

ORIGINAL RESEARCH

Wildlife speed cameras: measuring animal travel speed and day range using camera traps

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Animal tracking, image analysis, length-biased distributions, movement ecology, travel distance, video capture

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Abstract

Travel speed (average speed of travel while active) and day range (average speed over the daily activity cycle) are behavioural metrics that influence processes including energy use, foraging success, disease transmission and human-wildlife interactions, and which can therefore be applied to a range of questions in ecology and conservation. These metrics are usually derived from telemetry or direct observations. Here, we describe and validate an entirely new alternative approach, using camera traps recording passing animals to measure movement paths at very fine scale. Dividing the length of a passage by its duration gives a speed observation, and average travel speed is estimated by fitting size-biased probability distributions to a sample of speed observations. Day range is then estimated as the product of travel speed and activity level (proportion of time spent active), which can also be estimated from camera-trap data. We field tested the procedure with data from a survey of terrestrial mammals on Barro Colorado Island, Panama. Travel speeds and day ranges estimated for 12 species scaled positively with body mass, and were higher in faunivores than in herbivores, patterns that are consistent with those obtained using independent estimates derived from tracked individuals. Comparisons of our day range estimates with independent telemetry-based estimates for three species also showed very similar values in absolute terms. We conclude that these methods are accurate and ready to use for estimating travel speed and day range in wildlife. Key advantages of the methods are that they are non-invasive, and that measurements are made at very high resolution in time and space, yielding estimates that are comparable across species and studies. Combined with emerging techniques in computer vision, we anticipate that these methods will help to expand the range of species for which we can estimate movement rate in the wild.

Introduction

The pace at which mobile organisms move is a fundamental biological characteristic, with relevance to physiology, behaviour and ecology. Research on these processes has typically measured movement rate at one of two temporal scales: short term, reflecting speed within bouts of activity (including studies of locomotion), and long term, reflecting the movement distance integrated over the

whole activity cycle. The short-term metric (henceforth travel speed, Pyke 1981) affects the rate at which resources and predators are encountered, as well as the rate at which energy is expended (Schmidt-Nielsen 1972; Pyke 1981), thus reflecting energetic constraints, dietary needs, predation risk and behavioural responses to these. The long-term metric (henceforth day range, Carbone et al. 2005) represents an important measure of animals' use of space, with relevance to macro-ecology (Jetz et al.

2004; Carbone et al. 2014), population processes (Werner and Anholt 1993; Miller et al. 2014), human-wildlife interactions (Woodroffe and Ginsberg 1998; Graham et al. 2009) and epidemiology (Cross et al. 2005).

Travel speed and day range are traditionally measured by tracking individuals' trajectories, either through telemetry (Turchin 1998) or by following habituated individuals (typically primates, Sigg and Stolba 1981; Galdikas 1988). Telemetry requires that animals are captured and tagged, while following individuals usually requires long periods of habituation. In both cases, the methods are, at least initially, invasive. Also, the frequency of position fixes typically used in these studies is often too low to provide accurate measures of distance travelled (Rowcliffe et al. 2012), although GPS tracking devices can in principle deliver appropriate resolution (Kays et al. 2015). For these reasons, travel speed and day range studies have historically been limited in number and reliability.

Here, we describe an alternative approach for quantifying both travel speed and day range, based on images of animal movement captured by camera traps. Using video or near-video rapid-fire settings, and tracing movement paths within sequences of animals crossing their detection zones, camera traps can record movement in the form of sequential positions at known times. These data can therefore be used in the same way as telemetry data to derive measures of movement distance over a known time at a very fine scale (at least one fix per second). This yields a high resolution measure of travel speed, but camera traps are triggered by movement, so speeds measured in this way represent only active animals. To estimate day range (longer term average speed), we therefore need to take account of periods of inactivity, when animals are immobile and so unobserved by camera traps.

We therefore describe methods for the following steps: (1) extracting replicate observations of travel distance and duration at fine scale; (2) estimating average travel speed for a population of animals from these observations and (3) estimating average day range for a population of animals by combining estimates of travel speed and activity level. We apply these methods to a community of terrestrial animals in Panama, and validate the resulting estimates by comparing body mass scaling patterns and, where possible, specific day range estimates with independent estimates for the same species in the same habitat from the literature. These methods build on our previous work, which used movement-speed and turning-angle estimates from camera traps to parameterize simulations of movement (Rowcliffe et al. 2012), and developed methods to estimate activity level from camera-trap data (Rowcliffe et al. 2014). The novelty of this paper lies in: (1) a more detailed consideration of field methods; (2) a

new, statistically robust approach to the estimation of average travel speed; (3) the combination of travel speed with activity level to estimate day range and (4) empirical validation of the methods.

Materials and Methods

Generating image sequences

As for any sample, the sample of speed observations obtained from sequences of images must be representative of the wider 'population' from which it comes, and it is therefore critical that both camera hardware and survey design are specified to achieve this. In terms of hardware, four conditions must be met. First, cameras need to be remotely triggered to minimize disturbance, typically using passive or active infrared detectors. Second, where sensors are used to trigger cameras, reaction time should be rapid (generally below 1 s) in order to avoid the possibility that faster-moving animals can pass before recording starts. Third, frame rate should be high (at least 1 s^{-1}) in order to ensure that most passages generate at least two frames between which to measure speed. For camera-trap models that support multiple images per trigger, it is therefore advisable to use this setting with the maximum possible images per trigger, as well as setting cameras to trigger again immediately following each trigger. Finally, images need to be time stamped as precisely as possible, preferably with sub-second precision. Precision only to the nearest second when more than one frame is taken per second is problematic because it can yield duration observations of zero, hence apparently infinite speed, although we suggest a method to deal with this situation in the field application section below.

In terms of survey design, there are two conditions: recordings must happen at (1) a substantial number of locations that are (2) randomly selected with respect to the movements of animals (Rowcliffe et al. 2013). Surveys that over-represent particular landscape features, whether by chance or by design, would yield a biased estimate of speed if the focal species' behaviour is also related to those features. For example a small sample that happens to over-represent trails, or a survey that deliberately targets trails may result in over estimation of speed if animals use trails for faster, more directed movement bouts. Conversely, cameras placed at baits or scent lures may underestimate speed because animals investigating or eating the bait move relatively slowly. Measuring movement speed therefore requires sampling designs in which camera points are preselected either randomly (e.g. Kays et al. 2011), or in a grid formation (e.g. Jansen et al. 2014).

Extracting speed data from image sequences

The speed at which an animal passes in front of a camera trap can be measured by dividing the distance travelled by the duration of the sequence. The distance travelled is the summed linear distance between animal positions on the ground, which are identified by viewing images in the field and reconstructing the movement path on the ground within (NB not between) camera detection zones relative to nearby landmarks such as trees and rocks. The total distance moved between positions (d) can then be measured using a tape or hip chain. The duration of each passage (t) is the difference between time stamps of the first and last images.

Ideally all sequences obtained should be processed in this way for analysis, however, animals sometimes visibly respond to cameras, either by fleeing or by stopping to investigate. Sequences showing such reactions should be excluded from speed calculations, leaving only those in which no reactions are visible, and in which unbiased speeds can therefore reasonably be assumed.

Computational methods

Having generated a sample of $i = 1, 2, \dots, n$ total distances d_i , and passage durations t_i , the i th speed observation s_i is the ratio of these: $s_i = d_i/t_i$. The overall travel speed estimate for the population is some average of these speed observations. However, animals are more likely to contact cameras when they move faster (Hutchinson and Waser 2007), and we therefore expect our sample to be biased towards faster movements. More specifically, the random encounter model equation (Rowcliffe et al. 2008) describes a linear relationship between speed and trap rate, leading us to expect that the probability of sampling a given speed should be proportional to itself. In this case, the observed distribution is known as size-biased (Patil 2002). To overcome this bias, the mean speed, μ can be estimated by maximum likelihood, with the likelihood function taking the general form:

$$L(\mu, \theta | s_1, \dots, s_n) = \prod_{i=1}^n \frac{s_i f(s_i | \mu, \theta)}{\mu}$$

where $f()$ is the true probability density function (PDF) of speed in the absence of sampling bias, and θ represents additional parameters of the PDF (Patil 2002).

To model speed, a continuous non-negative PDF is required, and we identified three such distributions as potentially appropriate (while recognizing that there may be other possible distributions). First, a gamma distribution with rate θ :

$$f_{\text{gamma}}(s_i | \mu, \theta) = \frac{\theta^\alpha}{\Gamma(\alpha)} s_i^{\alpha-1} e^{-\theta s_i},$$

where α , the shape parameter, is given by: $\alpha = \mu\theta$.

Second, a log-normal distribution with standard deviation of the logarithm θ :

$$f_{\text{lognormal}}(s_i | \mu, \theta) = \frac{1}{s_i \theta \sqrt{2\pi}} \exp\left(-\frac{(\log(s_i) - \varepsilon)^2}{2\theta^2}\right),$$

where ε , the mean of the logarithm, is given by: $\varepsilon = \log(\mu) - \frac{\theta^2}{2}$.

Finally, a Weibull distribution with shape θ :

$$f_{\text{Weibull}}(s_i | \mu, \theta) = \frac{\theta}{\lambda} \left(\frac{s_i}{\lambda}\right)^{\theta-1} \exp\left(-\left(s_i/\lambda\right)^\theta\right),$$

where λ , the scale parameter, is given by the following equation: $\lambda = \frac{\mu}{\Gamma(1+1/\theta)}$.

In these expressions, $\Gamma()$ is the gamma function (Davis 1972). The best distribution for a given set of data can be selected on the basis of AIC (Burnham and Anderson 2002). Approximate parameter variance can be estimated by inverting the Hessian matrix at the maximum likelihood estimates (Bolker 2008).

The above method yields an estimate of travel speed (the average speed at which a population of active animals moves). Day range, the rate of movement over longer time scales, is the product of this travel speed and the proportion of time spent active (activity level). Activity level and its variance can also be estimated from camera-trap data, using the analytical methods detailed in Rowcliffe et al. (2014), and we use this approach here.

Having estimated travel speed while active μ and the proportion of time spent active p , day range is simply the product of these values:

$$v = \mu p$$

with standard error estimated by Goodman's (1960) variance of products formula:

$$SE(v) = v \sqrt{\left(\frac{SE(\mu)}{\mu}\right)^2 + \left(\frac{SE(p)}{p}\right)^2 + \left(\frac{SE(\mu)}{\mu}\right)^2 \left(\frac{SE(p)}{p}\right)^2}.$$

Application to a tropical mammal assemblage

Field data come from randomly placed camera traps (RC55; Reconyx, Holmen, WI) deployed from February 2008 to February 2009 on Barro Colorado Island (9°9'N, 79°51'W), Republic of Panama (Leigh 1999). The cameras

were triggered by passive infrared motion sensors, set to make 10 low-resolution (1 mega pixel) photographs at a rate of 1.4 frames per second on average for every motion trigger event, and to be able to trigger again immediately without delay. The study site and general camera trapping methods are detailed further in Kays et al. (2011).

Overall, a total of 6312 trap nights at 789 locations yielded 17,226 animal passages of >40 different vertebrate species. We used a subset of passages for speed measures, chosen systematically by taking measurements from the first three passages of each species at each camera deployment in which the animal's position was clearly visible in at least two consecutive images. This yielded 2181 speed observations for 19 terrestrial mammal species (excluding bats, birds, reptiles and very infrequent mammals). Here, we focus on 12 species for which we obtained at least 26 speed observations, a total of 2158 observations. A cut-off of 26 was used because the species with the next largest sample size had only eight observations, which we deemed too small to yield reliable results.

We tracked animal movement paths across the ground with a measuring tape to give the total distance moved, as described in the data extraction section above (see Video S1). We did this in situ, before removing the cameras from their deployment locations. Because time was recorded to the nearest second at a frame rate sometimes greater than two per second, and some speed observations were derived from only two frames, apparently zero-duration observations occurred due to rounding of time stamps. To nonetheless obtain accurate speeds for all observations, we took advantage of the fact that each trigger resulted in ten frames, regardless of how many of those were used to track distance, and calculated duration as the number of intervals over which distance was tracked, multiplied by the average duration of an interval across the entire trigger:

$$t_i = (r_i - 1) \frac{m_{10} - m_1}{9}$$

where r_i is the number of frames over which distance was measured, and m_1 and m_{10} are, respectively, the time stamps of the first and tenth images of the trigger.

We assessed the validity of our travel-speed and day-range estimates for Panamanian mammals in two ways. First, we examined whether travel speed and day range scaled positively with body mass within the size range of our sample, as they are known to do from previous studies of travel speed (McMahon 1975; Garland 1983a; Heglund and Taylor 1988) and day range (Garland 1983b; Carbone et al. 2005). To do this, we regressed travel speed and day range estimates for the 12 species in our Panamanian sample against species body mass, using

log transforms in order to quantify scaling relationships in the form of regression slopes (scaling exponents, b). We also explored whether scaling relationships varied with diet, categorized as either herbivore (including granivores and frugivores), or faunivore (including carnivores, myrmecovores and omnivores). Average body masses for Barro Colorado Island species were taken from local animal capture data (R. Kays, unpubl. data) where possible, otherwise from regional field guides by Emmons and Feer (1990) or Reid (1997). Scaling exponents were statistically compared using Wald tests, with test statistic W assessed on the chi-squared distribution with one degree of freedom:

$$W = \frac{(b_1 - b_2)^2}{SE(b_1)^2 + SE(b_2)^2}.$$

However, because we expect scaling exponents to differ between taxa (Carbone et al. 2005), unequal representation of different taxa between samples could cause differences in scaling exponents that are not attributable to observation method. To compare overall multi-taxon scaling exponents between camera trap and other methods, we therefore additionally used a randomization test, in which a null empirical distribution of scaling exponents was generated by fitting scaling relationships to 1000 random samples from the Carbone et al. (2005) data, with the same sample size and ratio of herbivores to faunivores in each sample as in the camera-trap data.

Our second validation approach was to compare our estimates of day range derived from camera traps directly with independent estimates derived from telemetry for the same species in the same or similar habitats. We found such estimates for three species: ocelot in Madre de Dios, Peru (Emmons 1988), agouti on Barro Colorado Island (Aliaga-Rossel et al. 2008) and opossum in Central Valley, Costa Rica (Vaughan and Hawkins 1999). Fix frequencies in these tracking studies were 2–12 per hour, which are too low to give an absolute estimate of day range, and likely underestimate distance moved by factors of about 2–5 (Rowcliffe et al. 2012, Fig. 4). We therefore used the species-specific correction factors calculated by Rowcliffe et al. (2012) to adjust telemetry estimates upwards before comparison with camera-trap estimates of day range. This method used correlated random walk simulations, with the frequencies and angle distributions of turns parameterized using the same camera-trap images as in this study, in order to estimate the amount of unobserved distance travelled between fixes of a given frequency. These simulations yielded species-specific functions for the relationship between relative apparent travel distance, expressed as a proportion of the true distance, and fix frequency. We used these functions to estimate

relative apparent travel distances (r) for each species given the fix frequencies reported, and divided the published day range estimates by r to derive corrected day ranges for comparison with camera-trap estimates.

Analyses were conducted in R 3.1.1 (R Core Team 2014). Speed distribution models were fitted using the package *bbmle* 1.0.17 (Bolker 2014).

Results

In nine of 12 species, log-normal was the most strongly supported of the three size-biased distributions fitted to travel speeds, particularly in those species with higher sample sizes (Table 1). Speed estimates based on the log-normal distribution were on average 28% higher than estimates using either of the other size-biased models, but were still consistently lower than unweighted mean estimates by a factor of nearly two on average (30–53% lower, Fig. 1). Given overwhelming support for the size-biased log-normal distribution model, we based all subsequent results on this distribution for all species.

Average travel speed ranged 3-fold between the fastest (ocelot) and slowest (mouse) species in our sample

(Table 1, Fig. 2A). Larger species and faunivores tended to travel faster than did smaller species and herbivores, with a further tendency to steeper body-mass scaling for faunivores than herbivores (Table 2). Reasonable precision was obtained for all travel speed estimates, with maximum and minimum coefficients of variation (CV) of, respectively, 18% for opossum ($n = 26$) and 3% for agouti ($n = 980$), and CV generally <10% for species approaching or exceeding a sample size of 80 (Fig. 3).

Day ranges varied five-fold across the species sampled (Table 1, Fig. 2B). Again, larger species and faunivores tended to travel further than smaller species and herbivores, although the difference in scaling exponents between faunivores and herbivores was small and non-significant (Table 2). Coefficients of variation for day range varied from 19% (opossum) to 4% (agouti). Variance in activity level estimates contributed little to these figures because sample sizes were so much higher for activity level estimates. Estimated day range CV trends below 10% for species with sample sizes approaching or exceeding 250 (Fig. 3).

Overall, our camera-based estimates of day range showed somewhat lower body mass scaling than found by

Table 1. Summary of sample sizes, body masses, diet categories, movement parameters estimated using camera traps, and model comparisons (Δ AIC) for alternative travel speed distributions for twelve Panamanian forest mammal species. Travel speeds and day ranges are based on log-normal distribution fits in all species. For brevity, the abbreviated common names given in brackets are used in the text. Activity level estimates (the proportion of time spent active) are taken from Rowcliffe et al. (2014).

Species	Sample size		Body mass (kg)	Diet	Activity level (SE)	Travel speed ms^{-1} (SE)	Day range km (SE)	Speed distribution Δ AIC		
	Activity	Speed						Gamma	Log-normal	Weibull
Mouse (mouse) unknown species	96	43	0.1	H	0.299 (0.04)	0.094 (0.012)	2.42 (0.46)	4.93	0	4.09
Tome's spiny rat (rat) <i>Proechimys semispinosus</i>	893	132	0.4	H	0.397 (0.023)	0.115 (0.009)	3.95 (0.40)	12.57	0	8.79
Red-tailed squirrel (squirrel) <i>Sciurus granatensis</i>	572	66	0.4	H	0.197 (0.011)	0.117 (0.015)	2.00 (0.27)	8.94	0	5.73
Common opossum (opossum) <i>Didelphis marsupialis</i>	119	26	1.1	F	0.374 (0.03)	0.153 (0.027)	4.93 (0.96)	0.17	0.11	0
Central American agouti (agouti) <i>Dasyprocta punctata</i>	10 292	953	3.5	H	0.282 (0.007)	0.134 (0.004)	3.25 (0.12)	65.49	0	46.69
White-nosed coati (coati) <i>Nasua narica</i>	459	125	4.0	F	0.404 (0.021)	0.158 (0.014)	5.49 (0.57)	2.04	1.23	0
Nine-banded armadillo (armadillo) <i>Dasyus novemcinctus</i>	121	40	4.2	F	0.366 (0.031)	0.204 (0.032)	6.47 (1.15)	10.36	0	6.7
Northern tamandua (tamandua) <i>Tamandua mexicana</i>	128	39	4.2	F	0.556 (0.061)	0.195 (0.025)	9.37 (1.57)	0.51	0	0.84
Lowland paca (paca) <i>Cuniculus paca</i>	999	195	8.0	H	0.342 (0.02)	0.171 (0.009)	5.04 (0.39)	24.12	0	27.61
Ocelot (ocelot) <i>Leopardus pardalis</i>	317	93	11.9	F	0.349 (0.036)	0.279 (0.019)	8.42 (1.04)	0.46	7.47	0
Red brocket deer (brocket) <i>Mazama temama</i>	816	181	22.8	H	0.524 (0.04)	0.153 (0.01)	6.94 (0.70)	7.97	0	6.61
Collared peccary (peccary) <i>Tayassu tajacu</i>	2965	265	25.2	H	0.381 (0.014)	0.153 (0.009)	5.04 (0.35)	23.04	0	14.65
Total	17 777	2158								

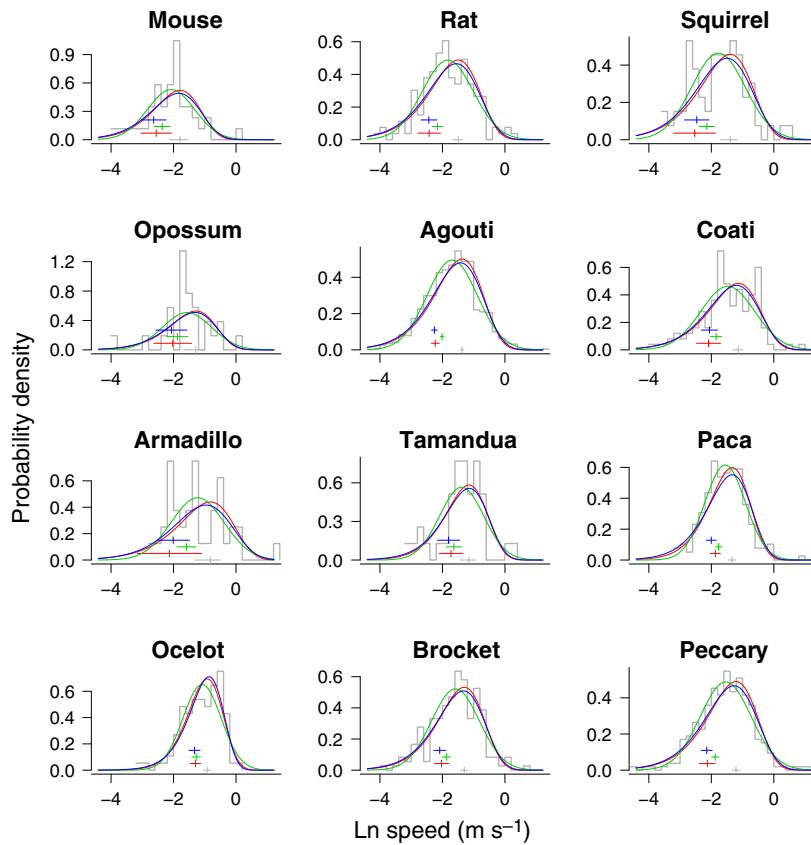


Figure 1. Distributions of speed observations (grey steps) and fitted size-biased distributions assuming three different parametric models: gamma (red), log-normal (green), Weibull (blue). Estimated average speeds and 95% confidence intervals are indicated by, respectively, vertical and horizontal lines, colour coded as above, with unweighted estimates in grey.

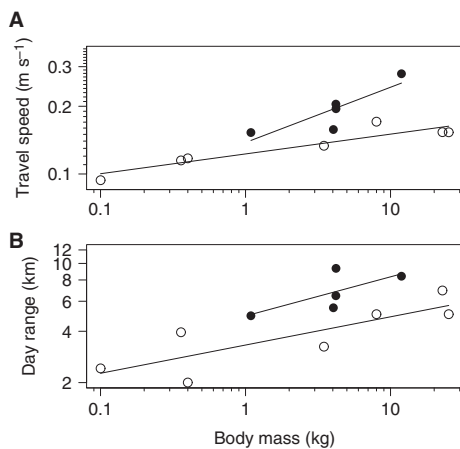


Figure 2. Average travel speeds (A) and day ranges (B) of 12 Panamanian mammal species, estimated from camera-trap image sequences, as a function of body mass and diet. Axes are log-scale, and trend lines are fitted power functions of the form $y = cx^b$, for faunivores (solid points) and herbivores (open points). Scaling exponents (b) are: faunivore travel speed = 0.25 (SE 0.08); herbivore travel speed = 0.09 (SE 0.02); faunivore day range = 0.23 (SE 0.13); herbivore day range = 0.17 (SE 0.05).

Carbone et al. (2005) (Fig. 4). Scaling exponents were significantly different in a straight comparison between data sets (Wald test $W = 9.4$, $P < 0.001$), however, the randomization test accounting for different taxonomic representation suggested no significant difference between scaling exponents ($P = 0.16$).

Camera-based estimates of day range were between 1.9 and 7.3 times higher than predicted by the linear regression using telemetry estimates (Fig. 4), broadly consistent with expectations of underestimation given the relatively low fix frequencies typical of telemetry studies (Rowcliffe et al. 2012). However, correcting for unobserved tortuosity in the three species for which direct comparisons were possible (ocelot, agouti and opossum), camera-based estimates of day range were within 11% of, and not significantly different from, telemetry-based estimates (Fig. 5).

Discussion

Travel speed and day range are fundamental properties of animal movement that are difficult to measure in wild

Table 2. Linear model results for \log_e -transformed camera-trap-based estimates of travel speed and day range as functions of body mass and diet category, either with or without interaction terms.

Model	Parameter	Travel speed				Day range			
		β	SE	t	P	β	SE	t	P
With interaction	Intercept	-1.981	0.101	-19.592	<0.0001	1.593	0.233	6.84	<0.001
	Mass	0.246	0.065	3.798	<0.01	0.229	0.149	1.539	0.16
	Diet(H)	-0.117	0.110	-1.059	0.32	-0.393	0.254	-1.545	0.16
	Mass: Diet(H)	-0.158	0.068	-2.325	<0.05	-0.064	0.156	-0.408	0.69
No interaction	Intercept	-1.785	0.068	-26.193	<0.0001	1.673	0.123	13.648	<0.0001
	Mass	0.102	0.024	4.31	<0.01	0.171	0.043	4.016	<0.01
	Diet(H)	-0.324	0.080	-4.063	<0.01	-0.477	0.143	-3.326	<0.01

β , parameter coefficients; P , significance of coefficients; SE, coefficient standard errors; t , coefficient t statistics.

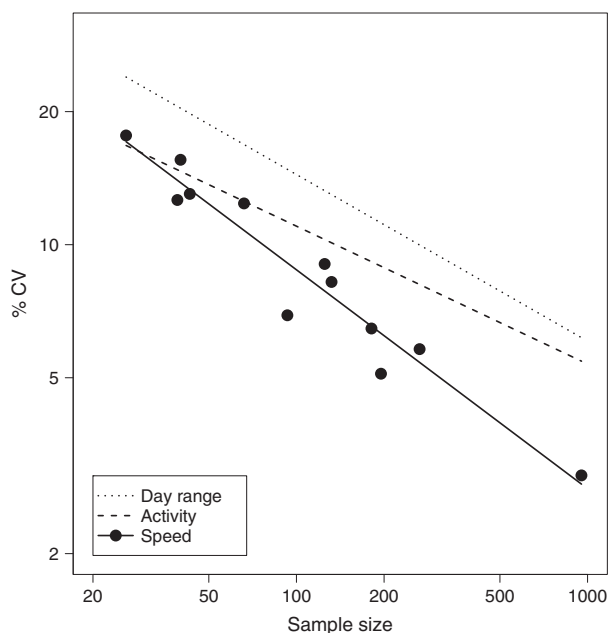


Figure 3. Coefficients of variation for speed, activity level and day range estimates for 12 Panamanian forest mammals as a function of sample size. Sample sizes for activity level and speed were very different in our sample (Table 1), so in order to show results for consistent sample size, we give the day range trend derived as $CV(v) = [CV(\mu)^2 + CV(p)^2 + CV(\mu)^2 CV(p)^2]^{0.5}$, where v , μ and p are, respectively, predicted day range, speed and activity trend values, and CVs are expressed as proportions. The trend for activity level is derived from Rowcliffe et al. (2014). Axes are log-scale, and trend lines are fitted power functions of the form $CV = cn^b$.

animals. The methods presented here provide a new means to measure these properties cost-effectively and non-invasively in a wide range of species, including many for which such information is currently lacking. Specifically, we have shown how average travel speed and day range can be estimated for animal populations from snapshots of animal movements captured by remote cameras. Application to the terrestrial mammal assemblage of

Barro Colorado Island, Republic of Panama, suggested that the methods are acceptably accurate. Comparison of our day range estimates with independent data sets showed patterns across species that were consistent with expectations from previous studies, and absolute values that were very similar to independent estimates corrected for low fix frequency.

In terms of scaling trends, speed of locomotion for a given gait has been found to scale with body mass with exponents in the range 0.18–0.25 (McMahon 1975; Heglund and Taylor 1988). The travel-speed scaling exponents 0.08 and 0.21 that we found for herbivores and faunivores, respectively, using camera-trap data are thus in the right region. That they are somewhat lower would be expected purely on the basis of smaller sample size and body mass range in this study (Isaac et al. 2013). However, this apparent difference may also be genuine, because published expectations derive from trends across species for a particular gait, whereas our results integrate across all gaits while active (including brief periods of stationarity), and changes in the mix of gaits used with increasing size likely influence the result. We were unable to find good evidence on how the mix of gaits might change with body mass, but speculate that herbivores might plausibly show increasing use of slower gaits with increasing size, whereas the mix of gaits used by faunivores might be faster and more consistent across the size range, a pattern that could explain our speed scaling observations. We encourage future tests of this hypothesis.

Day range scaling exponents of 0.13, 0.35 and 0.44 have been found for Artiodactyla, Rodentia and Carnivora respectively (Carbone et al. 2005). Our estimates of 0.16 and 0.19 for herbivores and faunivores, respectively (the latter group largely corresponding to Carnivora) fell in the same region, although distinctly lower than expected in the case of faunivores. However, sample sizes for faunivores were small, both in terms of species (4) and speed

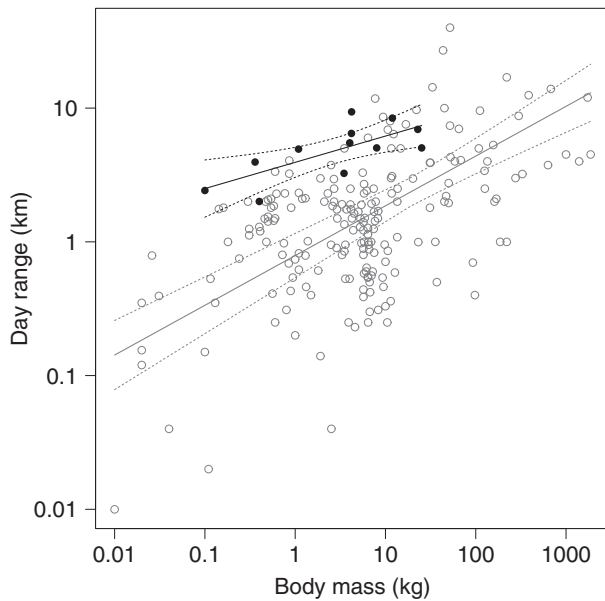


Figure 4. Day range – body mass relationships for 12 Panamanian forest mammals estimated using camera traps (filled circles; scaling exponent 0.2 SE 0.06), and for 86 terrestrial non-primate mammal species estimated by previous studies using telemetry [open circles, data from Carbone et al. (2005), scaling exponent 0.37 SE 0.04]. Trend lines are linear regression predictions with 95% confidence intervals for log-transformed data. Telemetry estimates were expected to be lower due to low temporal resolution of tracking in most studies.

observations per species (26–125), and the mis-match between our scaling estimates and those of Carbone et al. (2005) is again likely the result the much smaller, narrower sample (Isaac et al. 2013), together with low precision (approximate 95% confidence interval for faunivore scaling 0.06–0.59). Yet, despite the limited sample size in terms of numbers of species and body mass range used for validation, our estimated scaling exponents did not differ significantly from those of Carbone et al. (2005).

While our estimates of day range from camera traps were very close to those from telemetry (Fig. 5), this validation rests on the reliability of the method used to correct the telemetry estimates for infrequent fixes (Rowcliffe et al. 2012), and some caution may therefore be appropriate when evaluating the reliability of the comparison. The correction depends on accurately characterizing the tortuosity of movement in the tracked population, so one possible source of bias in the telemetry estimates is that the turn data used to parameterize the correction did not come from the same populations as the telemetry studies. However, comparator studies were specifically chosen to represent closely matched habitats, and we believe it is therefore likely that the tortuosity observed in our cameras was very similar to that in the populations tracked by telemetry. In thinking through the mechanisms

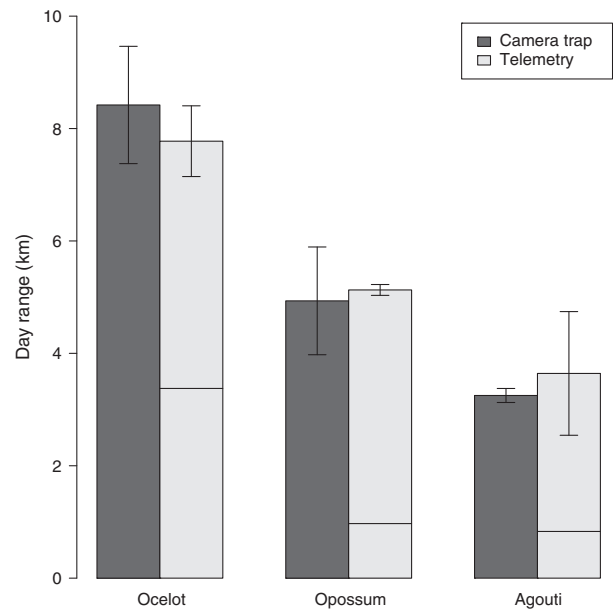


Figure 5. Day range estimates for three species compared between camera trapping (this study) and radio tracking [agouti: (Aliaga-Rossel et al. 2008); ocelot: (Emmons 1988); opossum: (Vaughan and Hawkins 1999)]. Raw tracking estimates (lower lines on telemetry bars) were corrected for underestimation due to the use of summed straight line distances from intermittent fixes, using the simulation approach described in Rowcliffe et al. (2012). Error bars are standard errors. Wald tests for comparison of estimates between methods: ocelot $W = 0.28$, $P = 0.6$; opossum $W = 0.04$, $P = 0.84$; agouti $W = 0.13$, $P = 0.72$.

underpinning the correction of telemetry data, and how these relate to the real-world mechanisms that lead to underestimation of travel distance, we can see no other obvious sources of bias.

There are several advantages of using camera traps, rather than telemetry or direct observations, to derive animal movement parameters. Camera traps are minimally invasive, not requiring that animals are captured and tagged or habituated to obtain movement information. This potentially makes movement measures possible for animals that cannot readily be tagged or observed, and opens the possibility of studying the movements of whole communities of terrestrial animals with single surveys. Moreover, the measurements can be made at a very high resolution in time and space, giving precise absolute measures of movement rate that are directly comparable across species and sites. In contrast, telemetry studies can be problematic in this respect because sampling intervals vary greatly, depending on the context and goals of the study, leading to variable degrees of bias in apparent movement distances (Rowcliffe et al. 2012).

An important characteristic of camera-based estimation is that the data are obtained from short sequences from

many individuals in the population, rather than long sequences of few individuals, as is typical of traditional methods. This may be seen as either an advantage or a disadvantage, depending on the research questions. The strength of the camera-based approach lies in providing a robust, representative sample of movement rates at the population level, whereas telemetry and direct observation studies often struggle to track more than a few individuals. On the other hand, individual-level questions clearly require data from known individuals, and cameras will be able to provide this level of detail only in rare cases where the focal species is both individually recognizable and intensively observed. In addition, although camera traps can now be used to estimate home range structure if individuals are recognizable (Pedersen and Weng 2013), telemetry remains better suited to this objective.

As in any estimation method, care is needed to avoid violations of assumptions that lead to bias. The key assumptions in this case are representative sampling of speeds, and, in the case of day range estimation, full activity at the peak of the daily activity cycle. This second assumption is required by the activity level model, and is discussed fully by Rowcliffe et al. (2014). Below we highlight four potential sources of non-representative sampling of speeds.

First, increasing probability of capture as animals move faster is unavoidable, but can be corrected by using a size-biased distribution to estimate average speed. However, we note that the underlying distribution assumed has some influence on the estimated average, making it important that the chosen distribution is a good fit. The log-normal distribution was the best of the three models in most cases, and visual inspection of Figure 1 suggests that this was a reasonable fit in absolute as well as relative terms. However, the empirical distributions arguably look slightly asymmetric on the log scale in some cases, suggesting possible room for improvement in the distribution used. Alternatively, we note that the non-parametric equivalent of the size-biased distribution would be the harmonic mean, and estimation might be usefully refined by exploring the desirability of using either this or alternative parametric distributions.

Second, targeting cameras at particular habitat or structural features may over-sample speeds characteristic of the monitored locations, motivating the requirement to randomize camera placements. Our results show that this does not necessarily hamper the accumulation of adequate sample sizes, however, it does mean that the method may not be applicable to data collected for the purposes of, say, mark-recapture analysis, in which a strongly directed placement strategy is typically used.

Third, we assume that camera traps can obtain unbiased speed observations, without themselves influencing animal movement. In practice, animals can detect

camera traps (Séquin et al. 2003; Meek et al. 2014), and sequences sometimes show obvious responsive movements, clearly violating this assumption. However, many species show little or no visible response to cameras, and we expect that unbiased speed observations are attainable in this case after removing obviously responsive sequences. Our validation results provide some evidence that this expectation is reasonable, at least for the species and study site considered, although future work could usefully address this assumption more directly.

Finally, inadequate equipment may fail to record speeds representatively and accurately. We caution against using camera traps that have a lag of approaching or greater than 1 s between animal trigger and first image registration, or that fire at a frame rate of fewer than 1 s^{-1} , since these specifications would likely under-sample faster movements.

A practical limitation of the method as implemented in the field test presented here is the manual measurement of path distances in the field, which is time consuming, and can be very difficult in environments lacking clear landmarks. An alternative is to track paths digitally within images, and use depth reconstruction algorithms to computationally map these paths onto real-world ground trajectories, from which true distances can be extracted. Various approaches requiring little or no additional field-work are theoretically possible to achieve this, and we are currently working to explore these and develop the necessary tools. Image analysis can potentially be further automated by extraction of the animal silhouette from pixel differences between subsequent images (Ren et al. 2013; Weinstein 2015), and ultimately even automated identification of species (Yu et al. 2013; Swinnen et al. 2014).

There is also scope for further work on statistical aspects of these methods. For example we have treated speed observations as independent, whereas they are in fact structured by point of observation, potentially introducing spatiotemporal correlations through repeated observations on individuals, or through associations between habitat and movement. We therefore anticipate that introducing random effects at the sample point level (and where possible the individual animal level) could provide more robust results in some cases. It would also be useful to develop methods for quantifying spatial variation in speeds, for example across habitats.

Conclusions

Our results suggest that camera trapping is ready to use as a technique for estimating rates of animal movement in the field, and we anticipate that future technological advances will make the methods increasingly accessible and easy to apply. We also note that the use of camera trapping is currently expanding hugely (Rowcliffe and

Carbone 2008; Burton et al. 2015). We therefore conclude that the methods developed here have the potential to expand the range of species in which we can study movement ecology, including poorly studied, rare and elusive species for which there is currently little or no information on movement.

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References

- Aliaga-Rossel, E., R. W. Kays, and J. M. V. Fragoso. 2008. Home-range use by the Central American agouti (*Dasyprocta punctata*) on Barro Colorado Island, Panama. *J. Trop. Ecol.* **24**:367–374.
- Bolker, B. M. 2008. *Ecological models and data in R*. Princeton University Press, Princeton, NJ.
- Bolker, B. M. 2014. *bbmle: Tools for general maximum likelihood estimation*. R package version 1.0.17. Available at <http://CRAN.R-project.org/package=bbmle> (accessed 14 April 2016).
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edition. Springer, New York, NY.
- Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, et al. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *J. Appl. Ecol.* **52**:675–685.
- Carbone, C., G. Cowlshaw, N. J. B. Isaac, and J. M. Rowcliffe. 2005. How far do animals go? Determinants of day range in mammals. *Am. Nat.* **165**:290–297.
- Carbone, C., D. Codron, C. Scofield, M. Clauss, and J. Bielby. 2014. Geometric factors influencing the diet of vertebrate predators in marine and terrestrial environments. *Ecol. Lett.* **17**:1553–1559.
- Core Team, R. 2014. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Australia.
- Cross, P. C., J. O. Lloyd-Smith, P. L. Johnson, and W. M. Getz. 2005. Duelling timescales of host movement and disease recovery determine invasion of disease in structured populations. *Ecol. Lett.* **8**:587–595.
- Davis, P. J. 1972. Gamma function and related functions. Pp. 253–294 in M. Abramowitz and I. A. Stegun, eds. *Handbook of mathematical functions with formulas, graphs, and mathematical tables*. Dover, New York, NY.
- Emmons, L. H. 1988. A field study of ocelots (*Felis pardalis*) in Peru. *Revue d'Ecologie (Terre et Vie)* **43**:133–158.
- Emmons, L. H., and F. Feer. 1990. *Neotropical rainforest mammals: a field guide*. University of Chicago Press, Chicago, IL.
- Galdikas, B. M. 1988. Orangutan diet, range, and activity at Tanjung Puting, Central Borneo. *Int. J. Primatol.* **9**:1–35.
- Garland, T. 1983a. The relation between maximal running speed and body mass in terrestrial mammals. *J. Zool.* **199**:157–170.
- Garland, T. 1983b. Scaling the ecological cost of transport to body mass in terrestrial mammals. *Am. Nat.* **121**:571–587.
- Goodman, L. A. 1960. On the exact variance of products. *J. Am. Stat. Assoc.* **55**:708–713.
- Graham, M. D., I. Douglas-Hamilton, W. M. Adams, and P. C. Lee. 2009. The movement of African elephants in a human-dominated land-use mosaic. *Anim. Conserv.* **12**:445–455.
- Heglund, N. C., and C. R. Taylor. 1988. Speed, stride frequency and energy cost per stride: how do they change with body size and gait? *J. Exp. Biol.* **138**:301–318.
- Hutchinson, J. M. C., and P. M. Waser. 2007. Use, misuse and extensions of “ideal gas” models of animal encounter. *Biol. Rev.* **82**:335–359.
- Isaac, N. J. B., D. Storch, and C. Carbone. 2013. The paradox of energy equivalence. *Glob. Ecol. Biogeogr.* **22**:1–5.
- Jansen, P. A., J. A. Ahumada, E. Fegraus, and T. O'Brien. 2014. TEAM: a standardised camera trap survey to monitor terrestrial vertebrate communities in tropical forests. Pp. 263–270 in P. D. Meek, P. J. S. Fleming, A. G. Ballard, P. B. Banks, A. W. Claridge, J. G. Sanderson, and D. E. Swann, eds. *Camera Trapping in Wildlife Research and Management*. CSIRO Publishing, Melbourne, Australia.
- Jetz, W., C. Carbone, J. Fulford, and J. H. Brown. 2004. The scaling of space use in animals. *Science* **306**:266–268.
- Kays, R., S. Tilak, B. Kranstauber, P. A. Jansen, C. Carbone, J. M. Rowcliffe, et al. 2011. Camera traps as sensor networks for monitoring animal communities. *Int. J. Res. Rev. Wireless Sensor Networks* **1**:19–29.
- Kays, R., M. C. Crofoot, W. Jetz, and M. Wikelski. 2015. Terrestrial animal tracking as an eye on life and planet. *Science* **348**:aaa2478.
- Leigh, E. G. 1999. *Tropical forest ecology: a view from Barro Colorado Island*. Oxford University Press, New York, NY.
- McMahon, T. A. 1975. Using body size to understand the structural design of animals: quadrupedal locomotion. *J. Appl. Physiol.* **39**:619–627.
- Meek, P. D., G.-A. Ballard, P. J. S. Fleming, M. Schaefer, W. Williams, and G. Falzon. 2014. Camera traps can be heard and seen by animals. *PLoS ONE* **9**:e110832.
- Miller, C. S., M. Hebblewhite, Y. K. Petrunenko, I. V. Seryodkin, J. M. Goodrich, and D. G. Miquelle. 2014. Amur tiger

- (*Panthera tigris altaica*) energetic requirements: implications for conserving wild tigers. *Biol. Conserv.* **170**:120–129.
- Patil, G. P. 2002 Weighted distributions. Pp. 2369–2377 in A. H. El-Shaarawi, W. W. Piegorsch, eds. *Encyclopedia of Environmetrics*. Wiley, Chichester.
- Pedersen, M. W., and K. C. Weng. 2013. Estimating individual animal movement from observation networks. *Methods Ecol. Evol.* **4**:920–929.
- Pyke, G. H. 1981. Optimal travel speeds of animals. *Am. Nat.* **118**:475–487.
- Reid, F. 1997. *A field guide to the mammals of Central America and southeast Mexico*. Oxford University Press, Oxford.
- Ren, X., T. X. Han, and Z. He. 2013. Ensemble video object cut in highly dynamic scenes. Conference on Computer Vision and Pattern Recognition, IEEE pp. 1947–1954.
- Rowcliffe, J. M., and C. Carbone. 2008. Surveys using camera traps: are we looking to a brighter future? *Anim. Conserv.* **11**:185–186.
- Rowcliffe, J. M., J. Field, S. T. Turvey, and C. Carbone. 2008. Estimating animal density using camera traps without the need for individual recognition. *J. Appl. Ecol.* **45**:1228–1236.
- Rowcliffe, J. M., C. Carbone, R. Kays, B. Kranstauber, and P. A. Jansen. 2012. Bias in estimating animal travel distance: the effect of sampling frequency. *Methods Ecol. Evol.* **3**:653–662.
- Rowcliffe, J. M., R. Kays, C. Carbone, and P. A. Jansen. 2013. Clarifying assumptions behind the estimation of animal density from camera trap rates. *J. Wildl. Manage.* **77**:876.
- Rowcliffe, J. M., R. Kays, B. Kranstauber, C. Carbone, and P. A. Jansen. 2014. Quantifying levels of animal activity using camera-trap data. *Methods Ecol. Evol.* **5**:1170–1179.
- Schmidt-Nielsen, K. 1972. Locomotion: energy cost of swimming, flying, and running. *Science* **177**:222–228.
- Séquin, E. S., M. M. Jaeger, P. F. Brussard, and R. H. Barrett. 2003. Wariness of coyotes to camera traps relative to social status and territorial boundaries. *Can. J. Zool.* **81**: 2015–2025.
- Sigg, H., and A. Stolba. 1981. Home range and daily march in a hamadryas baboon troop. *Folia Primatol.* **36**:40–75.
- Swinnen, K. R. R., J. Reijnders, M. Breno, and H. Leirs. 2014. A novel method to reduce time investment when processing videos from camera trap studies. *PLoS ONE* **9**:e98881.
- Turchin, P. 1998. *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*. Sinauer, Sunderland, MA.
- Vaughan, C. S., and L. F. Hawkins. 1999. Late dry season habitat use of common opossum, *Didelphis marsupialis* Marsupialia: Didelphidae) in neotropical lower montane agricultural areas. *Revista de Biología Tropical* **47**:263–269.
- Weinstein, B. G. 2015. MotionMeerkat: integrating motion video detection and ecological monitoring. *Methods Ecol. Evol.* **6**:357–362.
- Werner, E. E., and B. R. Anholt. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *Am. Nat.* **242**:272.
- Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. *Science* **280**:2126–2128.
- Yu, X., J. Wang, R. Kays, P. A. Jansen, T. Wang, and T. Huang. 2013. Automated identification of animal species in camera trap images. *EURASIP J. Image Video Process.* **1**:1–10.

Supporting Information

Additional supporting information may be found online in the supporting information tab for this article.

Video S1. Video of example animal passages past camera traps and a field measure of distance moved.

Data S1. R code for all analyses.

Data S2. R code for size-biased distribution fitting functions.

Data S3. R code for adding error bars to plots.

Data S4. List of nlsModel objects modelling relative path distance as a function of fix frequency (as presented in Rowcliffe et al. 2012).

Data S5. Data set from which speed observations derived.

Data S6. Species body mass data.

Data S7. Activity level estimates from Rowcliffe et al. (2014).

Data S8. Data set of day range estimates used in Carbone et al. (2005).

Data S9. Key to the meaning of column headings for all data files.