

Species occurrence data reflect the magnitude of animal movements better than the proximity of animal space use

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Abstract. Animal ecologists often use stationary point-count surveys, such as camera traps, to collect presence-absence data and infer distribution, abundance, and density of species. Rarely do these surveys explicitly consider variations in the magnitude of animal movement despite movement assumptions being implicit in their interpretation. For example, ecologists assume the frequency of species detections at a site is associated with the intensity of local space use, but it may be more indicative of transit through that point en route to other areas. This assumption remains untested, and a resolution is critical to accurate interpretation of species occurrence data. We compared fisher (*Pekania pennanti*) detections collected from a camera trap array with detailed Global Positioning System-telemetry data to test whether, at the population level, the spatial and temporal patterns of detections reflected the proximity of space use to sampling sites, or variability in the magnitude of animal movement across the study area. We also used an occupancy modeling framework to quantify the relative contributions of space use proximity and movement magnitude to estimated probabilities of site occupancy and detectability. We demonstrate that, at the population level, detection frequency and estimates of detection probability and occupancy are more closely associated with the magnitude of animal movement around a survey device than the proximity of animal space use. Variations in the magnitude of animal movement within and between species should receive greater consideration when interpreting occurrence data to correctly infer ecological processes. Not accounting for species movement, especially in multi-species surveys, may bias inferences of ecologic processes and result in misspecified management recommendations.

Key words: abundance; activity center; camera trap; detection; Global Positioning System telemetry; movement; occupancy; *Pekania pennanti*; space use; species occurrence data.

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INTRODUCTION

Animal ecologists quantify populations and communities by counting animals across space and time. Point surveys of individuals or species are commonly collected from stationary sampling locations (i.e., survey sites) through a variety of field methods (avian point-count surveys, mist-netting surveys, live-trapping surveys,

camera trap surveys, etc.) and are generally referred to as species occurrence data (SOD): the sequence of species detections at a single position in space and time (Scott et al. 2002). However, although mobile animals move in and around survey sites, rarely does the interpretation of SOD explicitly consider the influence of animal movement. Movement—changes in location through time—is a dynamic space-time process

that makes it difficult to accurately characterize where and when animals are located, and how the cumulative locations of individuals over time define patterns of population distribution and relative abundance (Hooten et al. 2017), as is the goal of point-count surveys.

Ecological inferences derived from SOD assume that spatial variation in species occurrence among survey sites represents variation in relative abundance, whereas temporal variation in species occurrence within a survey site reflects variation in the proximity of animal space use (i.e., the activity center of Royle et al. 2013, also see Turchin 1998, MacKenzie 2006, Burton et al. 2015). However, rarely have researchers explicitly tested the assumed relationships between measures derived from SOD (e.g., occurrence, detection probability, or occupancy—occurrence corrected for detection probability) and inferred ecological processes (abundance or density, space use, and habitat selection) despite this being a prerequisite to accurate data interpretation (Burton et al. 2015). A few studies have attempted to incorporate individual movement data empirically into estimates derived from SOD by combining occurrence from both point-count and telemetry data sets (Gopalaswamy et al. 2012, Sollmann et al. 2013, Popescu et al. 2014). However, a basic and general question remains: How does variability in the magnitude of species movement, vs. variability in the proximity of species space use, affect a survey's ability to sample a population? This question focuses on species rather than individual identification—a common goal of point-count surveys—and therefore assumes that movement and space use from a random sample of individuals are representative of the population.

One approach to investigate assumptions inherent in SOD is to statistically relate occurrence data from common survey methods to simultaneously collected movement data around survey sites. Developments in Global Positioning System (GPS) technology enable biologists to obtain detailed individual movement patterns through GPS telemetry rather than relying on traditional tracking techniques (Kays et al. 2015, but also see Ranacher et al. 2016). Each GPS point collected from a GPS collar on an active animal is considered an animal location, and its distance to survey sites can be quantified. With

the survey site as the sampling unit, we define the proximity of species space use as the mean distance between a survey site (e.g., camera trap) and all GPS locations, regardless of individual animal identity, collected through space and time (P_j ; analogous to the Royle et al. 2013 activity center, but quantified at the population rather than individual level):

$$P_j = \frac{1}{N} \sum_{i=1}^N d_i \quad (1)$$

where N is the total number of GPS locations collected across all individuals within the study, i represents each GPS location, and d_i is the distance between a survey site, j , and i . Again, with the survey site as the sampling unit, we define the magnitude of species movement (M_j) as the variation in d_i through space and time (Fig. 1);

$$M_j = \frac{1}{N-1} \sum_{i=1}^N (d_i - P_j)^2 \quad (2)$$

This framework ensures that each survey site has a value for both P and M .

For mammals, camera traps are increasingly used to obtain SOD for a variety of ecological research and conservation applications across increasingly large spatial and temporal scales (Burton et al. 2015, Steenweg et al. 2017). However, cameras lack the high resolution of individual movement patterns that can be derived from radiotelemetry or GPS telemetry (Pacifi et al. 2017). Therefore, cameras and telemetry provide fundamentally different kinds of information, and our objective was to use one method to assess assumptions inherent in the other.

We used fisher (*Pekania pennanti*) detection data collected from a camera trap array, paired with data collected from concurrent overlapping GPS-collared fishers, to test whether variability in species detection frequency is better explained by the proximity of species space use (P_j), or variation in the magnitude of species movement (M_j), across three temporal detection resolutions (surveywide presence-absence, monthly and weekly detections). Movement variability will dictate how frequently animals become available for detection at a point sample (camera trap), particularly for wide-ranging species sampled in continuous habitat (Efford and Dawson 2012).

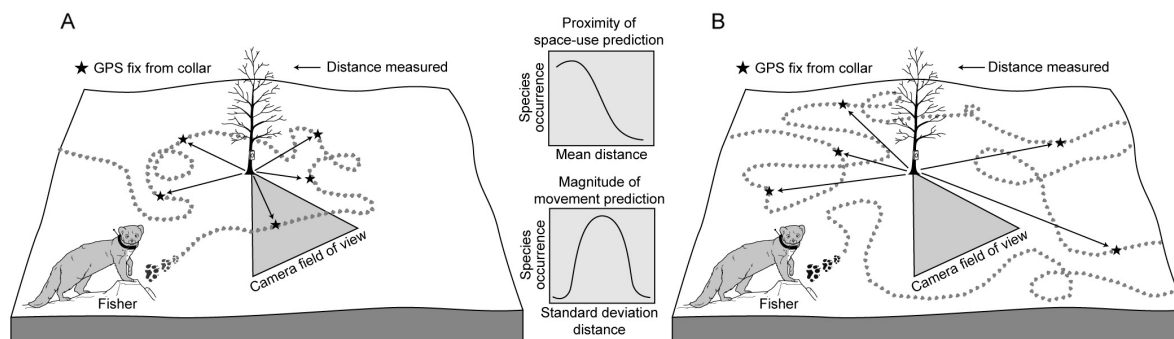


Fig. 1. Species occurrence data are the result of species detection within the detection zone of a stationary survey device. We tease apart population-level contributions of the magnitude of animal movement and proximity of space use to the detection of species at camera traps by comparing the mean distance between Global Positioning System (GPS) locations of all sampled individuals and each camera trap (P_j , proximity of space use) and standard deviation of distances between GPS locations and a camera trap (M_j , movement magnitude) of fisher (*Pekania pennanti*) GPS-telemetry fixes. Panel (A) represents a camera site with high proximity of space use (small P_j), low movement magnitude (small M_j), and high detection probability within the camera's field of view. Panel (B) represents a camera site with low proximity of space use (large P_j) and high movement magnitude (large M_j) resulting in low detection probability within the camera's field of view.

For this reason, we hypothesized that variability in the frequency (or probability) of species occurrence would be better explained by the magnitude of fisher movements around a site, M_j , than by the proximity of fisher space use to the site, P_j . As the temporal sampling resolution of the species detections increases (from survey presence-absence to monthly or weekly counts), there should be an increasing sensitivity to the magnitude of fisher movement relative to a site: Binary presence-absence data should be least sensitive to movement, as the species must be detected only once during the entire survey to be considered present. We therefore predict that variability in M_j will better explain survey-wide presence-absence than monthly or weekly counts.

Currently, typical point surveys assume that SOD are representative of animal activity in space and time, thus making implicit assumptions about animal movement, to which resulting ecological inferences could be sensitive (Burton et al. 2015, Neilson et al. 2018). We sought to explicitly quantify the contribution of animal movement to variations in SOD and evaluate how the inference of ecological process might change if the magnitude of species movement, rather than proximity of species space use, is the better predictor of SOD.

METHODS

Study system and data collection

Fisher are a medium-sized (2–7 kg; F. Stewart, *unpublished data*) Mustelid native to North American forests (Powell 1982). They have moderate body and home range size (Lindstedt et al. 1986) representative of mammal species investigated in many previous camera trap surveys (Burton et al. 2015), making them an attractive model for evaluating the contribution of movement parameters to SOD. We sampled fisher occurrence in central Alberta, Canada, in an area known as the Cooking Lake Moraine (CLM; Fig. 2). This 1596 km² landscape of rolling knob-and-kettle topography supports a diverse mammal community (F. Stewart, *unpublished data*) and is dominated by small wetlands, with trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and scattered pockets of spruce (*Picea glauca* and *Picea mariana*). It is a patchwork of exurban development, agriculture, protected forested areas, and privately owned green space. It is surrounded by unsuitable agricultural lands on all sides, making this a fairly closed population, but still functionally connected to disjunct fisher populations to the north and west (Stewart et al. 2017).

We established 64 camera trap sites in a 4 × 4 km² systematic grid cell array across the

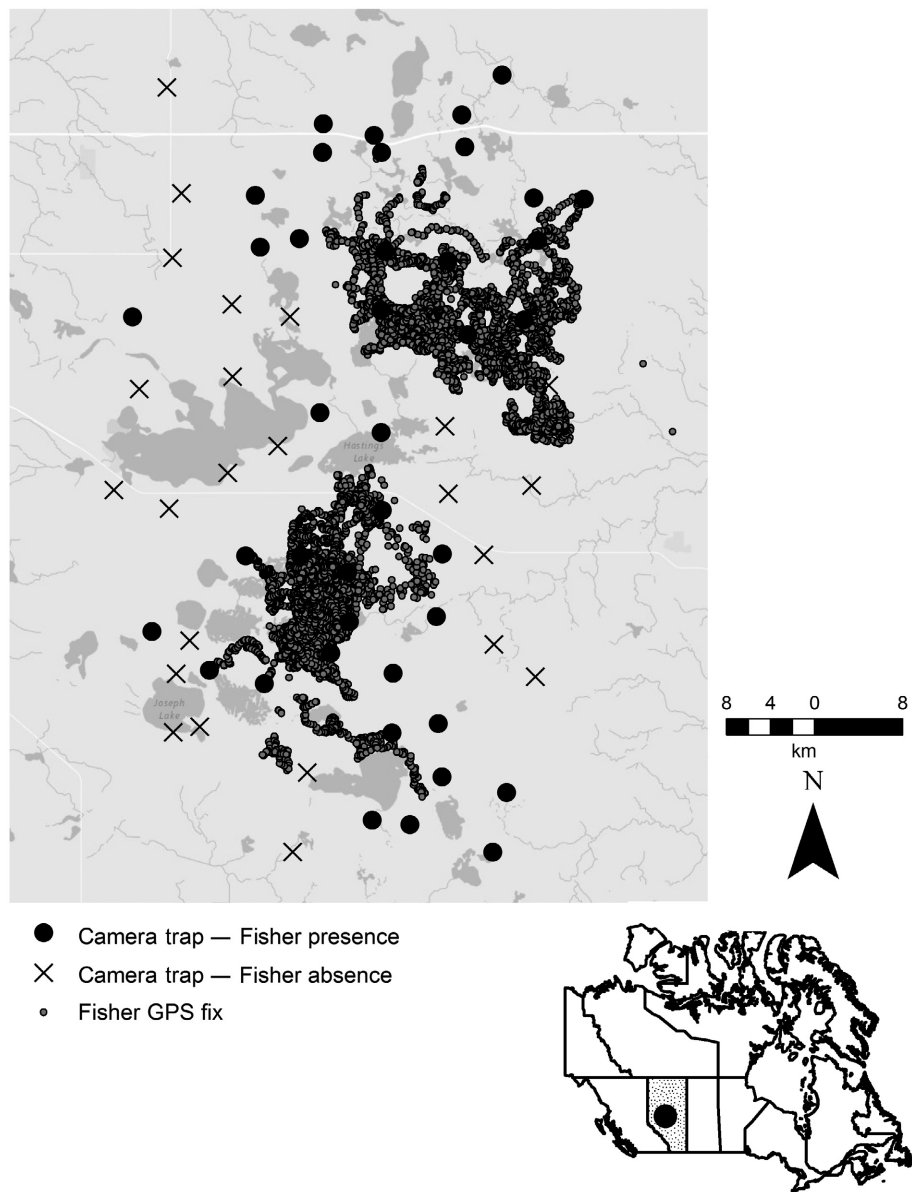


Fig. 2. Fisher Global Positioning System fixes from 10 individuals are overlaid on the spatial distribution of 64 camera trap sites deployed through winter 2015/2016 on Alberta's Cooking Lake Moraine. For spatial reference, dark patches refer to lakes and rivers whereas white lines refer to roads.

CLM (Fig. 2). At each site, the camera photographed the area surrounding a tree baited with ~5 kg of beaver meat and a commercial scent lure (O'Gorman's Long Distance Call). Fisher detections were recorded using Reconyx infrared cameras (models PC900 and PC85; sensu Fisher et al. 2014). Camera traps were deployed from December 2015 to April 2016 and

checked monthly. From these temporally continuous data, we binned fisher detections weekly (0–15), monthly (0–4), and as presence–absence (0/1) across the whole survey.

We live-trapped and GPS-collared 10 fisher individuals (5 male: 5 female) from November 2015 through March 2016. We distributed traps in a stratified random design that aimed to sample

animals distributed as randomly as possible relative to camera traps, and assumed collared animals are representative of the true distribution of fishers in this population. Fishers were captured in covered cage traps (Tomahawk 109 live-trap, Tomahawk, Wisconsin, USA) and sedated with a combination of ketamine (100 mg/mL, 12 mg/kg) and midazolam (5 mg/mL, 0.3 mg/kg). We fitted fishers with GPS tracking collars (E-obs Collar1A, Grünwald, Germany) containing a GPS microchip, a triaxial accelerometer, and ultra-high-frequency transmitter for telemetry and data download. The GPS was programmed with a 5-min fix schedule when the accelerometer recorded a speed >10 cm/s.

All data were collected under Canadian Council of Animal Care permits approved by Inno-Tech Alberta (2070M-A02/048/15-P01), and the University of Alberta (AUP00000518) Animal Handling and Care Committees.

Statistical methods

We used both regression and occupancy modeling frameworks to test whether fisher detections across the camera trap array were more closely related to the proximity of fisher space use (P_j) or magnitude of fisher movement (M_j) around each camera trap. Our basic response data format involved a site by weekly fisher detection matrix at each camera trap; this SOD is denoted as Y_{jt} , the presence/absence (or count) of any fisher detected at camera trap j in each survey t . When investigating temporal variation in SOD, this matrix was collapsed into monthly counts (0–4) and total survey presence-absence (0/1). Our predictor data set is comprised of two main variables measured at the site level: M_j and P_j . We measured the distance d_i (in m) between each camera ($N = 64$) and all GPS-telemetry points, and then calculated summary statistics of these distances—minimum, maximum, mean (P_j ; Eq. 1), and standard deviation (M_j ; Eq. 2)—using the Generate Near Table tool in ArcGIS 10.4.1 (Environmental Systems Research Institute, Redlands, California, USA). Mean, standard deviation, minimum, and maximum distance metrics are all highly correlated (Appendix S1: Table S1); to avoid multicollinearity, we did not include more than one metric as a predictor variable within each of our models.

We treated the mean of distances d_i between camera i and all GPS locations as a measure of fisher space use proximity P to camera site j

(Eq. 1). We hypothesized that camera detection frequencies (Y_j) would be negatively related to fisher proximity of space use (P_j): If fishers are physically situated close to a camera site, there will be more detections than if fishers are situated far from a camera site (Fig. 1). We predicted a negative relationship between camera detection frequencies and fisher minimum distance to be a sampling artifact—fisher must de facto be close to the camera to be detected, but this is not particularly informative. To quantify the magnitude of fisher movement (M_j) relative to a camera trap, we calculated the standard deviation of the distances d_i between camera trap j and all GPS locations (M_j ; Eq. 2). We hypothesized that camera detection frequencies would demonstrate a negative quadratic relationship with fisher movement magnitude (M_j): High or no variability in fisher movements would result in fewer detections as it would represent fewer opportunities for fisher to pass through a camera field of view (Burton et al. 2015), whereas intermediate variation in animal movements should result in more camera detections (Fig. 1). We conducted two analyses to test both spatial and temporal assumptions of SOD.

Spatial variation in species occurrence data

Ecologists assume that spatial variation in SOD reflects variation in relative abundance across survey sites; sites with many detections are situated in habitats with high frequency of animal use. We hypothesized that species detections were better explained by variation in the magnitude of species movement (M_j ; Eq. 2) than the proximity of species space use (P_j ; Eq. 1), such that:

$$Y_j \sim \alpha + \beta M_j + \varepsilon$$

To test this hypothesis, we regressed camera detection data, against the mean (i.e., proximity of space use; P_j), standard deviation (i.e., magnitude of movement; M_j), and maximum distances of fisher GPS locations relative to all camera traps using generalized linear models in R (R v3.3.3, R Foundation for Statistical Computing 2017).

Another way to consider SOD is as serial, binomial, detection histories—for example, the detection history 01110 observes three occurrences in five sessions. In the original formulation of occupancy modeling, detections of stationary species are obtained at discrete patches closed to

movement, and hence, the zeros in detection histories are considered as error—a failure to detect a species when present. Detection histories are used to estimate probability of detection given presence (p) using maximum-likelihood estimation (MacKenzie et al. 2002). For mobile animals in continuous habitat, p represents frequency of site use (Efford and Dawson 2012), with zeros entrained by both the error and the movement of animals around the sampling site (see Burton et al. 2015, Fig. 1). We hypothesized that variability in site detection probability (p) is explained by the magnitude of animal movement (M_j), whereas probability of site occupancy (ψ) is explained by proximity of animal space use (P_j). We predict as follows:

$$\psi(\cdot)p(M_j) \text{ and } \psi(P_j)p(\cdot)$$

where each camera site ($N = 64$) is the sampling unit. We competed a null model, $\psi(\cdot)p(\cdot)$, against models that assumed occupancy (ψ), detection probability (p), or both, varied as a function of movement magnitude (M_j), and proximity of space use (P_j). Further, we predict p to change with the temporal resolution of sampling (monthly or weekly counts as sample replicates). All occupancy models were performed in PRESENCE software v11.7 (Hines 2006) and competed in an information-theoretic framework based on Akaike information criterion (AIC) scores (Burnham and Anderson 2002).

Temporal variation in species occurrence data

Temporal variation in SOD—for example, a monthly 0111 detection history—is assumed to reflect changes in animal movements, which induces variations in the proximity of animal space use around the survey point. If this is true, we predict that sensitivity to the effects of the proximity of species space use (P_j), or magnitude of species movement (M_j), on SOD should increase with temporal sampling resolution: Survey presence-absence should be least sensitive, as the species must become available only once during an entire survey to be considered present. Within both our regression and occupancy frameworks, models involving monthly counts as the response variable should better fit the data than models involving survey presence-absence data, but models involving weekly counts as the response variable should fit the data best.

To investigate the effects of temporal resolution on SOD, we competed suites of models with occurrence data measured as survey presence-absence (0/1), monthly counts (0–4), or weekly counts (0–15) of fisher detections. For these generalized linear models, we used the residual deviance to compare model fit as a measure of model sensitivity. Survey presence-absence data were modeled using a binomial family function (logit link), and weekly count data were modeled using a Poisson family function (log link). Monthly count models used a multinomial regression in the R package *nnet* (version 7.3-12; Venables and Ripley 2002), an extension of logistic regression for response variables with count data (0–4) that is not Poisson distributed (Zuur et al. 2007). Suites of regression models within each temporal resolution were competed using AIC scores (Burnham and Anderson 2002). For occupancy models, we compared two suites of temporal models where species detection histories were composed of either four monthly or 15 weekly detection histories. We used the residual deviance ($-2 \log$ likelihood) to compare model fit. Results are presented as mean \pm standard error unless otherwise specified.

RESULTS

Sixty-four cameras were deployed for a total of 102 d (6528 trap days) and collected 95,128 photographs (i.e., animal detections) from December 2015 through early April 2016. Of these detections, 12,156 were of fisher. Fisher were observed on 43 of 64 cameras (naïve occupancy = 0.67). From 10 GPS-collared individuals, we obtained 28,088 fixes with 2808 ± 1137 fixes per individual. Global Positioning System fixes were on average $15,188 \pm 1281$ m away from any camera (Fig. 2). Microsatellite analysis from hair samples collected throughout the study revealed that at least 32 fishers occupied the CLM during the winter of 2015/2016 (Stewart et al. 2017). We therefore obtained GPS information from 31% of the minimum known population.

Spatial variation in species occurrence data

Variability in fisher SOD was best explained by variation in the magnitude of movement (M_j), rather than the proximity of space use relative to cameras (P_j). As predicted, a quadratic model

with M_j better explained variation in fisher occurrence than did linear relationships. In no models did the proximity of space use (P_j) explain SOD better than a null model (Fig. 3A).

Similarly, within the occupancy modeling framework, detection probability (p) was best explained by the magnitude of movement (M_j), rather than the proximity of species space use

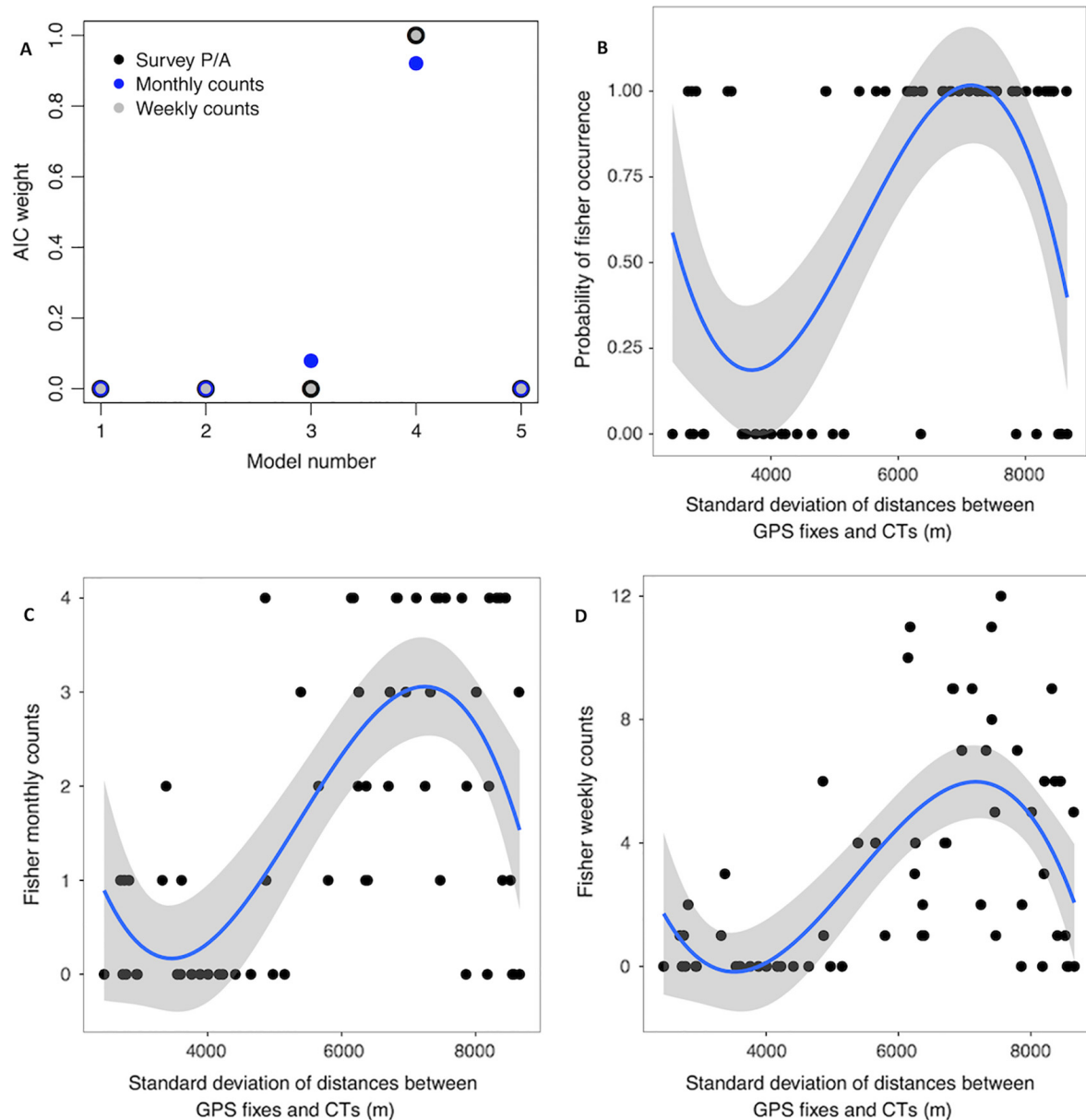


Fig. 3. Generalized linear models across three temporal resolutions all demonstrate that the standard deviation of the distances between Global Positioning System collar fixes and camera traps best predict the probability of species presence-absence, monthly counts, and weekly counts. Models presented in panel (A) include fisher species occurrence data as the response variable, with predictors of: (1) null model; (2) mean distance (i.e., proximity of space use; P_j); (3) standard deviation distance (i.e., movement magnitude; M_j); (4) standard deviation distance quadratic; and (5) maximum distance. Panels (B–D) demonstrate the top model from panel (A) at each temporal resolution (survey presence-absence, monthly counts, and weekly counts).

(P_j) relative to cameras. We competed a total of 45 monthly and 45 weekly models involving all possible combinations of maximum, mean (P_j), and standard deviation (M_j) distances as both occupancy (ψ) and/or detection probability (p) covariates (Appendix S1: Table S2). The best-supported models all suggested the magnitude of movement (M_j) best explained detection probability (p). The proximity of space use (P_j) best explained site occupancy (ψ) only when M_j was included as a detection covariate (Table 1).

Temporal variation in species occurrence data

The relationship between species occurrence and magnitude of movement (M_j) demonstrates a consistent negative quadratic pattern across all temporal resolutions (survey, monthly, and weekly; Fig. 3B–D). In contrast to our temporal prediction, binary presence–absence was more sensitive to M_j than were monthly or weekly species detections (model residual deviance = 72.58 for survey presence–absence temporal resolution; 76.65 for monthly temporal resolution; and 165.72 for weekly temporal resolution; Fig. 3B).

Estimated occupancy varied slightly with temporal resolution (monthly: $\psi = 0.68$, $p = 0.65$; weekly: $\psi = 0.64$, $p = 0.32$). Akaike information criterion ranking of occupancy models differed between monthly and weekly temporal resolutions; however, top models always involved movement magnitude (M_j) as an occupancy (ψ) and/or detection

probability (p) covariate (Table 1). For monthly models, p did not vary with survey month but did vary with M_j (ER [evidence ratio] model 1 and 2 = 3.87), and ψ varied with the maximum distance between a GPS fix and the camera (ER model 2 and 3 = 70.1). For weekly models, p varied by survey week and M_j (ER model 7 and 8 = 1.96), and ψ varied with M_j (ER model 6 and 7 = 9.3). In contrast to our temporal prediction, occupancy models measured on a monthly temporal resolution demonstrate more sensitivity to this relationship than models measured on a weekly temporal resolution (monthly models deviance ranged between 255 and 300; weekly models deviance ranged between 790 and 857; Table 1).

DISCUSSION

Species occurrence data from camera traps better reflect the degree to which animals move, rather than the space that animals use. Variation in the magnitude of movement (M_j) around a camera trap, rather than proximity of space use (P_j) to the camera trap, best explained species detections regardless of the temporal sampling resolution. Similarly, M_j best explained detection probability, and P_j only explained occupancy probability when M_j was included as a detection probability covariate. In addition, presence–absence was more sensitive to M_j than were monthly or weekly counts (Fig. 3).

Table 1. Selection of top occupancy models for fisher in Alberta's Cooking Lake Moraine across both monthly and weekly sampling periods.

Model†	AIC‡	ΔAIC	AIC weight	Model likelihood	K§	–2LL¶
Monthly sampling						
1. $\psi(\text{MAXIMUM}), p(M_j)$	263.51	0.00	0.79	1.00	4	255.51
2. $\psi(\text{MAXIMUM}), p(M_j + \text{SURVEY})$	266.22	2.71	0.20	0.26	7	252.22
3. $\psi(\cdot), p(M_j)$	274.74	11.23	0.00	0.00	3	268.74
4. $\psi(P_j), p(M_j)$	274.82	11.31	0.00	0.00	4	266.82
5. $\psi(\cdot), p(\cdot)$	304.93	41.42	0.00	0.00	2	300.93
Weekly sampling						
6. $\psi(M_j), p(M_j + \text{SURVEY})$	826.95	0.00	0.77	1.00	18	790.95
7. $\psi(\text{MAXIMUM}), p(M_j + \text{SURVEY})$	831.42	4.47	0.08	0.11	18	795.42
8. $\psi(\cdot), p(M_j + \text{SURVEY})$	831.82	4.87	0.07	0.09	17	797.82
9. $\psi(P_j), p(M_j + \text{SURVEY})$	832.54	5.59	0.05	0.06	18	796.54
10. $\psi(\cdot), p(\cdot)$	861.69	34.74	0.00	0.00	2	857.69

† Occupancy (ψ) and detection probability (p) were either constant (\cdot), varied by SURVEY, or varied by the MAXIMUM, STANDARD DEVIATION (M_j), or MEAN (P_j) distance between a camera trap and Global Positioning System fixes.

‡ Akaike information criterion.

§ Number of parameters in the model.

¶ –2 log likelihood of the model (deviance).

The role of movement in species detections is an implicit assumption in species occurrence research (Turchin 1998, MacKenzie 2006, Royle et al. 2013, Burton et al. 2015), and the conservation strategies derived therefrom (Morin et al. 2017, Royle et al. 2017), but rarely is movement explicitly quantified. We therefore recommend that the magnitude of species movement receives greater consideration when analyzing SOD from stationary surveys. These results may be especially important for species with large movements relative to the size of the study area (cf. Efford and Dawson 2012).

Considerable debate on the relationships between SOD, density, and abundance is waged within the ecological literature (Linden et al. 2017, Steenweg et al. 2016, Broadley 2017, Parsons et al. 2017), with ramifications for conservation and management (Fuller et al. 2016). Previous work acknowledges the potential for a nonlinear relationship between occupancy and abundance when animals display variable movement patterns between detection devices (Efford and Dawson 2012, Noon et al. 2012), and spurs calls for research that tests the assumptions of animal movement within these relationships (Ellis et al. 2014, Steenweg et al. 2016). In our test, temporal and spatial variations in species occurrence at a sampling site reflected the magnitude of animal movements, rather than the explicitly assumed variation in proximate space use and variation in relative abundance, respectfully (Turchin 1998, MacKenzie 2006, Royle et al. 2014, Burton et al. 2015). New methods are in continual development for different ways to think about the continuous sampling of camera trap data, and the resulting inferences on abundance and movement (Moeller 2017, Neilson et al. 2018).

The method of sampling also influences SOD. For example, considerable debate exists about the use of attractants in trap studies, as this method may affect both animal movement and detection probability. Bait is required for thousands of point-survey studies; of hundreds of camera trap studies reviewed by Burton et al. (2015), two-thirds targeted the camera at some form of attractant, with bait or lure being used in one-third of the studies. The effect of bait will vary by target species, and for elusive carnivores such as the fisher, is argued to be the most effect use of research funds (du Preez 2014). We do not

expect bait to have affected detection probability in this study, as spatially explicit capture–recapture modeling (Royle et al. 2013) did not detect any effect of trap behavior at the population level (J. Bugar, *unpublished data*). However, investigating the tortuosity of GPS movement paths of individuals relative to baited sites would be a valuable test of whether maximizing detection probability with bait truly comes at the expense of inflating species detections by increasing movement at a sampling site, relative to movements on the surrounding landscape.

Challenging the consistency of multiple data types represents an alternate tactic for addressing assumptions inherent in SOD. Popescu et al. (2014) demonstrated that camera traps reflected fisher space use in California, as fisher telemetry relocations correlated to the probability of detection by cameras; however, the spacing of cameras was much denser than in our study. In another method comparison example, Chauvenet et al. (2017) demonstrated that distance sampling provided more accurate European boar (*Sus scrofa*) density estimates than spatially explicit individual camera-based models because distance sampling was more robust to heterogeneity in boar group size. Our results build upon this literature in two ways: (1) by assessing animal space use and movement as separate, though associated, processes, and (2) by assessing multiple measures of SOD—occurrence and detectability-corrected occupancy.

Species occurrence data methods in general, and camera traps specifically, often measure occurrence of multiple species simultaneously. Two-thirds of reviewed camera studies compared relative abundance of multiple species by contrasting observed detection rates of each (Burton et al. 2015). For example, O'Brien et al. (2003) demonstrate European wild boar to be more abundant than either Malay tapir (*Tapirus indicus*) or Sambar deer (*Cervus unicolor*) across multiple areas. Similar conclusions have been made across continents and across methods, where more vagile species receive higher frequencies of detection when compared to less vagile species, and are inferred as being more abundant (Gompper et al. 2006, Monterroso et al. 2013, 2014, Carreras-Duro et al. 2016). However, our research suggests frequency of detections is not an accurate or robust index of relative abundance across species,

as it is likely conflated by differences in species' propensity for movement. We recommend that relative abundance as a population index needs to be standardized by some measure of species movement propensity, such as expected home range size or movement rate (Broadley 2017), to ensure it is a meaningful metric for species comparisons within, and between, studies. Moreover, devices with consistent capacity for animal detection need to be deployed in a sampling density reflective of the movement ecology of each species (*sensu* Linden et al. 2017). Species detection rates are affected by many factors other than abundance; the expected relationships between sampling design, detectability, and ecological inference will be species specific (Burton et al. 2015), and likely influenced heavily by species density (Kjellander et al. 2004, Broadley 2017).

We demonstrate the ubiquity and importance of movement when interpreting different temporal resolutions of SOD (survey presence-absence, monthly, and weekly counts). This relationship is reflected in sampling design literature. For example, MacKenzie and Royle (2005) suggest the temporal resolution of SOD should scale with species rarity: Surveying more sites less frequently is more efficient for rare species, whereas surveying few sites more frequently may be better for conspicuous species. These trade-offs in survey effort have been considered across bats (Weller and Lee 2007), birds (Bried et al. 2011), reptiles (Sewell et al. 2012), and plants (Garrard et al. 2008). Much less frequently has movement variability been considered when interpreting the SOD generated by those designs, but this could be evaluated with the methods described here.

We demonstrate that inferences from ecological investigations using SOD may reflect the magnitude of species movement better than species space use. This result has important implications for how we interpret projections from wildlife distribution (or ecological niche) models (Peterson 2003), how we model future biodiversity projections from landscape and climate change (Anderson et al. 2006, Elith et al. 2009), and how we understand large-scale ecological patterns and processes.

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