

Scale dependence in occupancy models: implications for estimating bear den distribution and abundance

TAMMY L. WILSON^{1,†} AND JOSHUA H. SCHMIDT²

¹Southwest Alaska Network, U.S. National Park Service, 240 W. 5th Avenue, Anchorage, Alaska 99501 USA

²Central Alaska Network, U.S. National Park Service, 4175 Geist Road, Fairbanks, Alaska 99709 USA

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Abstract. Monitoring programs are typically designed to identify long-term trends in animal abundance, however estimating abundance at a relevant scale can be logistically prohibitive. This is particularly true for species that occur at low densities or those with large home ranges. In such cases, occupancy surveys are often employed in place of more expensive abundance estimation techniques such as mark-recapture because precise estimation of occupancy probability generally requires fewer data. Although choice of plot size is a critical design element of occupancy monitoring, relatively little effort has been expended to develop or test plot size recommendations. Animal movement between surveys can complicate efforts to obtain an optimal plot size, but surveys of fixed objects, such as nests, dens, or burrows can provide insight about scale effects because the population exposed to sampling does not change during the duration of the survey. We used repeated aerial occupancy surveys to obtain estimates of brown bear (*Ursus arctos*) den distribution and abundance in a portion of Katmai National Park and Preserve in Alaska. We then used these data to assess the importance of plot size selection and highlight the effects of spatial grain on the resulting inference and utility for monitoring. Scale effects in estimates of mean den-based site occupancy, but not total den abundance demonstrated that careful selection of sample unit size is important if estimating occupancy probability is a primary monitoring objective. We expect occupancy surveys based on important structures such as nests or dens could have wide applicability for many species.

Key words: abundance monitoring; aerial survey; Alaska; habitat maps; Katmai National Park and Preserve; spatial grain; species distribution monitoring; *Ursus arctos*.

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† **E-mail:** tlwilson@nps.gov

INTRODUCTION

Although population abundance is often of primary interest for species conservation and management, estimating abundance at a relevant scale can be logistically prohibitive. Limiting the scope of inference to accommodate expensive mark-resight surveys may be one solution, but this approach may compromise information on species distribution necessary for conservation planning (Brown et al. 1995). Monitoring species

distribution is useful for exploring habitat selection and hypothesized population shifts due to stressors in time and space (Guisan and Thuiller 2005). Modeling species distributions requires detection/non-detection data or simple counts and is typically less expensive than data required for in-depth population monitoring (MacKenzie 2005). Though fundamental, animal occurrence data has well-known biases and limitations, such as imperfect detection (MacKenzie 2005) and scale sensitivities (Wiens et al. 2009), that

continue to attract considerable research effort.

Occupancy models are one of many statistical tools that can be used to provide spatially explicit information related to the distribution and abundance of unmarked animal populations while accounting for imperfect detection (MacKenzie et al. 2002, Royle and Dorazio 2008). Occupancy approaches use repeated detection/non-detection surveys at sites to account for bias caused by failing to observe the target species at sites where the species is actually present (MacKenzie et al. 2002). The standard closed-population occupancy model can also be modified to produce abundance estimates when detection and abundance are correlated (Royle and Nichols 2003). Similar to species distribution models (Seo et al. 2009) and resource selection functions (Boyce 2006), occupancy models are sensitive to the scale of observation (MacKenzie et al. 2006, Efford and Dawson 2012, Ellis et al. 2014). For this reason, it is important to choose the extent of the study and sample unit size (spatial grain) carefully when conducting occupancy analyses. Multi-scale analysis may therefore be necessary in order to plan monitoring activities (Ellis et al. 2014) and make inference about habitat requirements (Urban and Swihart 2009). The effects of scale are particularly important for low density species with life histories requiring extensive field efforts to sample (i.e., bears).

Developing adequate sampling approaches to monitor changes in bear (*Ursus* sp.) populations through time has been a topic of interest for many years (e.g., Becker and Quang 2009, De Barba et al. 2010, Thompson et al. 2010, Walsh et al. 2010), however, the effort required to obtain estimates of abundance with enough precision for effective monitoring and management can be prohibitively expensive (Reynolds et al. 2011). This has resulted in limited population-level information for bears throughout much of their range. If alternative metrics related to key components of population health and structure could be more simply sampled (e.g., den-based occupancy), it may be possible to monitor attributes important for bear conservation without measuring abundance directly.

Winter dens serve as sites for hibernation and parturition for bears, and are thus key components of bear life history strategies (Vroom et al.

1980, Van Daele et al. 1990, Pigeon et al. 2014). Immobile objects unique to an individual (such as dens) can be particularly useful for addressing questions of animal distribution for wide-ranging animals because these structures are fixed on the landscape and represent a critical component of animal behavior and ecology (Stanley and Royle 2005, Wilson et al. 2010, Price and Rachlow 2011). Den sites also provide an excellent opportunity to examine scale dependences in distribution and abundance, because they remain at a fixed location on the landscape within a given year, simplifying the closure assumption at every grain of analysis.

During the spring of 2013, we conducted repeated aerial surveys for brown bear dens in a study area located in central Katmai National Park and Preserve, Alaska (Katmai). We used single-season occupancy models to explore the importance of plot size on estimates of den-based occupancy and the abundance of dens in our study area. Our primary objectives were to: (1) estimate den-based site occupancy and abundance for brown bears; (2) assess the effects of survey unit size on estimates of den-based site occupancy and abundance; and (3) discuss the implications of scale sensitivities on using occupancy models for monitoring.

METHODS

Study area

The study area was a 2500-km² portion of Katmai National Park and Preserve located in the Bristol Bay watershed north of Lake Grosvenor and south of Nonvianuk Lake (Fig. 1). The Bristol Bay watershed supports large runs of sockeye salmon (*Oncorhynchus nerka*), an important food source for brown bears (Hilderbrand et al. 2004). Large prey (e.g., moose, *Alces alces*), small prey (e.g., arctic ground squirrels, *Spermophilus parryi*), and abundant berry producing plants (e.g., blueberry, *Vaccinium ovalifolium*) are also available. These abundant resources contribute to one of the densest brown bear populations in the world (Sellers et al. 1999). The terrain is complex, with mountains, broad plateaus, moraines, lake shores, and bottomlands at elevations ranging from 10 to 1640 m. Most of the study area consists of tundra and short vegetation, but the lower hillsides support alder (*Alnus* sp.) thickets;

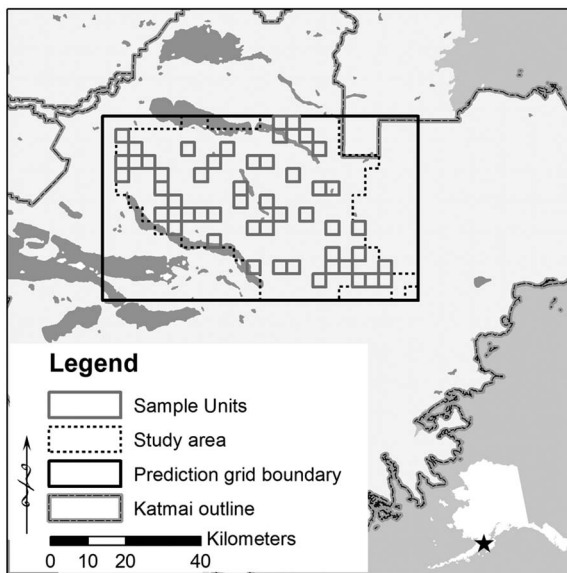


Fig. 1. The study area is located in Katmai National Park and Preserve, Alaska, USA. The inset on the lower right shows the location of Katmai (black star) in Alaska (white).

cottonwood (*Populus* sp.) and spruce (*Picea* sp.) forests dominate the river bottoms and lake shores. The study area has a moist subarctic climate that is affected by large maritime storms. Most of the 50+ cm of precipitation falls as cool summer rain, but large winter storms deposit snow in the mountainous regions of the park. Although data about snow conditions are limited, the snowpack generally begins to recede as brown bears emerge from their dens in May.

Survey design

We placed a 3800-km² rectangular prediction grid composed of 12.25-km² grid cells over the 2500-km² study area (Fig. 1). We chose this grid size to roughly match the expected underlying bear density recorded during a recent survey (Harper 2009). At this scale, we expected approximately one bear den per grid cell on average and an overall occupancy of 1.0 if bears maintained exclusive home ranges of the same relative size (i.e., ideal despotic distribution). Post-hoc, we divided or combined cells to obtain three additional grids to explore the effects of grid cell size on results from occupancy models: a quarter grid (X/4) containing 3.06-km² cells, a

half grid (X/2) containing 6.13-km² cells, and a double grid (2X) containing 24.50-km² cells. We conducted den surveys at the 1X scale (12.25 km²), using simple random selection to obtain 50 random sample units from the 1X grid cells within our geographic area of interest (Fig. 1). The sample data for the X/4 and X/2 scales was obtained by dividing the sample units as described above, resulting in 200 and 100 sample units, respectively. We obtained sampled grid cells for the 2X scale by combining adjacent 1X sampled grid cells using the next-nearest neighbor rule, resulting in 21 combined sample units. The sampled grid cells from each grid size were marked as occupied or not using the GPS den locations obtained from the aerial den survey described below.

Field methods

An observer-pilot team searched for bear dens at 50 randomly selected 1X grid cells (sites) within the study area using a small aircraft (Super cub [PA-18A] or Cessna 185 [C-185]). Surveys were conducted during den emergence before deciduous trees leafed-out between 1 and 31 May 2013. All 50 sites were surveyed once before any replicate surveys. Logistical, weather, and safety concerns dictated when repeated surveys would be flown with those in the most mountainous terrain requiring calm, clear conditions. We originally intended to survey each site three times, but weather and logistical difficulties prevented resampling of some sites. The entire site was flown 100–300 m above the ground depending on terrain, wind, and visibility conditions (e.g., snow cover). We made sure that each site was sampled completely, recognizing sites with complex terrain and vegetation features (e.g., hills and conifers) required more time to sample than simpler sites.

During surveys, we searched for holes large enough to accommodate a brown bear. Den identification was aided by other signs of bear activity, including: tracks in the snow, mounded soil, and smashed vegetation (Fig. 2). Upon detecting a den during a survey flight, we flew multiple passes to photograph the den, and mark the spatial location (i.e., latitude and longitude) with a handheld GPS unit. We assumed that all dens belonged to brown bears, because black bears are rarely observed in Katmai. We recorded

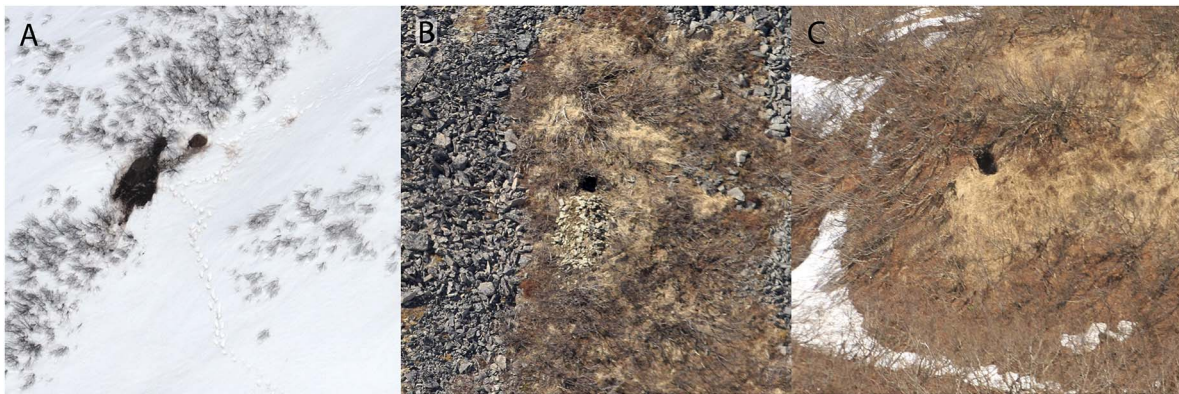


Fig. 2. Brown bear dens photographed in Katmai National Park and Preserve during den surveys in May 2013. The images show the different signs of bear use. Panel (A) shows den with two entrances, stained snow, fresh tracks, and a large soil mound; (B) shows den with a large soil mound; and (C) shows den with smashed vegetation.

a detection (1) if ≥ 1 dens were observed in a cell during a survey flight, and a non-detection (0) otherwise. If a site was sampled fewer than three times, we added missing observations (NA) to the end of the encounter history. Positional error was unavoidable for our aerial survey, and den locations occasionally fell outside of the surveyed grid cell. In these instances, the den was considered to be located inside the surveyed grid cell nearest the recorded locations if the expected error polygon intersected the surveyed cell (~ 250 m; T. L. Wilson, *unpublished data*).

Data analysis

Occupancy models typically assume population closure, which means that the ecological state of interest (site occupancy or population abundance) do not change during the course of the survey. We began the surveys in late spring when snow was still covering many dens. Dens that were covered by snow were present but not available for detection, therefore the expected increase in den availability as the snow melted during the survey could be considered a part of the observation process, which we modeled by including a survey date covariate. We used the UNMARKED package version 0.10–4 (Fiske and Chandler 2011b) in R version 3.0.2 (R Core Team 2014) to fit single-season occupancy (MacKenzie et al. 2002) and abundance (Royle and Nichols 2003) models. For details about model formulae and sample code, please see Royle and Dorazio

(2008).

Our suite of eight models included covariates accounting for temporal heterogeneity in detection (survey date) and spatial heterogeneity between sites (Table 1). We tested the spatial covariates for multicollinearity prior to selecting the final suite of models containing covariates on occupancy probability or abundance, and did not allow correlated covariates ($r_{\text{pearson}} > 0.50$) to appear in the same model. We tested all possible two-variable, non-correlated combinations of three variables, each derived from the 60-m National Elevation Dataset (NED): elevation (m), slope (degrees), and northness (a cosine transformation of aspect). We expected that these variables could be related to occupancy and abundance at a given site. We were unable to include additional covariates due to poor availability of ecologically relevant spatial datasets in our study area. To obtain covariates for analysis and prediction at each grid scale, we computed the mean values of measures within the grid cells. We standardized covariates $(\bar{X} - X_i)/SD$ to aid convergence of the maximum likelihood algorithm. We used AIC to rank candidate models. We used the highest-rated two-variable model to generate predictions of occupancy and abundance at each grid scale. We used empirical Bayesian methods to obtain confidence intervals for the derived parameters: mean occupancy, and total abundance (Fiske and Chandler 2011a). We used plots of predicted values to examine how

Table 1. Models used to evaluate bear den occupancy in Katmai National Park and Preserve. Covariates are separated by a comma in additive models. All spatial covariates derived from the 60-m National Elevation Dataset. Slope is in degrees, and North is aspect with a cosine transformation.

Model	Description
p(.).s(.)	constant model
p(date)s(.)	detection by date occupancy
p(date)s(slope)	constant
p(date)s(north)	detection by date occupancy by slope
p(date)s(elev)	detection by date occupancy by north
p(date)s(elev^2)	detection by date occupancy by elevation
p(date)s(north,slope)	detection by date occupancy by elevation quadratic
p(date)s(elev,north)	detection by date occupancy by additive northness and slope
	detection by date occupancy by additive elevation and northness

covariates were related to both detection and occupancy. We made predictive occupancy maps using coefficients from the highest-rated two-variable model in ArcGIS (Environmental Systems Research Institute, Redlands, California, USA).

RESULTS

As expected, both the occupancy and abundance models predicted that the probability of detecting dens increased as the season progressed (Fig. 3). The time-dependent model of detection (including the day of year covariate) was selected at grid scales X/4, X/2, and 1X for both the occupancy and abundance estimators. Boundary conditions (near 100% occupancy) affected model selection at the 2X scale, and many occupancy models produced convergence errors (Figs. 3 and 4). The constant model was

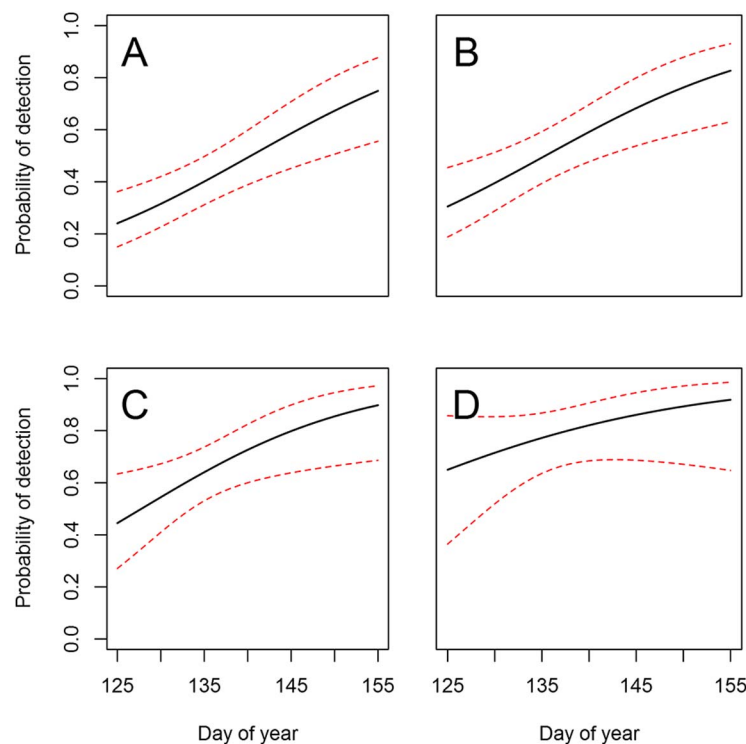


Fig. 3. Predicted probability of detection for a range of dates derived from the best-fitting two-variable occupancy models. Data were obtained from repeated surveys of a study area in Katmai National Park and Preserve, Alaska, USA. Results from models fit at each of four grid cell sizes are presented: (A) quarter (X/4), (B) half (X/2), (C) whole (1X), and (D) double (2X). Aerial den surveys were conducted between day 128 and 150. The dashed lines represent 95% confidence intervals.

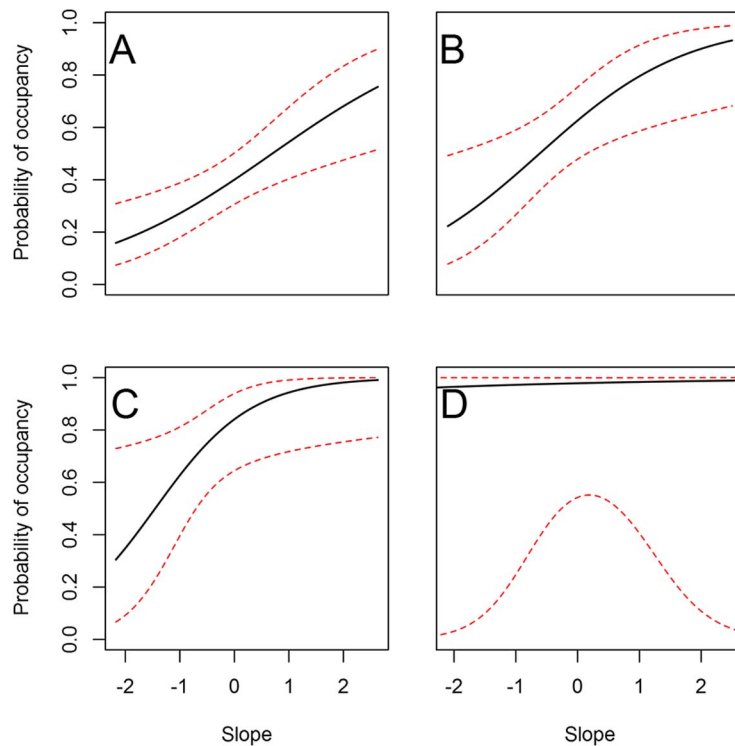


Fig. 4. Predicted probability of occupancy for a range of slope values derived from the best-fitting two-variable occupancy models. Data were obtained from repeated surveys of sample units within a study area in Katmai National Park and Preserve, Alaska, USA. Results from models fit at each of four grid cell sizes are presented: (A) quarter ($X/4$), (B) half ($X/2$), (C) whole ($1X$), and (D) double ($2X$). The dashed lines represent 95% confidence intervals.

selected for both occupancy and abundance at the $2X$ scale, suggesting uniform occupancy and abundance across the cells at the largest grain (Table 2).

Models containing the covariates slope and northness contributed most of the model weight for $X/4$, $X/2$, and $1X$ grids for both occupancy and abundance (Table 2). Slope was the most important predictor of site occupancy and abundance, contributing to all of the models supported by AIC at scales $<2X$ (Table 2). The probability that a site was occupied by a den and den abundance both increased with mean slope at all scales (Fig. 4). The probability of den occupancy and den abundance were generally greater on south-facing slopes, although the 95% confidence intervals overlapped 0 at most scales (Table 3, Fig. 5). With the exception of the $X/2$ standard occupancy model, northness was only included as a single-variable extension of the preferred

slope model.

The mean estimated probability that a site within the prediction grid area contained bear dens (often interpreted as proportion of sites occupied) increased with increasing cell size (Fig. 6A). Similarly, as cell size expanded, the mean predicted number of dens per cell increased: $X/4 = 0.57$ ($SD = 0.25$); $X/2 = 1.05$ ($SD = 0.43$); $1X = 1.96$ ($SD = 0.71$); $2X = 4.09$ ($SD = 0.82$). Although the estimated total abundance at each site gets larger with increasing cell sizes, the study area-wide estimates of total abundance remained consistent (Fig. 6B). The Royle-Nichols model predicted between 653 ($CI = 317$ – 1362) dens on the $1X$ prediction grid and 749 ($CI = 452$ – 1252) dens on the $X/4$ prediction grid.

Maps of den occurrence clearly show the effects of scale sensitivity on predicted occupancy probability (Fig. 7). The $X/4$ grid map shows the most spatial detail in predictions, reflecting the

differences in site occupancy estimates between sites. Spatial detail was reduced, and overall cell occupancy probabilities increased as grid cell size increased. All sites within the prediction grid were predicted to be occupied with probability 1.0 at the 2X grid cell size.

DISCUSSION

We found that den-based site occupancy estimates were strongly dependent on sample unit size. Maps of predicted probability of object occupancy demonstrate how scale affects interpretation of distribution. Our results demonstrate that careful consideration of the scope of inference desired and animal biology are necessary when designing site occupancy studies. We expect that with additional testing and development, site occupancy surveys for dens, nests, or burrows could also be a viable alternative to population abundance surveys for many species that are difficult or expensive to monitor through direct observation.

The estimated total number of dens in the prediction area remained relatively consistent with increasing grid cell size, despite progressively increasing estimated occupancy probabilities. This makes sense because larger areas necessarily have more dens, and the Royle and Nichols (2003) model incorporates abundance-induced heterogeneity into the detection model. Several unpublished reports suggest that the brown bear population in Katmai is between 101 and 156 bears per 1000 km², which would translate into an estimated abundance of approximately 384–593 bears in our prediction grid. Our estimates of den abundance were about twice the expected density. One explanation for this is that the site has unusually good bear denning habitat, drawing bears from outside the study area. An alternative explanation that there would be more than 1 den/bear, is also plausible given that dens may persist on the landscape for many years. Sign persistence is a known limitation of using indirect indicators (e.g., dens) for monitoring (Stanley and Royle 2005, Price and Rachlow 2011) and is an issue that deserves further attention in the context of using dens for monitoring bear populations. However, if we assume that dens deteriorate at a constant rate, then changes in den-based estimates could be

directly interpreted as changes in bear abundance or occupancy. A possible avenue for further development includes: modeling den persistence using a capture-mark-recapture approach (e.g., Wilson et al. 2014), paired with the incorporation of additional animal signs that would improve confidence in annual use (e.g., Wilson et al. 2010). Also of concern for any future monitoring program are the large confidence intervals surrounding den abundance estimates. These should be reduced by adopting a fully Bayesian analysis approach using informed priors (McCarthy and Masters 2005, Schmidt and Rattenbury 2013) and incorporating spatial autocorrelation (Wilson et al. 2010). Further gains in confidence can also be achieved through development of mechanistic spatial covariates that better model spatial heterogeneity due to brown bear habitat selection.

The predicted distribution of bear dens (Fig. 7) shows that some sites were better habitat for brown bear denning than others, but scale sensitivities are apparent. For example, if we interpreted that all sites with occupancy probability <0.5 were unoccupied, then the eastern portion of the prediction grid would be unoccupied for the X/4 or X/2 grids, but occupied for all larger grids. Based on the pattern observed in our data, we would expect that much of the prediction grid would appear unoccupied if the grids were subdivided further (e.g., X/8, where there would only be 0.25 dens/grid cell). Despite this scale sensitivity, our models correctly identified steep-moderate slopes as an important characteristic of brown bear den habitat (Van Daele et al. 1990, Ciarniello et al. 2005, Libal et al. 2012). Although a detailed investigation of denning ecology was beyond the scope of this study, our findings demonstrate that when appropriate covariates are available, the den-based site occupancy approach could be used to identify habitat features important to bears at a landscape scale.

Scale sensitivity is a fundamental property of measuring animal distribution (Johnson 1980, Wiens 1989), and occupancy analysis is not immune from substantial scale effects (Urban and Swihart 2009, Efford and Dawson 2012). Our results demonstrate scale effects due to grain, but extent can have similar effects for brown bear summer locations (Ciarniello et al. 2007) and den

Table 2. AIC tables for all models from the bear den occupancy analyses (A) and the bear den abundance analysis (B) in Katmai National Park and Preserve. The models are presented in the order of greatest support. Four grid scales were analyzed and presented separately: $2X = 27.50 \text{ km}^2$, $1X = 12.25 \text{ km}^2$, $X/2 = 6.13 \text{ km}^2$, and $X/4 = 3.06 \text{ km}^2$.

Scale	Model	nPars	AIC	ΔAIC	AIC weight	Cumulative weight
A) MacKenzie occupancy models						
X/4	p(date)s(slope)	4	461.33	0.00	0.62	0.62
	p(date)s(north,slope)	5	462.36	1.03	0.37	0.99
	p(date)s(.)	3	471.19	9.85	0.01	0.99
	p(date)s(north)	4	472.10	10.76	0.01	1.00
	p(date)s(elev)	4	473.18	11.85	0.00	1.00
	p(date)s(elev,north)	5	474.08	12.74	0.00	1.00
	p(date)s(elev^2)	5	475.08	13.75	0.00	1.00
X/2	p(.)s(.)	2	484.75	23.42	0.00	1.00
	p(date)s(north,slope)	5	310.63	0.00	0.63	0.63
	p(date)s(slope)	4	311.98	1.34	0.32	0.95
	p(date)s(north)	4	311.98	7.33	0.02	0.97
	p(date)s(.)	3	317.96	8.26	0.01	0.98
	p(date)s(elev,north)	5	318.89	8.58	0.01	0.99
	p(date)s(elev)	4	319.21	10.05	0.00	1.00
1X	p(date)s(elev^2)	5	320.69	11.96	0.00	1.00
	p(.)s(.)	2	329.67	19.04	0.00	1.00
	p(date)s(slope)	4	177.62	0.00	0.58	0.58
	p(date)s(north,slope)	5	178.75	1.13	0.33	0.91
	p(date)s(.)	3	181.88	4.26	0.07	0.98
	p(date)s(elev,north)	5	184.37	6.75	0.02	1.00
	p(.)s(.)	2	187.15	9.54	0.00	1.00
2X	p(date)s(elev^2)	5	188.18	10.57	0.00	1.00
	p(date)s(north)	4	191.85	14.23	0.00	1.00
	p(date)s(elev)	4	195.60	17.33	0.00	1.00
	p(.)s(.)	2	71.28	0.00	0.25	0.25
	p(date)s(.)	3	71.66	0.38	0.21	0.46
	p(date)s(elev,north)	5	72.23	0.95	0.15	0.61
	p(date)s(north)	4	72.62	1.34	0.13	0.74
	p(date)s(elev)	4	72.73	1.45	0.12	0.86
	p(date)s(slope)	4	73.51	2.23	0.08	0.94
	p(date)s(north,slope)	5	74.59	3.31	0.05	0.99
	p(date)s(elev^2)	5	76.93	5.64	0.02	1.00
B) Royle-Nichols abundance models						
X/4	p(date)s(slope)	4	459.43	0.00	0.71	0.71
	p(date)s(north,slope)	5	461.34	1.91	0.27	0.98
	p(date)s(.)	3	468.60	9.17	0.01	0.99
	p(date)s(north)	4	470.28	10.85	0.00	1.00
	p(date)s(elev)	4	470.58	11.15	0.00	1.00
	p(date)s(elev,north)	5	472.28	12.85	0.00	1.00
	p(date)s(elev^2)	5	472.34	12.92	0.00	1.00
X/2	p(.)s(.)	2	482.45	23.02	0.00	1.00
	p(date)s(slope)	4	309.60	0.00	0.65	0.65
	p(date)s(north,slope)	5	311.22	1.61	0.29	0.94
	p(date)s(.)	3	316.13	6.53	0.02	0.96
	p(date)s(north)	4	317.49	7.88	0.01	0.97
	p(date)s(elev)	4	317.99	8.39	0.01	0.98
	p(date)s(north,slope)	5	319.07	9.47	0.01	0.99
1X	p(date)s(elev^2)	5	319.86	10.26	0.00	1.00
	p(.)s(.)	2	327.06	17.46	0.00	1.00
	p(date)s(slope)	4	175.30	0.00	0.58	0.58
	p(date)s(north,slope)	5	177.30	2.00	0.21	0.79
	p(date)s(.)	3	178.91	3.61	0.10	0.89
	p(date)s(elev)	4	180.70	5.40	0.04	0.93
	p(date)s(north)	4	180.89	5.59	0.03	0.96
	p(date)s(elev,north)	5	182.57	7.27	0.02	0.98
	p(date)s(elev^2)	5	182.69	7.39	0.01	0.99
	p(.)s(.)	2	181.06	8.76	0.01	1.00

Table 2. Continued.

Scale	Model	nPars	AIC	Δ AIC	AIC weight	Cumulative weight
2X	p(.)s(.)	2	68.94	0.00	0.27	0.27
	p(date)s(.)	3	69.42	0.48	0.21	0.48
	p(date)s(slope)	4	70.39	1.45	0.13	0.61
	p(date)s(elev)	4	70.59	1.66	0.12	0.73
	p(date)s(north)	4	70.90	1.96	0.10	0.83
	p(date)s(north,slope)	5	71.78	2.85	0.07	0.90
	p(date)s(elev^2)	5	72.15	3.21	0.05	0.95
	p(date)s(elev,north)	5	72.47	3.53	0.05	1.00

Note: 2X models fit poorly, and many produced convergence errors due to estimates near $\psi = 1$. Model selection statistics are provided for reference only.

Table 3. Coefficients from the best supported model at all scales, and for both methods. The 95% confidence intervals are listed in parentheses. Bold text indicates coefficients where 95% confidence intervals do not overlap zero.

Scale	Model	Intercept (<i>p</i>)	Date	Intercept (<i>s</i>)	Northness	Slope
X/4	Occupancy	-10.58 (-16.07, -5.09)	0.07 (0.04, 0.12)	-0.41 (-0.81, -0.00)		0.64 (0.25, 1.04)
	Royle-Nichols	-10.27 (-15.41, -5.12)	0.07 (0.03, 0.11)	-0.59 (-0.96, -0.22)		0.41 (0.17, 0.65)
X/2	Occupancy	-10.76 (-17.28, -4.23)	0.08 (0.03, 0.13)	0.50 (-0.10, 1.09)	-0.46 (-0.97, 0.05)	0.84 (0.33, 1.46)
	Royle-Nichols	-10.04 (-15.82, -4.26)	0.07 (0.03, 0.11)	0.05 (-0.39, 0.49)	-0.09 (-0.37, 0.19)	0.37 (0.12, 0.63)
1X	Occupancy	-10.47 (-19.19, -1.76)	0.08 (0.02, 0.15)	1.59 (0.62, 2.56)		1.07 (0.12, 2.02)
	Royle-Nichols	-8.66 (-15.65, -1.66)	0.06 (0.02, 0.10)	0.64 (0.08, 1.21)		0.34 (0.06, 0.63)
2X	Occupancy	1.32 (0.66, 1.98)		3.22 (0.71, 5.72)		
	Royle-Nichols	-0.41 (-1.89, 1.06)		1.29 (0.34, 2.24)		

Note: Blank cells represent coefficients that were not present in the best model as selected by AIC.

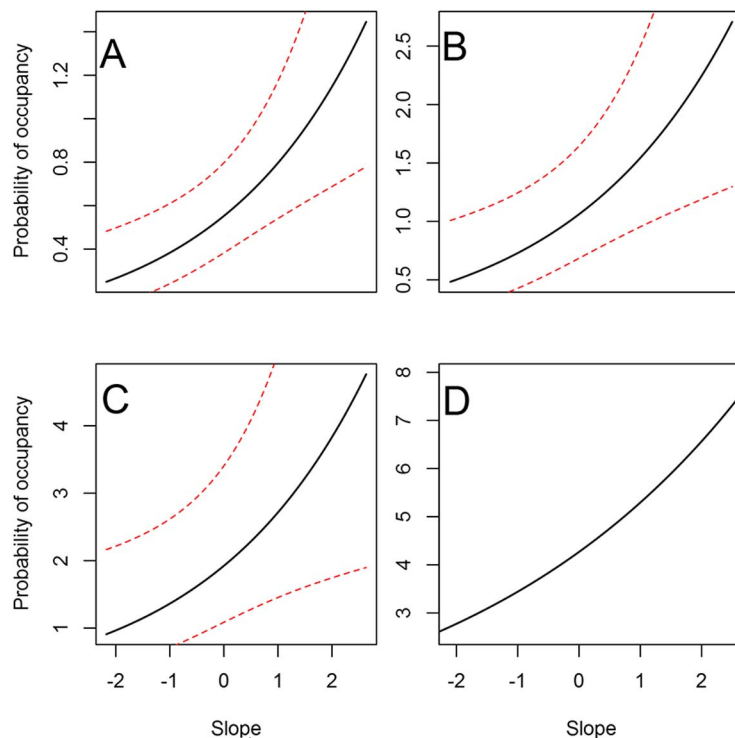


Fig. 5. Predicted den abundance for a range of slope values derived from the best-fitting two-variable abundance models. Data were obtained from repeated surveys of a study area in Katmai National Park and Preserve, Alaska, USA. Results from models fit at each of four grid cell sizes are presented: (A) quarter (X/4), (B) half (X/2), (C) whole (1X), and (D) double (2X). The dashed lines represent 95% confidence intervals.

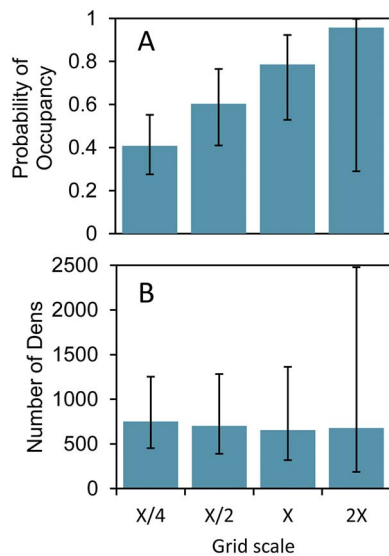


Fig. 6. Panel (A) shows mean probability of den occupancy $X/4 = 0.408$ (CI = 0.276–0.552); $X/2 = 0.604$ (CI = 0.410–0.765); $1X = 0.786$ (CI = 0.529–0.923); $2X = 0.957$ (CI = 0.290–0.998), and panel (B) shows total den abundance $X/4 = 749$ (CI = 452–1252); $X/2 = 701$ (CI = 389–1281); $1X = 653$ (CI = 317–1362); $2X = 677$ (CI = 187–2477) for four different grid cell sizes in Katmai National Park and Preserve, Alaska, USA.

site selection (Pigeon et al. 2014). It is therefore critical to consider both grain and extent during every aspect of occupancy studies, including study design, reporting, and interpretation. Furthermore, the presence of scale effects in occupancy models warrants that care should also be taken when comparing study results from occupancy analyses conducted at different scales.

The optimal scale at which to study ecological relationships has intrigued researchers for many years (e.g., Wiens 1989, Hobbs 2003, Ciarniello et al. 2007). There may be no optimal scale for studying any particular ecological process, so multi-scale analyses are recommended (Urban et al. 1987, Hobbs 2003). However, ecological processes are often thought to operate at characteristic levels that can be used to guide design for data collection (Urban et al. 1987). For example, for any given set of spatial objects, there exists a grain size and extent for which all sites are occupied (saturation), or few sites are occupied (scarcity). These boundaries are a function of underlying object density, species ecology, animal movement (Efford and Dawson 2012), and study area extent. Fig. 6 illustrates that occupancy analysis should be conducted at a grain and

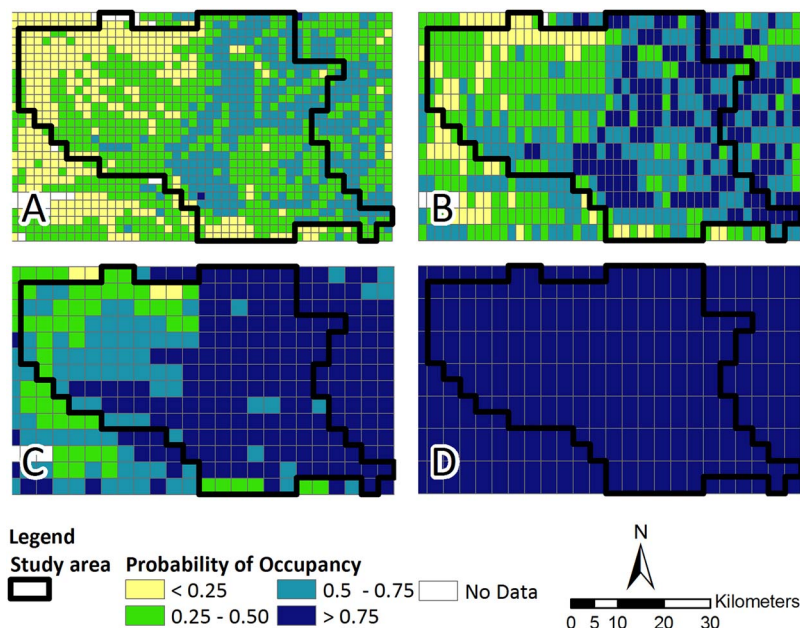


Fig. 7. Maps of the predicted den occupancy in Katmai National Park and Preserve, Alaska, USA. Results from best-fitting two-variable occupancy models at each of four grid cell sizes are presented: (A) quarter ($X/4$), (B) half ($X/2$), (C) whole ($1X$), and (D) double ($2X$).

extent that assures the estimator is not operating near either boundary (MacKenzie et al. 2006:157–158).

The occupancy literature contains contrary advice about choosing a meaningful sample unit size that does not lead to boundary estimates. Some authors recommend sample unit sizes that are larger than animal home ranges to account for the possibility that sample unit area is confounded with home range area (MacKenzie and Royle 2005, Efford and Dawson 2012) or hedge against violations of the closure assumption (O'Connell and Bailey 2011) because of animal movement. However, the power to detect trend in the occupancy parameter may be better if the sample unit is slightly smaller than the mean home range area of the species in question (Ellis et al. 2014). Scale dependencies in species distribution models may affect species differentially (e.g., Seo et al. 2009), and general prescriptions based on expected animal behavior (e.g., home range size) should be approached with caution. For example, the underlying spatial intensity of dens should be a function of home range because bears tend to select den sites within their home ranges (Schoen et al. 1987, Ciarniello et al. 2005). However, we reached saturation at the 2X grid cell size (i.e., probability contained ≥ 1 den = 1.0), which was much smaller than the grain size guidelines recommended based on simulations of moving animals (Efford and Dawson 2012). Although dens do not move and closure is ensured, the study area extent, and underlying density of dens within the study area, dictate the appropriate sampling grain. It is therefore best to let the study objectives and characteristics of the species of interest guide the data collection regime (Hobbs 2003, Ellis et al. 2014). Given the scale sensitivities observed here, it is important that researchers, conservationists, and managers define objectives carefully so that the results of occupancy analysis match the ecological phenomenon of interest and are comparable between studies.

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

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