Research Article

The Debate About Bait: A Red Herring in Wildlife Research

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ABSTRACT The use of bait (or attractants) to lure animals to a sampling site is common in wildlife research and important for optimizing species detection rates. The effect of bait on animal movement and space-use, however, is contested, fueled by concerns bait may affect animal movement and increase residency time. If founded, bait may bias parameter estimates from density, species distribution, resource selection, or behavioral models, produce spurious ecological inferences, and skew resulting management recommendations. To test whether animal movement varies with proximity to bait, we used high-resolution global positioning system telemetry data of 10 fishers (*Pekania pennanti*), temporally paired with 64 baited wildlife camera traps, to quantify the effect of bait on individual and population movement metrics. Although bait appeared to have a significant correlative effect on 1-hour movement segments, landscape characteristics had an effect 1.7 times greater, where the proportion of mixed forest and cultivation explained the majority of variability in animal movements. We contend that maximizing probability of detection and controlling or modeling local-scale landscape variability that could affect the probability of detection is a more important consideration in wildlife research than the effect of bait, which is eclipsed by differences incurred by natural habitat heterogeneity. Failing to maximize the probability of detection may obscure the modest bias potentially presented by the use of bait, or attractants, on ecological inference. © 2019 The Wildlife Society.

KEY WORDS animal movement, animal occurrence, attractants, bait, camera trap, *Pekania pennanti*, tortuosity.

Point sampling is used by biologists to survey animal density and distributions by sampling occurrence across space and time. For decades, the probability of animal encounters has been maximized by using attractants (Schlexer 2008). These methods are deployed across taxa and ecosystems, from marine to the alpine; they include live-trapping (Hoffmann et al. 2010), mist netting (Bibby 2000), non-invasive genetic tagging via hair trapping (Waits and Paetkau 2005), and more recently, camera trapping in terrestrial (O'Connell et al. 2010, Burton et al. 2015, Kays 2016) and aquatic (Harvey et al. 2007, Bacheler et al. 2013) environments. Attractants, of which bait is but one form, entice animals into the trap or detection device, and can encompass olfactory (e.g., scent lure for fish and terrestrial carnivore research; Long et al. 2012), auditory (e.g., prey calls for raptor research; Bildstein and Bird 2007), nutritional (e.g., salt licks for ungulate research; Côté 2000), visual (e.g., compact disks used as attractants at fur snares), and natural rewards—objects regularly used in the natural environment (e.g., trees, latrine sites, and nests; Schlexer 2008).

All attractants are designed to increase the probability of encounters between the animal and the sampling device beyond that expected by random chance. Maximizing the probability of detections given presence (p) is often imperative for statistical modeling, wherein data density limits the application and proper functioning of statistical models (MacKenzie et al. 2017). For example, two-thirds of terrestrial camera-trap studies directed the camera at some form of attractant, with bait or lure being supplied in a third of the studies (Burton et al. 2015). Baiting can be particularly important for rare and elusive species (Thompson 2004); 2 winters of lured but unbaited sampling produced 0 Rocky Mountain wolverine (*Gulo gulo*) detections (J. T. Fisher, InnoTech Alberta, unpublished data), whereas a beaver (*Castor canadensis*) carcass at each site the following year increased the estimated probability of detection (p) to 0.65 using non-invasive genetic tagging, and 0.99 using camera trapping (Fisher et al. 2013, Fisher and Bradbury 2014). Although bait has been argued to be the most effective use of research funds (du Preez et al. 2014*a,b*; although see Balme et al. 2014), it is also anecdotally labeled as a statistical and ethical red flag by animal care committees and some reviewers of manuscripts.

The contention is that maximizing encounter rates, probability of detection, and data density comes at a potential cost. How the use of bait affects animal

movement, and resulting space-use or residency time, and what effect these factors have on the interpretation of ecological process is unknown (Long et al. 2012, du Preez et al. 2014a). There is considerable variability in potential bait effects: shifting activity spatial and temporal patterns, competition, detection probability, or selection probability within a home range. How these might affect an inference, as bias or simply error around estimates, remains to be examined (Schlexer 2008, Long et al. 2012, Cusack et al. 2015). For example, density estimates from point sampling methods typically assume a half-normal decay function between the probability of individual detection and the distance to the center of an individual's home range (Efford 2004, Royle et al. 2013). The use of bait might violate this assumption by shifting the center of the individual's home range, and skewing resulting density estimates, an important metric for wildlife management (Williams et al. 2002). Alternatively, use of a baited site may amplify measures of species occurrence, biasing estimates of space-use and habitat selection. The effect of bait can be viewed as a gradient question, requiring animals of different distances to bait, rather than the comparison of baited to unbaited landscape locations. The effect of proximity to bait on an animal's movement could be tested using tortuosity calculations, the departure of an animal's path from a straight line (Turchin 1996, Benhamou 2004, Miller et al. 2011), of movement path segments. Increased tortuosity near a bait site suggests smaller, more exploratory movements characteristic of foraging, caching, or vigilance behaviors, rather than larger linear movements characteristic of travel or searching behaviors. Movement, however, is also affected by landscape heterogeneity, where foraging opportunities and associated olfactory cues, of which bait is but one, can vary with habitat characteristics (Johnson et al. 1992, Barraquand and Benhamou 2008). To our knowledge, no one has empirically evaluated the effect of bait on animal movement, density, or space-use, which requires simultaneously collected data sets on species occurrence and species movement.

Our objective was to determine whether animal movement varies with proximity to bait, and we investigated this relationship at population and individual scales. We hypothesized that variability in movement due to bait would be smaller than variability due to landscape heterogeneity. If animal movement is affected by the proximity of bait, we expected a negative correlation between tortuosity measures of fisher (*Pekania pennanti*) path segments and distance of the path segment to the nearest baited camera trap; path segments close to a trap should be more tortuous than path segments far from a trap, as fishers truncate longer movements to investigate the bait.

STUDY AREA

This study took place between December 2015 and March 2016 on and around Alberta's Beaver Hills Biosphere (BHB). The BHB is situated in east-central Alberta, Canada (53.381167°N, 113.062976°W). It is a 1,596-km² glacial moraine composed of small permanent water bodies and mixed forests of trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*), with pockets of white spruce (*Picea glauca*) and open meadows, intermixed with varied land uses including cultivation, agriculture, and exurban development (Fig. 1). The elevation of the BHB varies between 650 m and 760 m, annual precipitation varied between 450 mm and 500 mm, and average daily temperatures ranged between 17°C in the summer to −14°C in winter seasons (Government of Alberta 2018). This region of mixed boreal forest and aspen parkland provides habitat for a diversity of avian, amphibian, and mammalian species (Beaver Hills Initiative 2015), including moose (*Alces alces*), elk (*Cervus canadensis*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), northern flying squirrel (*Glaucomys sabrinus*), red squirrel (*Tamiasciurus hudsonicus*), snowshoe hare (*Lepus americanus*), porcupine (*Erethizon dorsatum*), striped skunk (*Mephitis mephitis*), least-tailed, short-tailed, and long-tailed weasel (*Mustela nivalis*, *M. ermina*, and *M. frenata*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), and fisher (Stewart 2018). Fisher gene flow exists with populations to the north (Stewart et al. 2017), but the extent of agriculture surrounding the BHB limits connectivity between this landscape and adjacent forested regions.

METHODS

Field Methods

To measure the effect of proximity to attractants on animal movement, we took advantage of 2 simultaneous studies on the BHB investigating fisher occurrence and fisher movement. We established camera sites within each cell of a systematic 4 × 4-km² grid cell array, resulting in 64 sampling sites (Fig. 1). We sampled fisher occurrence using a method we deemed most likely to detect effects on animal movement: large, regularly refreshed beaver carcass bait rewards, placed at camera traps during winter when food is limited. At each site, we directed a camera trap at a bait tree that had a commercial scent lure (O'Gorman's™ Long Distance Call, Broadus, MT, USA), and approximately 5 kg of beaver meat suspended 3 m above the ground (Stewart et al. 2018). We refreshed bait and lure monthly from December 2015 through April 2016. Combined, the spatial configuration and temporal sampling of sites reflect an average home range of fisher individuals within this study area (Burgar et al. 2018).

Concurrently (Nov 2015 through Mar 2016), we measured the movement of 10 resident adult fishers (5 male and 5 female) on the BHB using global positioning system (GPS) telemetry-collars (E-obs Collar1A™; Grünwald, Germany). Density estimates of fisher within this population range between 0.73 and 3.91 fishers/100 km² (Burgar et al. 2018); therefore, we obtained GPS movement data of ≥17% of the population. We captured fishers in covered cage traps (Tomahawk 109 Live-Trap; Tomahawk, WI, USA), sedated with midazolam (5 mg/ml, 0.3 mg/kg) and ketamine (100 mg/ml, 12 mg/kg), and fitted each fisher with a GPS-collar. We programmed collars for 5-minute
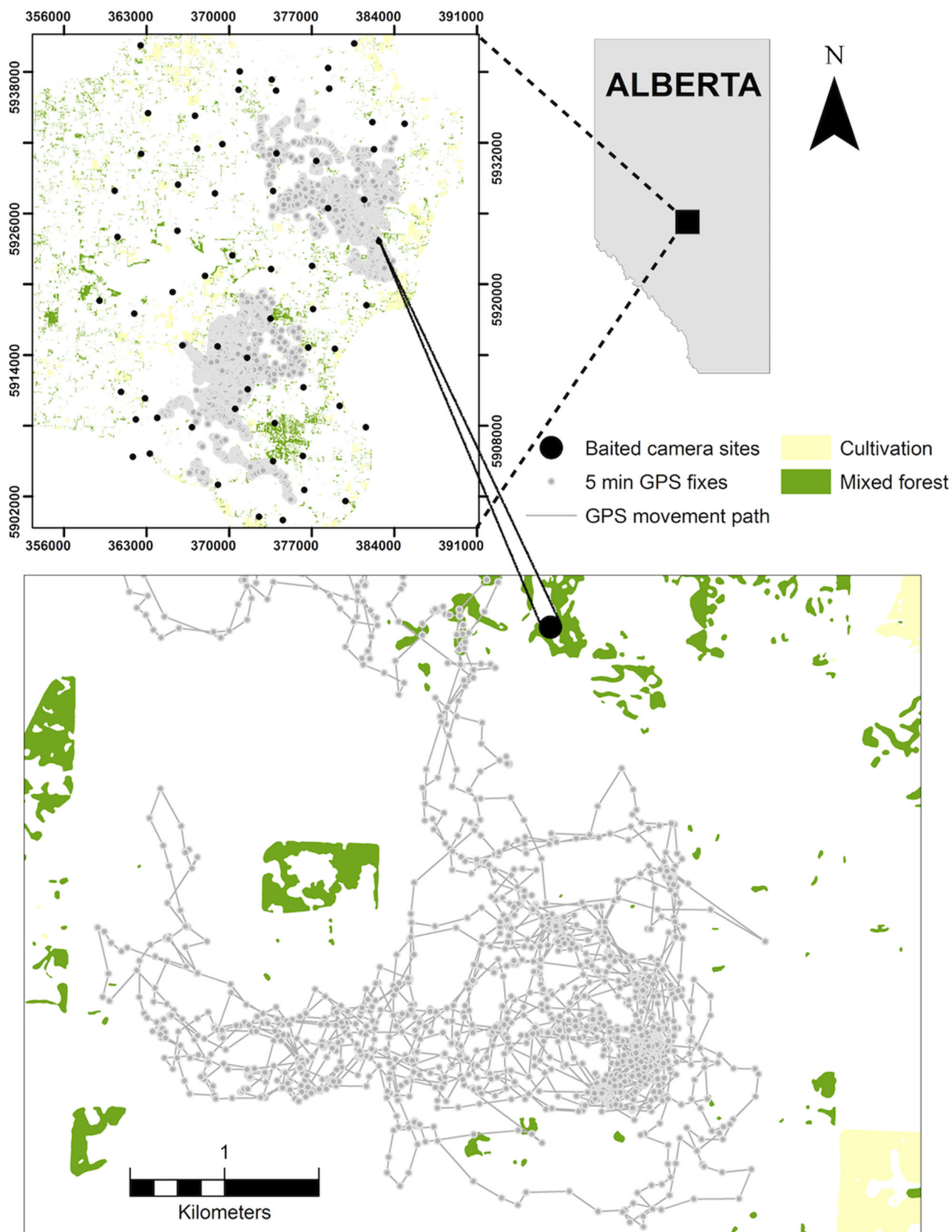
Figure 1. We collected fisher global positioning system (GPS) telemetry data from 10 fishers across Alberta's Beaver Hills Biosphere, Canada, 2015–2016, as a measure of movement, and compared movement data to the proximity of bait at 64 camera-trap sites. The proportion of cultivation and mixed forest explained variability in fisher movement much more so than bait proximity, as represented by green and yellow landscape features. White landscape features represent a combination of water, grassland, shrubland, development, coniferous forest, deciduous forest, linear features, block features, and protected areas, which did not significantly affect animal movement.

fixes if the animal was moving >10 cm/second; collars contained a tri-axial accelerometer for speed measurements, a GPS microchip for location measurements, and an ultra high frequency (UHF) transmitter for data download and telemetry. Data collection was approved under the Canadian Council of Animal Care permits administered by both the University of Alberta (AUP00000518) and InnoTech Alberta (2070M-A02/048/15-P01) Animal Care and Handling Committees.

Statistical Analyses

We tested whether the tortuosity of fisher movements, as measured by high-fix rate GPS telemetry, varies with proximity to baited camera sites; we assumed detection and non-detection data could approximate movement (Neilson et al. 2018, Stewart et al. 2018) and would reflect fisher's decisions about interacting with a baited site. We segmented fisher GPS telemetry paths by 12 units of 5-minute fixes to investigate this relationship on a temporal scale of 1-hour increments (12 × 5-min). This approach eliminated failed fixes from our analysis and corresponds to the recommended period for determining dependent occurrences in camera-trapping studies (Romero-Munoz et al. 2010, Hernandez-Santin et al. 2016). We then calculated the average location (as scaled Universal Transverse Mercator [UTM] co-ordinates: mean UTM easting by mean UTM northing), and tortuosity (cosine of the relative angle between consecutive GPS steps), of these 1-hour segments. Tortuous movements are represented by small numbers (<0), and more linear movements are represented by larger numbers (>0; Calenge 2016). Finally, we calculated the distance (i.e., proximity) between a segment's average location and the nearest bait. We summarized these data in the R package plyr (Wickham 2011) using the dplyr function.

We used a generalized linear mixed model (GLMM) framework in the R package nlme (Pinheiro et al. 2017) to weigh support for a statistical relationship between bait proximity and tortuosity of fisher movement. We regressed the average segment tortuosity against the bait proximity for each 1-hour segment of fisher movement. We also considered the effect of camera-trap location (UTM easting [UTMX] and UTM northing [UTMY]), fisher sex, and interactions between these predicting variables, on tortuosity. We scaled all predictor variables to ensure we could compare their parameter estimates. In a separate analysis, we included fisher identification as a random effect to investigate any among-individual variation (Nakagawa and Schielzeth 2010, Stewart and Mcadam 2014). We compared models in an information-theoretic framework based on Akaike's Information Criterion (AIC) scores, which balance variance explained by model fit, with model parsimony (Burnham and Anderson 2004); we did not compare models with and without random effects because the model selection process differs for fixed versus random effects (Greven and Kneib 2010).

Finally, to investigate the effects of landscape features on path segment tortuosity, we used ArcGIS v10.3 (Environmental Systems Research Institute, Redlands, CA, USA) geographic information system with LandSat digital map inventories from the Alberta Biodiversity Monitoring Institute (Landcover Map and Human Footprint Maps 2014), and Beaver Hills Initiative (Land Management Framework 2015). We quantified the proportion of natural and anthropogenic landscape features around bait sites. Tortuosity can be scale-dependent (Turchin 1998, Whittington et al. 2004), and fisher movement segments on the BHB were on average 1.6 km ± 0.01 km (SE) away from a baited camera. To ensure we encompassed the full inference space of fisher movement, we, therefore, measured landscape heterogeneity as the proportion of water, grassland, shrubland, cultivation, development, coniferous forest, deciduous forest, mixed forest, linear features (hard roads, vegetated roads, trails, seismic lines, pipelines, and transmission lines), block features (rural residential homes and oil well sites), and protected areas within a 1.5-km-radius buffer around bait sites as predictor variables in a final GLMM model. We used stepwise model selection (stepAIC function) in the R package MASS (Venables and Ripley 2002) to determine the most parsimonious model wherein landscape features explained variability in fisher movement.

We ensured all data met model assumptions through thorough data exploration (Zuur et al. 2009); we removed predictor variables with high multicollinearity (variance inflation factor >3) from the analysis. Average segment tortuosity was normally distributed so we used Gaussian models with an identity link (Crawley 2007). We conducted all analyses in R version 3.3.3 (R Core Team 2017) and results are presented as mean ± standard error unless otherwise specified.

RESULTS

We obtained movement data from 10 fisher individuals across 94 days of observation; GPS fixes represented an average of 2,808 ± 1,137 fixes/individual (Stewart et al. 2018). These fixes generated 3,432 1-hour movement segments (357.9 ± 167.7 segments/individual). Across all individuals, fishers demonstrated slightly tortuous movement segments ($\bar{x} = -0.06$, SD = 0.01), and segments occurred a maximum of 4.2 km from baited sites (min = 3.9 m).

Site location and landscape heterogeneity, not bait proximity, best explained variability in fisher movement tortuosity. Correlating movement tortuosity and bait proximity demonstrated a weak but significant association ($r = 0.035$, df = 3,430, $P = 0.038$). Regression model selection demonstrated that movement tortuosity was best explained by a positive and weak relationship with bait proximity ($\beta = 0.023 \pm 0.01$, $P = 0.02$), where a positive β coefficient implies movement is more tortuous closer to a bait site, and a strong negative relationship with bait location ($\beta = -0.040 \pm 0.01$, $P < 0.001$). Comparing the β coefficients (i.e., slopes) of these 2 predictors demonstrated the spatial location of the bait had a 1.7-fold effect size on fisher tortuosity when compared with bait proximity, indicating landscape characteristics (i.e., where a bait site is placed) around study sites had an important effect on

animal movement. Combined, this top model as measured by AIC accounted for 65% of the weight of evidence when compared with other models (Table 1).

Of landscape predictors, the spatial location, proportion of cultivation, and proportion of forests best explained fisher movement tortuosity. Movement segments were more tortuous around baited camera sites on the east side of the BHB ($\beta = -0.05 \pm 0.01$, $P < 0.001$) with high proportions of cultivation ($\beta = -0.45 \pm 0.17$, $P = 0.009$), and less tortuous around baited camera sites with high proportions of mixed forest ($\beta = 0.47 \pm 0.16$, $P = 0.004$). This model explained 45% of the weight of evidence; in the second-best landscape model, which explained 22% of the weight of evidence, fisher movement segments were more tortuous around baited camera sites with high proportions of deciduous forests ($\beta = -0.04 \pm 0.17$, $P = 0.82$), although this relationship was not significant (Table 2).

DISCUSSION

Fisher movement was influenced more by natural landscape heterogeneity than by proximity to bait. For fishers on BHB, individuals at the west end of the study grid had slightly tortuous movements, but individuals on the east end of the study grid had more tortuous movements despite the proximity of baits. Bait location had 1.7 times the effect of bait proximity on fisher movement tortuosity, which can be primarily explained by the proportion of mixed forest and cultivation around baited camera sites. These analyses demonstrate that landscape-movement associations have the potential to have a larger effect on wildlife data than the proximity to attractants.

The importance of correlative landscape predictors in this analysis suggests that the effect of bait on movement is eclipsed by habitat-associated variation in movement. We constructed the study in favor of creating a movement response in proximity to bait by conducting this analysis in winter when food is most limiting, when we could expect the greatest possible effect of bait, and by providing attractive, substantial, easily obtainable, and frequently replenished food rewards. Like most landscapes supporting a persistent population, however, the agricultural BHB landscape provides abundant natural prey (Stewart 2018).

Five kilograms of monthly beaver meat likely comprises a very small proportion of food resources available, and, therefore, is not a substantially greater inducement to change spatial behavior than any other food resource on the landscape.

This attraction distraction question has been modeled extensively as trap happiness, or a trap effect, wherein an animal once caught is more likely to be caught again (Nichols et al. 1984). This is a less direct measure of the effect of bait on the behavior of a free-moving organism than ours but still informative. In a separate study on the same BHB fishers, we quantified density estimates from baited camera-trap data using spatial capture-recapture methods (Royle et al. 2013). We demonstrated that there was no effect of trap behavior on density estimation at the study level but that trap behavior may vary between individual sites (Burgar et al. 2018), corroborating our analysis here. These analyses, however, are correlative and inferential; much of landscape ecology (in particular) is based on spatial signals collected across gradients of interest. To determine the causal effect of bait on animal movement or shifts in home range patterns, a productive future research avenue would be to quantify animal movement across a camera-trap array composed of sites with manipulated bait presence.

Throughout the history of ecological inquiry, traps have rarely randomly been placed in space or time because researchers recognize the importance of optimizing effort through increasing detection probability and spatial and temporal landscape variations. For small animals, decades of live-trapping researchers have placed traps along run poles for animals that might use these fine-scale habitat features (Chitty 1957), and amphibian researchers purposefully put pit-fall traps next to water bodies (Corn and Bury 1990). For larger animals (i.e., ungulates and carnivores), traps are commonly placed along stream beds or game trails because they are recognized areas of high residency time (Harmsen et al. 2010). If these natural features are purposefully used to increase the detection probability of species when compared with random trap placement, why are we so concerned about intentionally placed attractants? For example, Stewart (1979) demonstrates an interaction between trap placement

Table 1. Generalized linear model outputs of the effect of distance to bait (POB; m), sex, bait location (UTMX), and individual (ID) on the tortuosity of 1-hour fisher movement segments collected in the winter of 2016 in central Alberta, Canada. The location of the bait (UTMX) had 1.7 times the effect on fisher movement tortuosity than POB as demonstrated by model 1. Models with random effects (A and B) are not comparable using corrected Akaike's Information Criterion (AIC_c) to models without a random effect but are included here for reference.

Model	Intercept	POB[a]	Sex	UTMX[b]	POB:UTMX	Random effect	df	−2LL[c]	AIC_c	ΔAIC_c	w_i[d]
1	−0.06	0.02		−0.04			4	−3,046.26	6,100.53	0.00	0.65
2	−0.06	0.02		−0.04	−1.5EE−04		5	−3,046.26	6,102.54	2.01	0.23
3	−0.05			−0.04			3	−3,049.04	6,104.09	1.55	0.10
4	−0.06	0.02	0.05				4	−3,053.10	6,114.22	10.13	<0.01
5	−0.05	0.02					3	−3,054.29	6,114.59	0.37	<0.01
A	−0.05	0.02				ID	4	−3,054.09	6,116.18	0.00	0.49
B	−0.05	0.02		−0.03		ID	5	−3,055.99	6,122.01	5.83	0.51

[a] Proximity of bait.
[b] Spatial location of the bait.
[c] −2 log likelihood.
[d] AIC weight.

Table 2. Generalized linear model outputs and corrected Akaike's Information Criterion (AIC$_c$) model selection of the effect of landscape features on the tortuosity of 1-hour fisher movement segments collected in the winter of 2016 in central Alberta, Canada. Of landscape predictors, the spatial location, proportion of cultivation, and proportion of forests best explained fisher movement tortuosity.

Model	Intercept	POB[a]	UTMX[b]	CULT[c]	MIXED[d]	DECID[e]	df	−2LL[f]	AIC$_c$	ΔAIC$_c$	w_i[g]
1	−0.04		−0.05	−0.45	0.47		6	−3,051.18	6,114.39	0.00	0.45
2	−0.03					−0.04	4	−3,053.90	6,115.81	1.42	0.22
3	−0.07		−0.03		0.43		5	−3,053.54	6,117.10	1.29	0.12
4	−0.04	0.03	−0.05	−0.45	0.48		7	−3,051.74	6,117.51	0.41	0.09
5	−0.06		−0.03				4	−3,055.09	6,118.19	0.68	0.07

[a] Proximity of bait.
[b] Spatial location of the bait.
[c] Proportion of cultivation.
[d] Proportion of mixed wood forest.
[e] Proportion of deciduous forest.
[f] −2 log likelihood.
[g] AIC weight.

and habitat features for 3 Australian small-mammal species, and this interaction varied with season. For larger mammals, Cusack et al. (2015) investigated this issue by comparing mammal diversity at strictly game trail-based, and strictly randomly deployed cameras in Tanzania's Ruaha National Park; they reported that spatial and seasonal variations affected inferences on mammal community greater than camera placement. In a similar study, Kolowski and Forrester (2017) reported that camera traps at trail or log features had significantly higher mammal capture rates than did randomly placed camera traps. These studies highlight the vast and varied use of attractants in wildlife research to date, and that spatial, temporal, and methodological variations have a great effect on detection probability of multiple species.

Camera traps represent one mode of investigation wherein bait is an integral part of observational experiments, but they also answer parallel questions investigated by other methods. For example, camera traps provide promise for the exploration of behavioral patterns (Stewart et al. 2016, Caravaggi et al. 2017) and activity patterns in relation to species co-occurrence and anthropogenic activities (Ridout and Linkie 2009, Frey et al. 2017). As such, the findings presented here extend well beyond the focus of this method and are important to test in other systems with different methods and species. We demonstrate that the effect of bait can be easily quantified by wildlife practitioners with the appropriate data.

There is always potential for reported relationships to change between species, scales, and habitats of investigation. Although the study system used here has many generalities, our attraction distraction issue could be the result of a number of specificities that would benefit from future testing. If an effect of bait is observed within a study system, it could be partly explained by a mismatch between the scale of selection and the grain of sampling; the larger the ratio between the scale at which the attractant has some effect, and the scale at which sampling occurs, the bigger the potential problem. The scale of a bait response may be dependent upon the spatial and temporal extent at which an organism perceives the bait, the value of the bait, and how free (Fretwell and Lucas 1969) an organism is to access the bait. It is plausible that the effect of bait may influence animal movement more than presented here if landscape heterogeneity is reduced, the amount of bait reaches a certain mass, or individual organisms do not partition either space or time in the same structured manner as fishers. Varying the density of attractants, incorporating temporal relationships through investigation of species activity pattern overlap (Frey et al. 2017), and investigating these relationships in other systems will help to provide context for generalizable predictions of these caveats (Smith 2001, Kirby et al. 2017).

MANAGEMENT IMPLICATIONS

Given the increased data density provided by using attractants, we recommend that wildlife researchers consider the pros and cons of using bait in their studies relative to the potential effects of landscape heterogeneity, and do not *de facto* assume that bait alters natural ecological processes. Maximizing detection probability helps ensure confidence in statistical results, inferred ecological processes, and hence the efficacy of science-based decision-making resulting from wildlife research.

ACKNOWLEDGMENTS

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Associate Editor: Jason Marshal.