-smith, N. (1998) How high ambient temperature affects the daily activity and foraging time of a subtropical ungulate, the greater kudu (*Tragelaphus strepsiceros*). *Journal of Zoology*, **246**, 183–192.

Palomares, F. & Delibes, M. (1993) Determining activity types and budgets from movement speed of radio-marked mongooses. *Journal of Wildlife Management*, **57**, 164–167.

Pearson, O.P. (1960) Habits of *Microtus californicus* revealed by automatic photographic recorders. *Ecological Monographs*, **30**, 231–250.

Peichl, L. (2005) Diversity of mammalian photoreceptor properties: adaptations to habitat and lifestyle? *The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology*, **287**, 1001–1012.

Pereira, J.A. (2010) Activity pattern of Geoffroy's cats (*Leopardus geoffroyi*) during a period of food shortage. *Journal of Arid Environments*, **74**, 1106–1109.

R Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reid, F. (1997) *A Field Guide to the Mammals of Central America and Southeast Mexico*. Oxford University Press, Oxford.

Ridout, M.S. & Linkie, M. (2009) Estimating overlap of daily activity patterns from camera-trap data. *Journal of Agricultural, Biological and Environmental Statistics*, **14**, 322–337.

Rowcliffe, J.M. & Carbone, C. (2008) Surveys using camera-traps: are we looking to a brighter future? *Animal Conservation*, **11**, 185–186.

Rowcliffe, J.M., Field, J., Turvey, S.T. & Carbone, C. (2008) Estimating animal density using camera-traps without the need for individual recognition. *Journal of Applied Ecology*, **45**, 1228–1236.

Rowcliffe, J.M., Carbone, C., Jansen, P.A., Kays, R. & Kranstauber, B. (2011) Quantifying the sensitivity of camera-traps: an adapted distance sampling approach. *Methods in Ecology and Evolution*, **2**, 464–476.

Rowcliffe, J. M., Kays, R., Kranstauber, B., Carbone, C. & Jansen, P. (2014) Activity level estimation data. *Figshare*, http://dx.doi.org/10.6084/m9.figshare.1160536.

Shepard, E.L.C., Wilson, R.P., Quintana, F., Laich, A.G., Liebsch, N., Albareda, D.A. *et al.* (2008) Identification of animal movement patterns using tri-axial accelerometry. *Endangered Species Research*, **10**, 47–60.

Sherwin, C.M. (1998) Voluntary wheel running: a review and novel interpretation. *Animal Behaviour*, **56**, 11–27.

Suselbeek, L., Emsens, W.-J., Hirsch, B.T., Kays, R., Rowcliffe, J.M., Zamora-Gutierrez, V. & Jansen, P.A. (2014) Food acqusition and predator avoidance in a Neotropical rodent. *Animal Behaviour*, **88**, 41–48.

Xu, H., Nichols, K. & Schoenberg, F.P. (2011) Directional kernel regression for wind and fire data. *Forest Science*, **57**, 343–352.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Variation in speed with time of day.

Appendix S2. Variation in camera sensitivity with time of day.

Appendix S3. Activity and confounding detectability patterns used to generate simulated data for evaluating bias in the estimation of activity level.

Appendix S4. Data used in comparative analysis of activity level across multiple published sources.

Appendix S5. Model selection table for comparative analysis of activity level across multiple published sources.