Sampling scales define occupancy and underlying occupancy–abundance relationships in animals

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Abstract. Occupancy–abundance (OA) relationships are a foundational ecological phenomenon and field of study, and occupancy models are increasingly used to track population trends and understand ecological interactions. However, these two fields of ecological inquiry remain largely isolated, despite growing appreciation of the importance of integration. For example, using occupancy models to infer trends in abundance is predicated on positive OA relationships. Many occupancy studies collect data that violate geographical closure assumptions due to the choice of sampling scales and application to mobile organisms, which may change how occupancy and abundance are related. Little research, however, has explored how different occupancy sampling designs affect OA relationships. We develop a conceptual framework for understanding how sampling scales affect the definition of occupancy for mobile organisms, which drives OA relationships. We explore how spatial and temporal sampling scales, and the choice of sampling unit (areal vs. point sampling), affect OA relationships. We develop predictions using simulations, and test them using empirical occupancy data from remote cameras on 11 medium-large mammals. Surprisingly, our simulations demonstrate that when using point sampling, OA relationships are unaffected by spatial sampling grain (i.e., cell size). In contrast, when using areal sampling (e.g., species atlas data), OA relationships are affected by spatial grain. Furthermore, OA relationships are also affected by temporal sampling scales, where the curvature of the OA relationship increases with temporal sampling duration. Our empirical results support these predictions, showing that at any given abundance, the spatial grain of point sampling does not affect occupancy estimates, but longer surveys do increase occupancy estimates. For rare species (low occupancy), estimates of occupancy will quickly increase with longer surveys, even while abundance remains constant. Our results also clearly demonstrate that occupancy for mobile species without geographical closure is not true occupancy. The independence of occupancy estimates from spatial sampling grain depends on the sampling unit. Point-sampling surveys can, however, provide unbiased estimates of occupancy for multiple species simultaneously, irrespective of home-range size. The use of occupancy for trend monitoring needs to explicitly articulate how the chosen sampling scales define occupancy and affect the occupancy–abundance relationship.

Key words: abundance–occupancy; distribution–abundance; large mammals; mobile organisms; occupancy models; sampling; scale.

Introduction

The ubiquity of positive occupancy–abundance (OA) relationships is a foundational pattern in ecology (Passy 2012). It has long been observed that locally abundant species are regionally widespread (Andrewartha and Birch 1964) and that this pattern is generally consistent within species over time, and among species over space (Gaston et al. 2000). OA relationships have key implications for both the theoretical understanding of ecology and for guiding applied conservation. For example, these

macroecological patterns can help understand how local and regional ecological processes interact (Gaston and Blackburn 2000) and can illuminate how biological and ecological traits can affect large-scale patterns (Webb et al. 2009). In conservation, positive OA relationships point to a "double jeopardy" where rare species are at risk of extirpation both because small populations increase the risk of stochastic catastrophic loss, and because restricted distributions increase the risk that all populations experience unfavorable conditions simultaneously (Lawton 1995, Gaston et al. 2000).

Changes in occupancy are most likely driven by changes in abundance and not the other way around (Gaston and Blackburn 2003). Understanding the mechanisms underlying the shape of positive OA patterns, however, remains incomplete, but includes at least four factors. First, the positive relationship can be understood

with the most basic mathematical relationship between occupancy (a binomial process) and abundance (governed by a Poisson process). Any increase in abundance mathematically causes any spatial function of abundance to also increase (Royle et al. 2015). The result is a positive relationship between occupancy and abundance. Second, ecological drivers, such as different life-histories among species such as dispersal, can change OA relationships because occupancy responds quicker at high dispersal rates (e.g., in oceans) to changes in abundance (Blackburn et al. 2006). Thirdly, discrepancies in terminology account for some differences in the shape of OA relationships, for example, some studies calculate abundance of only occupied cells, while others consider all cells surveyed (Borregaard and Rahbek 2010). Finally, the issue of scale is paramount in ecology, both because species interact differently with the environment at different scales, and because our scale of observation affects our interpretation of ecological patterns (Wiens 1989, Levin 1992). Wilson (2008) showed that sampling artifacts can affect the shape of OA relationships, for example, when the extents of abundance and occupancy surveys do not match. More importantly, estimates of occupancy have been shown to depend on the size of grid cells (Gaston and Fuller 2009) and this can affect the OA relationship (He and Gaston 2000, Kunin et al. 2000).

Beyond positive vs. negative, the curvature of the OA relationship also has important applied implications when relying upon occupancy as a surrogate for abundance (MacKenzie and Nichols 2004). For example, when using occupancy for monitoring population trend of sensitive species, it is important to understand how an observed change in occupancy corresponds to a change in abundance. Estimated occupancy of Spotted Owls (*Strix occidentalis*), for example, was linearly related to abundance, and thus when used for trend monitoring, changes in occupancy correspond linearly to changes in abundance (Tempel and Gutiérrez 2013). When governed by a curvilinear OA relationship, however, a change in abundance may remain undetected when only monitoring occupancy. For example, the relationship between wolf (*Canis lupus*) occupancy and density is curved and, furthermore, the curvature depends on sampling grid size (Latham et al. 2014).

Occupancy models that correct for imperfect detection have revolutionized how we estimate and think about occupancy (MacKenzie et al. 2002, Bailey et al. 2013). Occupancy models are inherently hierarchical and rely on repeated sampling to estimate detection probability, providing estimates of site occupancy that are unbiased by observer error (MacKenzie et al. 2002). Early occupancy models were developed in discrete habitat patches, i.e., amphibians in ponds (MacKenzie et al. 2002). Sampling can be repeated across space (e.g., transects; Ellis et al. 2014), across time (e.g., repeated call surveys; MacKenzie et al. 2002), or by using multiple observers (Nichols et al. 2000). Point-location detection/non-detection data are often inexpensive and are ever-increasing with new

emerging technologies such as eDNA (Schmidt et al. 2013) and camera trapping (Burton et al. 2015). As a result, occupancy monitoring is rapidly being adopted as a surrogate for abundance monitoring, but without fully understanding the relationship between the two. Understanding changes in population occupancy over time is often predicated on positive and linear OA relationships (MacKenzie and Royle 2005). Despite the key connections between occupancy and abundance, little work (see Royle et al. 2013, Kéry and Royle 2016) has explicitly linked these two foundational concepts in ecology: occupancy models and OA relationships.

Criticisms of estimating population trend with occupancy models have recently emerged when occupancy is estimated in continuous habitat (Efford and Dawson 2012) and when organisms are mobile (Hayes and Monfils 2015), often violating the assumption of geographical closure. Moving beyond sampling discrete habitat patches (e.g., ponds; MacKenzie et al. 2002), ecologists now use a wide array of sampling units to collect occupancy data, commonly across continuous habitat, for example using an imaginary grid to discretize the landscape in discrete patches that are then classified as occupied or not (Noon et al. 2012). This move away from sampling discrete units of habitat contrasts with the original formulation of occupancy models (MacKenzie et al. 2002), but is consistent with data commonly used in the study of OA relationships, for example, sampling birds or plants in quadrats (Gaston et al. 2000). Estimates from occupancy models rely on a closure assumption that prohibits changes in occupancy state (occupied or not occupied) among repeated sampling sessions; i.e., sites must remain occupied or remain unoccupied throughout the entire survey. Dynamic models allow for changes among seasons or years only, and not within sampling occasions (MacKenzie et al. 2003), so dynamic models do not circumvent the closure assumption. The most common form of repeated sampling is over time (Bailey et al. 2013). When time between repeated occasions is long relative to movement speed of mobile organism, closure can be violated if organisms move among sampling cells (Hayes and Monfils 2015). One proposed solution for such violations is to redefine the estimated parameter from "occupancy" to "use" (Latif et al. 2016). Changes in definition that are driven by sampling scale, whether temporal or spatial, however, necessarily result in significant considerations for how occupancy estimates are used in trend monitoring, which we demonstrate in this paper.

Generally, occupancy is defined as the proportion of sites where a species is found (Gaston et al. 2000, MacKenzie et al. 2002), but the definition varies along temporal and spatial sampling scales (Royle and Dorazio 2008, Noon et al. 2012). Using occupancy for trend monitoring requires understanding the shape of species-specific OA relationships, but this understanding may be complicated by the potential interplay among sampling scales and species-specific life history, especially with the increased demand for simultaneous multi-species

monitoring (e.g., Noon et al. 2012) where each species may have a different OA relationships. When using occupancy for monitoring, it has been argued that the most useful spatial scale to sample occupancy is the scale where the relationship between occupancy and abundance remains close to 1:1 (Stanley and Royle 2005, Noon et al. 2012). Linden et al. (2017), for example, empirically showed that occupancy and abundance estimates have the highest correspondence when sampling at close to the home-range scale. This suggested approach to spatial sampling scale could potentially avoid both the grid saturation problem (Kunin et al. 2000) and the dilution effect (Gautestad and Mysterud 1994) when measuring occupancy. Selection of the temporal sampling scale, on the other hand, depends on the objective of the study and desire to minimize violations of closure (Royle and Dorazio 2008). Discrete ponds, for example, may be occupied at different times during a breeding season due to ecological differences among ponds. Surveying ponds throughout the total length of the breeding season will, therefore, violate the assumption of closure, but this choice remains appropriate if the objective is to understand how many ponds are occupied at any point during the breeding season (Royle and Dorazio 2008). However, for wide ranging mobile organism moving through continuous habitat, it will be difficult to address the violation of closure, and thus the interpretation of occupancy becomes unclear.

In this study, we first develop a conceptual framework for interpreting estimated occupancy of mobile animals in continuous space that can be applied across different spatial and temporal scales. Next, using this framework, we investigate the effects of spatial grain and sampling unit on the shape of the OA relationship. Because of the ubiquity of repeated sampling designs, we also consider the effect of temporal sampling extent (i.e., duration of the survey). Previous studies have shown that OA relationships become more curved with increasing spatial grain (He and Gaston 2000, Hui and McGeoch 2007). Following this work, we predict that similarly, the curvature of the OA relationship will increase with grain size. Thus, we expect that occupancy estimates will be higher with larger grain size, even when abundance remains constant. Similarly, we hypothesize that longer temporal durations will also increase occupancy estimates because of the increase in probability of closure violation (Rota et al. 2009). Many different sample units are used in occupancy and occupancy-abundance investigations (see *Conceptual framework for interpreting occupancy across scales*), but to our knowledge, there has been little or no research on the effects of sampling unit on occupancy–abundance relationships. Given occupancy is a spatial process, we also expect the choice of sampling unit to affect the OA relationship. We test these predictions using a simulation study. Simulations help control for confounding variables while forcing an explicit expression of underlying model assumptions. We further test our predictions with an empirical data set of 11 medium-large mammals collected from remote cameras in and around two national parks in the Canadian Rockies.

A note on terminology

The word "scale" can mean many things; for example, spatial scale can mean spatial grain, spatial extent, spatial lag, etc. Here we specify that we investigate spatial grain as the size of the grid cells that are used to discretize continuous space. For areal sampling, the grid-cell size determines the size of the sampling unit; for point sampling, the grid-cell size determines the distance between sampling locations (see *Methods* for more details on the differences between these two general forms of sampling). Similarly, temporal scale has equally as many definitions; here we investigate only temporal duration of sampling, i.e., total length of the survey. In the discussion, however, we explain how other spatial and temporal scales were either explored elsewhere in the literature, were tested in the appendix, or were controlled for. Finally, because occupancy can be interpreted in many different ways, we clarify here that, when referring to "occupancy," we mean the parameter being estimated during any occupancy sampling exercise. As we show in this manuscript, the meaning of this parameter is fluid and depends on sampling scales.

Conceptual framework for interpreting occupancy across scales

As explained above, occupancy-estimation designs often stray far from the original formulation by MacKenzie et al. (2002), with varying temporal and spatial sampling scales that necessarily affect the definition of occupancy. Here, we explain our conceptual framework that shows explicitly how these deviations from MacKenzie et al. (2002) affects the definition of occupancy being estimated. Occupancy surveys can vary in temporal scale from instantaneous direct observations of animals to cumulative sign of animals (e.g., scat, tracks, pictures, vocalizations) over a longer period of time. This accumulation of use is also referred to as occupancy integrated over time, or as asymptotic occupancy (Efford and Dawson 2012). Occupancy of individuals will be necessarily more closely related to abundance than occupancy of sign because sign from individuals can accumulate over an area as animals move during longer temporal windows. The definition of occupancy from sign, thus, depends on the movement rate of individuals throughout their annual home range, the temporal sampling window, and the spatial distribution of surveys relative to the size of the species home range (see large circles in Fig. 1). Considering occupancy relative to home-range sizes illustrates the effects of both spatial and temporal sampling scales. When occupancy surveys have a short temporal window relative to movement rates and home-range size, animal sign accumulates in a small area (Fig. 1A, C, E). Temporal sampling duration, therefore, changes the definition of occupancy because it affects the
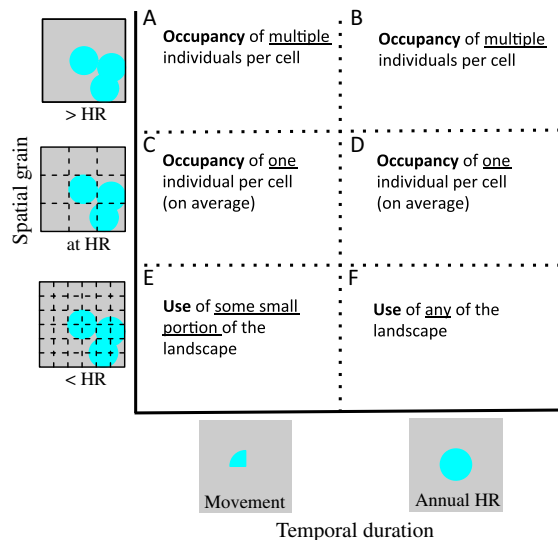
Fig. 1. Conceptual framework for how the definition of occupancy changes along spatiotemporal sampling scales. Spatial sampling grain (i.e., cell size) is described at three scales relative to annual home ranges (HR; large circles). Temporal sampling duration (i.e., survey length) is described relative to movement rate of the animal and total annual home range.

ranges, occupancy refers to the proportion of cells occupied (used) by each individual (Fig. 1E, F). Occupancy surveys are most directly related to abundance when cells size matches home-range size, allowing one individual to occupy each cell (Fig. 1C, D). Spotted owls provide an ideal example because they are highly territorial and each occupied territory has only one pair (Tempel and Gutiérrez 2013). Consequently, when grid cells and home ranges align, each occupied cell represents one pair of owls (Fig. 1C, D, but with non-overlapping home ranges). Due to their territoriality, owl pair occupancy at the spatial scale of the home range has a linear OA relationship (Tempel and Gutiérrez 2013). Thus, to ensure a closer link between occupancy and abundance, it has been recommended that occupancy studies sample at the home-range scale whenever possible (MacKenzie and Nichols 2004, Noon et al. 2012). Unfortunately, this can be difficult to achieve for many species because individuals often have overlapping home ranges and there is substantial variation in home-range size within species (e.g., between sexes). Moreover, it is impossible to standardize in multi-species surveys when home-range size varies among species.

Not only do spatiotemporal sampling scales affect the definition of occupancy, the sampling unit can as well (Fig. 2). When dealing with discrete habitat, occupancy can be interpreted as the proportion of discontinuous habitat patches (e.g., ponds) that are occupied (Fig. 2D; MacKenzie et al. 2002). When discretizing continuous habitat, however, the sampling unit is considered the cell, rather than the patch, and the occupancy parameter changes from patch occupancy to cell occupancy (Fig. 2A, B). For example, atlas data commonly gathers information about the presence of bird or plant species

proportion of the landscape occupied by each individual during the sampling period. Spatial grain (i.e., cell size), on the other hand, affects the number of individuals that occupy each cell. When cells are larger than average home ranges, occupancy refers to the occupancy of at least one individual (Fig. 1A, B). When cells are smaller than home

Fig. 2. Conceptual differences among three commonly used sampling methods to collect occupancy data and the resulting sampling units. Three common methods (areal sampling of individuals, areal sampling of use, and point sampling of use; rows A–C, respectively) are compared to (D) how occupancy models were originally characterized by MacKenzie et al. (2002).

within grids. Similarly, open-water fish hauls also sample individuals and cover an area. Sampling use rather than individuals provides some monitoring opportunities but further complicates the definition of occupancy. For mobile species, it is possible to move from areal-based sampling of use (e.g., track counts) to point-based sampling of use (Fig. 2C; e.g., camera traps, acoustic surveys), although this distinction is seldom explicit in the literature. A shift in sampling unit causes a corresponding shift in the definition of occupancy: either cell occupancy, patch occupancy, or site occupancy. How this change in sampling unit affects OA relationships is unknown, which is addressed in our simulations.

Methods

Simulating occupancy–abundance relationships

We examined the effects of temporal scale, spatial scale, and sampling unit on OA relationships using a simplified spatial capture–recapture (SCR) sampling framework used for abundance estimation (Efford et al. 2009, Royle et al. 2013). We first simulate point-location data to mimic our empirical remote camera data (see below where we vary sampling unit). This simulation framework would be similar for any point data such as acoustic surveys, eDNA samples, etc. We use a SCR framework to simulate animal locations with a homogenous Poisson point process (uniform movement density), and distributes home range centers within a sampling area. We focused on assuming perfect detection because imperfect detection should only affect precision of occupancy estimates and not the occupancy abundance relationship (see Appendix S1 where we verify this expectation). In the SCR sampling framework, individual detection at any point depends on: the baseline detection probability at the home range center, g_0; the home range scale parameter, σ; and the distance between the home range center and the point location, d, such that detection rates decrease with d, often through a bivariate normal decay function. However, to model our assumed perfect detection, we set $g_0 = 1$ and $\sigma = 0$, so that detection was perfect and did not vary with d (again, see Appendix S1 where we modified these parameters and tested the effects of relaxing our perfect detection assumption). We then truncated the area where individuals could be detected to $\sigma(5.99)^{0.5}$, the 95% center area of a bivariate normal decay (Royle et al. 2013). To evaluate estimation bias, we calculated the total area of occupancy as the overlapping total distribution of all annual home ranges in a population, where each home range is conceptualized as a circular area occupied by an individual through a year (Fig. 1B, D, F). Note that home range centers were Poisson distributed in space, meaning we did not restrict animal distribution by conspecifics (neither aggregation nor repulsion), and home ranges were permitted to overlap. Holt et al. (2002) investigated how different spatial distribution models

performed to describe OA relationships and found that, although the Poisson distribution did poorer than others when tested with empirical data, all models performed reasonably similarly. The Poisson model saturates quicker than other proposed models (e.g., negative binomial, which allows for spatial aggregation), but we used the Poisson model to develop our OA relationships because of its simplicity in describing OA patterns (Freckleton et al. 2005) and its correspondence with density estimation simulations (Efford et al. 2009, Royle et al. 2013).

We used a simulated landscape of 80×80 sampling units in continuous habitat. When considering each unit in simulated space as 1 km in real space, the total simulated area (6,400 km^2) was close to the size of our main study area, Banff National Park (6,641 km^2). We simulated between 1 and 150 animals reaching a maximum density of 23.4 animals/1,000 km^2 (a high, but comparable maximum density for a rare carnivore such as Grizzly bears, *Ursus arctos*). Each circular home range (large circles in Figs. 1 and 2) occupied an area of 100 km^2 (radius = 5.6 km). To simulate changes to spatial sampling scale (i.e., grain), we changed the spacing between sampling locations using three different sized lattices. Sampling lattices with 16, 64, and 256 point-sampling locations, resulted a spacing of 20, 10, and 5 km apart, respectively (i.e., 1 point sample per 400, 100, and 25 km^2, respectively). To simulate changes to temporal sampling scale (i.e., total survey duration), we changed the fraction of each 100-km^2 home range that animals were able to use. For example, to simulate a short, seasonal sampling window, we allowed animals to use only 0.25 of their home range, resulting in an area used that was 25 km^2 rather than 100 km^2. This assumption is true under diffusive movement of individuals such as a correlated random walk (Turchin 1998). All scenarios were simulated 1,000 times.

To simulate different sampling units, we simulated three data-collection methods commonly used for occupancy estimation (see Fig. 2). First, we laid a lattice of grid cells on the landscape within which the presence of individuals is recorded. This method produces data common to species atlas data (e.g., bird or plant counts) collected in many OA studies (Fig. 2A). Removal sampling of individuals, e.g., haul sampling of fish, would also produce data with this nature. Observed occupancy was calculated as the proportion of cells with at least one individual. Second, we systematically distributed point samples across the landscape as in the above simulations to record use, rather than recording individuals. This method produces data similar to acoustic and camera surveys by collecting point-samples of animal sign (Fig. 2C). Estimation in this sampling scenario essentially ignores any grid cells used to spread out sampling; we calculated observed occupancy as the proportion of point-sampling locations that landed on occupied areas. When a camera fell on any home range, it perfectly detected the presence of the individual(s) that use the area and was considered occupied. Third, we simulated an intermediate scenario between the two previous

methods where we used the same lattice of grid cells for areal sampling as in scenario A, but rather than tracking the presence of individuals, we tracked their use (see Fig. 2B). This method produces data similar to track counts and other transect data (e.g., Ellis et al. 2014), or similar to the data resulting from aggregating multiple point locations in a cell to produce a single estimate of occupancy per cell. For this third method, we calculated observed occupancy as the proportion of cells containing any portion of a home range. For all three sampling scenarios, we assumed perfect detection (but see Appendix S1 where simulated imperfect detection and showed there is little affect of detection probability on how sampling scales affect occupancy–abundance relationships).

Empirical test of the effects of samples scales on underlying occupancy abundance relationships

To test the patterns predicted by our simulations, we collected empirical data using 148 remote cameras for 11 medium-large mammal species. Cameras were deployed across three study areas in and around Banff and Waterton Lakes National Parks, Alberta, Canada (total area sampled: 3,700 km^2; Appendix S2: Fig. S1). In 2012, 72 cameras were deployed in a portion of Banff National Park and adjacent Kananaskis Country; in 2013, 48 cameras were deployed in Banff and the Ya Ha Tinda study area; and in 2014, 26 cameras were deployed in Waterton Lakes National Park study area. Camera locations were systematically distributed with one camera per 5 × 5 km cell to allow analysis at three hierarchical scales: 25, 100, and 400 km^2. These cell sizes correspond to the approximate home-range sizes of red fox (*Vulpes vulpes*; ~25 km^2), cougars (*Puma concolor*; 87–97 km^2 and 140–334 km^2 for females and males, respectively; Ross and Jalkotzy 1992), and grizzly bears (~520 km^2; Stevens and Gibeau 2005). Of the 148 cameras deployed 2012–2014, 146 collected data from 15 June to 15 October. Images were classified to species level in all study areas. We estimated occupancy for 11 medium-large mammal species: black bear (*Ursus americanus*), cougar, coyote (*Canis latrans*), elk (*Cervus canadensis*), grizzly bear, lynx (*Lynx canadensis*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*), red fox, white-tailed deer (*Odocoileus virginianus*), and wolf; refer to Steenweg et al. (2016) for more study area details.

To estimate occupancy for each species, we discretized camera data into two-week intervals, which was the shortest temporal grain that avoided numerical estimation errors for our data set (Steenweg et al. 2016). We estimated occupancy using a maximum likelihood approach in the statistical software, R (R Development Core Team 2015), using the package unmarked (Version 0.10-6; Fiske and Chandler 2015). To mimic sampling at larger spatial scales (i.e., grains of 100 and 400 km^2), we rarefied the 25-km^2 data by subsampling the sampling locations for each analysis within a larger grid cell. At the scale of a cougar home range, for example, we used

0.25 of the locations, using only one camera per group of four cameras within each 100-km^2 cell. At each scale, we randomly subsampled the data 200 times and tracked mean occupancy and standard error. To mimic sampling at smaller temporal scales (i.e., survey durations of 1, 2, and 3 months) we similarly subsampled the data, using random windows of 1, 2, or 3 months of data rather than the full 4 months of data. Using a random window (rather than random weeks) preserved any potential seasonal signal in the data had we only sampled for a particular month. We tested for the effects of survey duration and spatial sampling scale on occupancy estimates using mixed-effects generalized linear models in the metafor package in R (Viechtbauer 2010). We specified species as a random effect and incorporated variances of occupancy estimates. We then compared models with and without the fixed effects of either survey duration or spatial sampling scale using the Akaike information criterion corrected for sample size (AIC$_c$).

Results

Simulating occupancy–abundance relationships

Spatial and temporal sampling scales affected the OA relationship differently. When surveys were temporally short enough to allow only short-distance movements, OA relationships were shallower, appearing near linear (Fig. 3A, D, G). Increasing the temporal sampling extent, moving right along rows in Fig. 3, increased the curvature of the relationship. Thus for a fixed abundance, estimates of occupancy increased with increased temporal sampling extent. In contrast, increasing the spatial sample grain, moving up along columns in Fig. 3, did not affect the shape of OA relationship, but did decrease the precision of the occupancy estimate. Lower precision was due to a decline in sample size (see Appendix S3: Fig. S1).

The choice of sampling unit had a strong effect on the shape of the simulated OA relationship (Fig. 4). Regardless of the sampling unit, OA relationships were nonlinear, but the non-linearity depended on the type of sampling unit. Simulating areal sampling of individuals represents data commonly analyzed during investigations of the OA relationship. Point sampling of animal sign (Fig. 4C) reached an asymptote much slower than areal sampling of sign (Fig. 4B).

Empirical test of occupancy-abundance predictions

Concurring with our theoretical simulations in Fig. 3, increasing the spatial grain of real data from camera traps (point sampling) did not affect occupancy estimates. The model with the effect of spatial grain performed worse than the model without (ΔAIC$_c$ = 2.17), with a non-significant effect of spatial grain ($P = 0.25$; Appendix S4). Mean occupancy estimates remained relatively constant across spatial grain for data collected from remote cameras
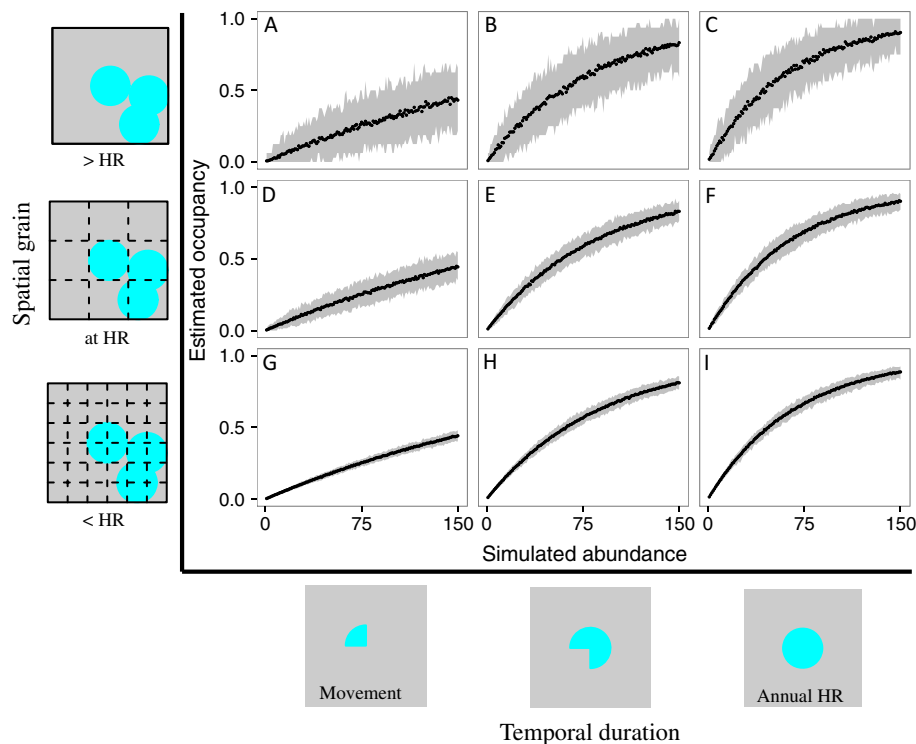
FIG. 3.   Combined effects of spatial and temporal sampling scales on occupancy–abundance relationships from point-sampled data on simulations of 1–150 individual home ranges (HR; teal circles). Mean and 95% confidence intervals of occupancy estimates presented from 1,000 simulations for each abundance level. Temporal sampling durations ranges from a survey length that only permits short animal movements (0.25 of HR), to long enough to allow animals to move throughout their entire home range. Spatial point-sampling grain ranges from grid-cell sizes that are small enough to capture only the movements of a short survey (0.25 HR), through grids that match the size of annual home ranges, to grids that are much larger than home ranges (4 × HR).

(Fig. 5B). This trend was consistent for all 11 species when sample size remained sufficiently high: grains of 25 and 100 km^2, but not 400 km^2. When sample size decreased to only 10 cameras (at spatial grain of 400 km^2), there was great uncertainty in occupancy estimates. The apparent increase in some occupancy estimates at such grain size (Fig. 5B) was due to small sample size, and paralleled similar declines in precision due to small sample size from our simulations (Fig. 3A–C; Appendix S3). In contrast, increasing the temporal sampling duration (survey length) of real data from camera traps significantly increased occupancy estimates (ΔAIC_c = 36.01) with a significant effect of survey length, (P < 0.0001; Appendix S4). Moreover, an estimate of 0.112 ±0.012 (mean ± SE) resulting in real estimate of 0.022, means that with every additional month surveyed, occupancy increases on average 2.2%, and this trend was consistent across 10 of 11 species (Fig. 5A). Thus, despite animal density remaining constant, occupancy estimates increased with longer surveys, matching expectations from our simulation results (Fig. 3).

DISCUSSION

Sampling scales affect the definition of occupancy for mobile species and, in turn, these fluid definitions affect the nature of OA relationships. The relationship between temporal sampling scale and the time it takes an animal to move throughout its home range affects occupancy estimates. Our simulations demonstrate that, for a given abundance, longer survey lengths result in higher occupancy (Fig. 3). Our camera data on 11 medium-large mammal species corroborate this conclusion for a wide range of occupancy estimates (0.2–0.8; Fig. 5A). This result is especially pertinent for rare species whose occupancy estimates could increase by an absolute occupancy of ~0.1 within four additional months of sampling. When relating spatial sampling scales to home range size, it may be prudent to sample for long enough to allow animals to move throughout their entire home range. Interestingly, changes to our temporal sampling window could also be interpreted as changes in home range size. Given equal densities, therefore, occupancy estimates will be higher for animals with larger home ranges because each individual covers a greater area. Sampling at a point over longer time periods is, in essence, a surrogate for sampling a spatial area, by integrating the space used by animals over time. The longer the sampling window, the more time animals have to move in front of the camera from elsewhere in their range. The area used, therefore, increases over time and is species specific (Fig. 5A).
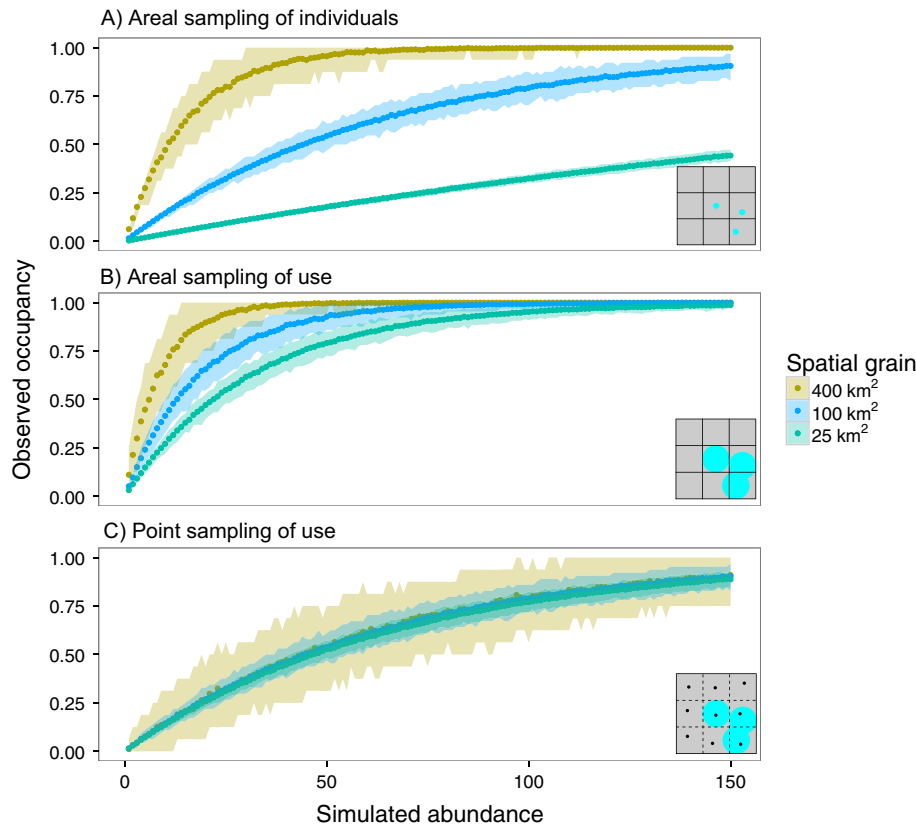
Fig. 4. Effect of sampling unit on occupancy–abundance relationships. Three sampling units include (A) areal sampling of individuals, (B) areal sampling of use, and (C) point sampling of use. Mean and 95% confidence interval of occupancy are from 1,000 simulations for each abundance level (1–150 individuals). Panel C is equivalent to combined data from Fig. 3C, F, and I. Small conceptual figures depict areal-sampling cells, home range centers (teal dots), distribution of sign around home range center (teal circles), and point-sampling locations (black dots).

Different from the effects of temporal scales, the shape of OA relationships surprisingly remained constant across spatial grain in our simulations of point sampling (Fig. 3), but precision changed due to concurrent changes in sample size (Appendix S3: Fig. S1). Our camera data also demonstrated this result when sample size was sufficient, i.e., when $n = 146$, or $n = 31$, but not $n = 10$ (Fig. 5B). The species included in our analysis spanned a wide range of life histories including carnivores, omnivores, and herbivores; group-living (e.g., wolves and elk) and solitary species (e.g., lynx, cougar); and territorial (e.g., grizzly bears) and non-territorial species (e.g., moose). The scale-invariance of the OA relationship under point sampling, therefore, appears robust to these large ecological differences among species.

Our results showing that OA relationships are unaffected by spatial sampling scale, contrasted with our predictions based on previous work that implicitly considered only areal sampling (He and Gaston 2000, Hui and McGeoch 2007, Wilson and Schmidt 2015). We reconcile this disagreement by considering the sampling unit. Many previous OA studies assumed complete or representative areal sampling of grid cells, and in this case, OA relationships are indeed dependent on spatial grain size (see Fig. 4A, which closely mimics the change in relationship due to spatial sampling scale demonstrated by He and Gaston [2000], compare Fig. 4A to their Figs. 1 and 2). In contrast, many recent occupancy studies use point sampling (e.g., remote cameras, acoustic surveys) where occupancy is defined as the presence of sign from one or more individuals at a point. In this case, the density of sampling points does not affect OA relationships (Fig. 4C). This change in sampling unit is only possible with a concurrent change in the definition of occupancy from presence of individuals, to presence of sign (Fig. 2). Efford and Dawson (2012) similarly emphasize that in most occupancy studies where individual identification or other means to assure geographical closure are lacking, it is difficult to guarantee independence among any indirect signs of animals (e.g., scat, tracks, pictures, vocalizations). When sampling use instead of individuals, the underlying pattern-generating process that describes occurrence also changes from a point-pattern process that describes individuals, to a surface-pattern process, for which theory is
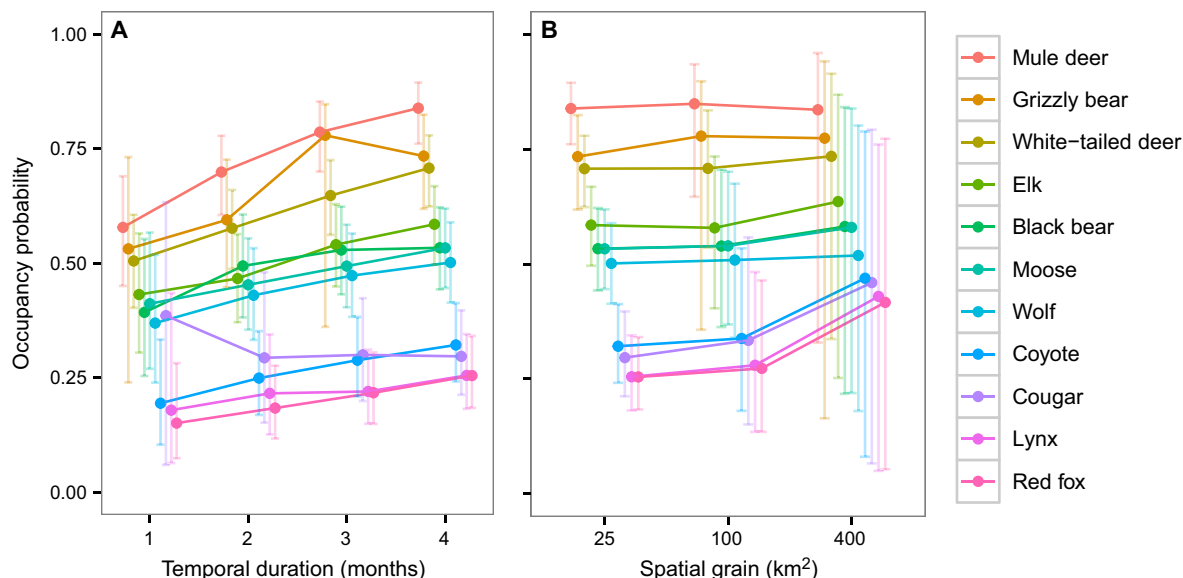
FIG. 5.   Effects of (A) temporal and (B) spatial sampling scales on occupancy estimates (mean and 95% confidence intervals) of 11 medium-large mammal species captured on remote cameras in the Canadian Rockies. (A) Temporal duration (survey length) varies while spatial grain (i.e., grid-cell size, and therefore spacing between point samples) remains at 25-km^2 cells. (B) The opposite: spatial grain varies, while temporal duration remains constant at 4 months of data. Cameras (n = 146) were deployed 15 June–15 October.

not well developed in spatial statistics (Gelfand et al. 2010). In our simulations, we conceptualize the presence of sign as a uniform home range area for each mobile individual. Substantial statistical theory is based on instantaneous sampling, both in space and time (Buckland et al. 2005). Moving from areal to point sampling, we move to a more instantaneous sampling of space, which prevents the breakdown of the OA relationship across spatial scales. In contrast, longer survey lengths are further from instantaneous, resulting in an OA relationship that is more curved because the occupancy parameter represents an integration of use over time (Efford and Dawson 2012). Therefore, point sampling of overall use for occupancy estimation, rather than of individuals, comes with the benefit of approximately instantaneous spatial sampling, but with the drawback of longer temporal samples (i.e., changing estimates; Fig. 5A). More research is needed to understand this trade-off in light of spatial statistical theory on surface patterns (Gelfand et al. 2010) as it emerges, but other aspects of sampling design effects on OA relationships are well known.

Fortin and Dale (2005) describe five aspects of sampling design that affect spatial patterns: grain, strategy, sample size, extent, and spatial lag. Here we investigated spatial grain, temporal extent, and one aspect of strategy (point vs. areal sampling). Furthermore, other sampling considerations, aspects of species life history (territoriality), or density dependence can also affect OA relationships (Efford and Dawson 2012). Our systematic sampling caused both spatial lag and sample size to remain fixed to grain (but see Appendix S3 where we allowed sample size to deviate and show that it only

affected the precision of estimates, not the shape of the curve). Spatial extent in our simulations and empirical investigations remained relatively constant although home ranges were able to extend beyond the sampling grid. Because cameras collect continuous data, temporal grain is equal to the length of each sample session (here, 2 weeks), but this choice only affects precision of occupancy estimates, not the mean estimates themselves (Steenweg et al. 2016). To more closely mimic closure, point samples could be spaced beyond what individual animals can move within the survey period (e.g., Fig. 1A, B). This spacing increases the independence among sampling locations, individuals will not be likely to be sampled at multiple locations, like most acoustic bird sampling protocols, but spreading out sampling cannot avoid multiple individuals being present at single locations. We simulated randomly distributed animals, which allowed for overlap among individuals. Aggregation of social animals, for example, will also increase the curvature of the OA relationship (Efford and Dawson 2012), but this increase should not interact with the general effects of spatial and temporal sampling scales on OA developed here. Although we simulated changes in abundance, we could not investigate how changes in abundance affected occupancy with our empirical data. This is typical of occupancy estimation data collected within one season, for example, and our purpose was to demonstrate that OA relationship can change only due to sampling scales or sampling units. Furthermore, we did not simulate density dependence between occupancy and abundance, but little is known about how individual species' distributions change with abundance. Home

range sizes of tigers (*Panthera tigris*) and oven birds (*Seiurus aurocapilla*), for example, decrease with density (Efford et al. 2016). This effect could materialize as changes in degree of overlap among individuals' home ranges (Ellis et al. 2014), which is complex, even for a territorial species with little range overlap (e.g., wolves [Webb and Merrill 2012]).

In our simulations, we only considered occupancy as a two-dimensional phenomenon, a measure of the distribution of these individuals across a given area. However, occupancy can be 0 dimensional (e.g., a point), one dimensional (a fish in a river), or three dimensional, depending on the ecology of the species of interest and the objective of the study. Arboreal and many oceanic organisms inhabit three-dimensional space, leading to the possibility of three-dimensional occupancy (e.g., Davies and Asner 2014). Fish occupancy in streams can be depicted as one dimensional if stream depth and width are ignored or not of interest (Falke et al. 2012). This one-dimensional occupancy could be similarly estimated for shoreline or intertidal occupancy. Perhaps non-intuitively, the original formulation of occupancy (MacKenzie et al. 2002) is essentially 0 dimensional. Point-sampling often necessarily involves sampling of some small space (e.g., the area in front of the camera). Similarly, ponds are multi-dimensional (at least two dimensional). But when interested in the proportion of ponds or points that are occupied, ponds become analogous to individuals, despite occupancy being a spatial metric. When measuring pond occupancy, the space that an occupancy metric describes becomes dimensionless. With multiple individual amphibians occupying single ponds, however, the OA relationship will also be concave. This non-linearity is true whenever one unit of occupancy (e.g., grid cell, pond, point) can be occupied by multiple individuals.

The linearity of the OA relationship is important to consider when using occupancy as a surrogate for abundance (MacKenzie and Nichols 2004). In our simulations, when survey length was restricted to the scales shorter than animal movements, the OA relationship appeared nearly linear (Fig. 3A, D, G). If these OA relationships were extended to higher abundances, a similar asymptotic shape would present itself due to overlap of the movements of individuals. Similarly, had we extended simulations of point sampling to higher animal densities in Fig. 4C, the shape would begin to have a similar curvilinear shape to other sampling units. Therefore, the linearity of the OA not only depends on temporal sampling scale (Fig. 5A), spatial grain when using areal sampling (Fig. 4A, B), but also the range of densities. Furthermore, there are ecological factors whose affects on OA relationships are species or context specific. For example, home range size (Efford and Dawson 2012), territoriality or aggregation (Efford and Dawson 2012, Noon et al. 2012), and body size (Webb et al. 2009) can all affect the curvature of the underlying OA relationship. Moreover, Webb et al. (2007) showed that increasing species

followed expectations from interspecific OA relationships (i.e., followed the interspecific curvature), but that rare and declining species tend to have OA relationships that departed from these expectations, making the implications of their decline less predictable. When using occupancy as a metric for population trend, therefore, it may be necessary to develop species-specific OA relationships (e.g., for wolves, Webb and Merrill [2012], e.g., for bobcats, Clare et al. [2015]). Furthermore, understanding where a species or population of interest lies on the OA relationship affects the usefulness of using occupancy as a surrogate for abundance. For many non-territorial species, occupancy necessarily saturates to 1 once density is sufficiently high. But regardless of curvature, rare species with low occupancy (e.g., coyote, cougar, red fox, lynx in Fig. 5) correspond to the lower portion of the OA relationship (e.g., only consider occupancy of 0–0.3), which can appear near linear regardless of scale (Fig. 3).

Conclusions

Our investigation into the linkage between these two foundational frameworks in ecology, AO relationships and occupancy modeling, provides three major insights. First, using the most common detection-corrected occupancy data (temporally repeated surveys), we showed how different scales of sampling necessarily change the underlying definition of occupancy. Second, estimates of detection-corrected occupancy that are used for trend monitoring would benefit from explicitly articulating how the chosen sampling scales affect the definition of occupancy, and how this choice affects the underlying relationship with abundance. Finally, occupancy without meeting the assumption of geographical closure is not occupancy. Discretizing space with grids for occupancy estimation works best for static organisms. We demonstrated, however, that a benefit of point-based sampling of mobile organisms is that their occupancy estimates are robust to changes in sampling grain regardless of species ecology. This result implies that point-sampling studies with non-identifiable individuals (e.g., using remote cameras, acoustic surveys, species-level eDNA) can estimate occupancy for multiple species using a fixed density of point-sampling locations, regardless of home ranges size of the animals, but we stress that the definition of occupancy may be species-specific, ranging from use by one individual to occupancy of multiple individuals. We hope this work will stimulate more acknowledgement and discussion of the implications of the fluid definition of occupancy.

We conclude with a call for more research linking the theory and practice of investigating OA relationships with occupancy estimation. Our novel results on how the choice of sampling unit can affect the relationship between sampling grain and the shape of OA relationships demonstrates the need to reconcile these two distinct bodies of literature further. Both areas of research would benefit from better integration. For example, OA theoreticians long identified that occupancy of rare

species can be underestimated due to imperfect detection (Gaston et al. 1998), yet many OA investigations to date continue to rely on species distributions that assume that non-detections are true absences (Kéry 2011, Yin and He 2014). Investigations into OA relationships would benefit from correcting occupancy for imperfect detection to avoid this negative bias, if following sampling-design considerations when collecting occupancy-estimation data (MacKenzie and Royle 2005, Bailey et al. 2007, Guillera-Arroita and Lahoz-Monfort 2012). In turn, we demonstrate in this paper that a greater understanding of the underlying intraspecific relationship between occupancy and abundance would improve the tracking of species of concern with occupancy estimation. Both groups of researchers should be aware of the effects of sampling scales and sampling unit on both the definition of occupancy and the underlying occupancy–abundance relationship.

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