

A peer-reviewed version of this preprint was published in PeerJ on 17 December 2013.

[View the peer-reviewed version](http://peerj.com/articles/227) (peerj.com/articles/227), which is the preferred citable publication unless you specifically need to cite this preprint.

Harris G, Farley S, Russell GJ, Butler MJ, Selinger J. 2013. Sampling designs matching species biology produce accurate and affordable abundance indices. PeerJ 1:e227 <https://doi.org/10.7717/peerj.227>

Sampling designs matching species biology produce accurate and affordable abundance indices

Wildlife biologists often use grid-based designs to sample animals and generate abundance estimates. Although sampling in grids is theoretically sound, in application, the method can be logistically difficult and expensive when sampling elusive species inhabiting extensive areas. These factors make it challenging to sample animals and meet the statistical assumption of all individuals having an equal probability of capture. Violating this assumption biases results. Does an alternative exist? Perhaps by sampling only where resources attract animals (*i.e.* targeted sampling), it would provide accurate abundance estimates more efficiently and affordably. However, biases from this approach would also arise if individuals have an unequal probability of capture, especially if some failed to visit the sampling area. Since most biological programs are resource limited, and acquiring abundance data drives many conservation and management applications, it becomes imperative to identify economical and informative sampling designs. Therefore, we evaluated abundance estimates generated from grid and targeted sampling designs using simulations based on geographic positioning system (GPS) data from 42 Alaskan brown bears (*Ursus arctos*). Migratory salmon drew brown bears from the wider landscape, concentrating them at anadromous streams. This provided a scenario for testing the targeted approach. Grid and targeted sampling varied by trap amount, location (traps placed randomly, systematically or by expert opinion), and traps stationary or moved between capture sessions. We began by identifying when to sample, and if bears had equal probability of capture. We compared abundance estimates against seven criteria: bias, precision, accuracy, effort, plus encounter rates, and probabilities of capture and recapture. One grid (49 km² cells) and one targeted configuration provided the most accurate results. Both placed traps by expert opinion and moved traps between capture sessions, which raised capture probabilities. The grid design was least biased (-10.5%), but imprecise (CV 21.2%), and used most effort (16,100 trap-nights). The targeted configuration was more biased (-17.3%), but most precise (CV 12.3%), with least

effort (7,000 trap-nights). Targeted sampling generated encounter rates four times higher, and capture and recapture probabilities 11% and 60% higher than grid sampling, in a sampling frame 88% smaller. Bears had unequal probability of capture with both sampling designs, partly because some bears never had traps available to sample them. Hence, grid and targeted sampling generated abundance indices, not estimates. Overall, targeted sampling provided the most accurate and affordable design to index abundance. Targeted sampling may offer an alternative method to index the abundance of other species inhabiting expansive and inaccessible landscapes elsewhere, provided their attraction to resource concentrations.

1 **Grant Harris**,¹ United States Fish and Wildlife Service, Albuquerque, NM, 87103, USA

2 **Sean Farley**, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK,
3 99518, USA.

4 **Gareth J. Russell**, Department of Mathematical Sciences, New Jersey Institute of Technology,
5 Newark, NJ, 07102, USA.

6 **Matthew J. Butler**, United States Fish and Wildlife Service, Albuquerque, NM, 87103, USA

7 **Jeff Selinger**, Alaska Department of Fish and Game, 43961 K-Beach Road, Soldotna, AK 99669,
8 USA.

9 ¹Corresponding author:

10 United States Fish and Wildlife Service

11 PO Box 1304

12 Albuquerque, NM 87103

13 e-mail: grant_harris@fws.gov

14 phone: 505-248-6817

15 **INTRODUCTION**

16 Wildlife biologists often rely on photographs or DNA in a capture-mark-recapture (CMR)
17 framework to estimate the abundances of sparsely distributed animals inhabiting expansive,
18 heavily vegetated and inaccessible terrain (*Karanth & Nichols, 1998; Boulanger et al., 2002;*
19 *Harris et al., 2010; Kindberg et al., 2011*). At issue is how to sample effectively and
20 economically under such conditions. In particular, are there alternative sampling designs to the
21 conventional grid?

22 Grid-based designs operate by enveloping study sites with a uniform cell size and sampling
23 within each cell (*e.g. Woods et al., 1999; Poole et al., 2001; Boulanger et al., 2002; Williams et*
24 *al., 2002; Boulanger et al., 2004; Kendall et al., 2009*). Although the approach is popular, grid
25 sampling harbors logistical challenges, and when improperly used, methodological flaws (see
26 below). An alternative sampling design could sample only at biologically important locations that
27 attract the target species (hereafter “targeted sampling”; *Karanth & Nichols, 1998; Sawaya et al.,*
28 *2012*). Obvious resistance to this approach stems from the biases introduced if some individuals
29 in the population failed to visit the sampling area.

30 While abundance estimation forms a cornerstone of wildlife biology, the size of many study sites,
31 challenging terrain and elusiveness of the target species makes acquiring abundance data
32 expensive. Yet most biological programs receive little funding, requiring professionals to pursue

33 economical methods to estimate abundance, while maintaining informative and scientifically
34 defensible designs. Given this reality, we evaluated the targeted sampling design by comparing it
35 to conventional grid sampling. If targeted sampling generates abundance estimates affordably
36 and precisely, with low bias and effort, then it could offer an informative and economical
37 alternative to estimating abundances of sparsely distributed animals inhabiting heavily vegetated
38 or topographically complex environments, provided the species attraction to resource
39 concentrations. Globally, many species having these characteristics are of high conservation
40 concern (*e.g. Fuller, 1995; Weber & Rabinowitz, 1996; Shackleton, 1997*). Often, abundance
41 data for such species are deficient, unable to inform population status, threat assessments, or
42 provide direction for properly conserving and managing populations of these animals.

43 **Grid and targeted sampling**

44 Grid sampling aims to ensure that all individuals within the population have the same probability
45 of capture (*Nichols & Karanth, 2002; Williams et al., 2002*). While the theory is sound,
46 implementation has at least 3 disadvantages. First, to ensure that all individuals encounter traps,
47 users often scale grid cells to match the average home range size of the target species (*Boulanger*
48 *et al., 2004a; Boulanger et al., 2006*). Problems arise when biologists lack home range
49 information for their population under study, home range sizes vary between surveys, or home
50 range sizes vary widely within a population. When home range data are lacking, then
51 practitioners can rely on home range sizes from the same or related species elsewhere, hoping
52 that the cell size used is appropriate (*Boulanger et al., 2006; Sawaya et al., 2012*). If animals
53 change their behavior in response to concentrated or dispersed resources, making their home
54 ranges shrink or expand, then home range sizes will vary between years (*i.e.* surveys). This
55 makes it challenging for a defined grid size to always be appropriate. If home range sizes have

56 much variation in the population, then a mean value has little biological relevance (*McNab,*
57 *1963; Powell, 2000; Boulanger et al., 2006*). By relying on the home range mean, a segment of
58 the population will have home range sizes below the cell size, so traps may not be available to
59 capture them. In each case, using home range data to guide the size of the grid cell may result in
60 the grid being too large, causing an unequal probability of capture. This raises capture
61 heterogeneity, thereby increasing error in the CMR approach (*Williams et al., 2002; Boulanger et*
62 *al., 2004*). Since many studies sampling with grid configurations do not biologically justify the
63 grid resolution chosen, they lack information to evaluate this heterogeneity violation (*e.g. Woods*
64 *et al., 1999; Boulanger et al., 2004; Mowat et al., 2005; Boulanger et al., 2008a; Kendall et al.,*
65 *2008*). In any event, for grid sampling, the solution relies on using small cell sizes to ensure that
66 all individuals have a chance of being captured.

67 Of course, this begs the question of how small cell sizes must be. Although we discuss this point
68 later, it invokes the second issue. Many study sites are large (10,000s of km²) and include areas
69 difficult to access, due to vegetation types, terrain, or insecure political situations. Sampling in
70 these areas is logistically difficult or unsafe, and when using small cells sizes, the projects can
71 become prohibitively expensive (*Kendall et al., 2009; Harris et al., 2010; Sawaya et al., 2012*).
72 A third issue with grid sampling is the same trapping effort covers an entire study area that varies
73 in species densities. This seems inefficient. Overall, these problems risk generating ineffective
74 and expensive sampling designs, which can discourage project implementation (*Woods et al.,*
75 *1999; Boulanger et al., 2002; Kendall et al., 2009*).

76 Resources influence a species' distribution, by attracting animals from the wider landscape into
77 relatively smaller areas. Therefore, places that concentrate important biological resources often
78 contain a high density of the target species (*MacArthur, 1972; Karanth et al., 2002*). Hence,

79 targeted sampling focuses effort in high use areas (places that attract the target animal), which
80 may reduce the amount of area to sample, number of traps, and sampling logistics (*e.g.* scent
81 marking stations, water holes, trails; *Karanth & Nichols, 1998; Sawaya et al., 2012*). Each of
82 these factors lowers project costs. Because the sampling design matches species biology and
83 more animals are sampled in less area, it should increase capture probabilities (*Karanth et al.,*
84 *2002*). Further, targeted sampling may facilitate sampling insecure study sites, if the resource
85 concentrations – and hence high densities of the target species – occur in safer areas where they
86 can be sampled.

87 The estimator would fail if numerous individuals in the population did not frequent the sampling
88 area, or if the proportion that visited changed over time. Then, traps in a targeted configuration
89 would not be available to all individuals equally, in amounts that could vary between surveys,
90 causing bias. This would render the sampling assumptions unreasonable, and the final abundance
91 estimates unreliable (*Karanth & Nichols, 1998, Williams et al., 2002*). Further, changes in
92 abundances between years would reflect behavioral responses of the species, or an artifact of
93 sampling design, and not actual variation of the species abundances. The sampling techniques
94 would not generate estimates, but indices. Of course, these are the same issues encountered when
95 sampling animals with grids, when home range sizes vary between surveys, or when cells are too
96 large, so traps fall outside of some animals' home ranges rendering them unavailable for capture.

97 Our goal is to identify sampling designs that provide accurate, affordable and defensible
98 abundance estimates. Therefore, we compared abundance estimates generated from grid and
99 targeted sampling designs against a known population size. Our evaluations relied on geographic
100 positioning system (GPS) location data from female brown bears (*Ursus arctos*) inhabiting the
101 Kenai Peninsula of south-central Alaska, USA. Here, migratory salmon drew brown bears from

102 the wider landscape, concentrating them at anadromous streams (*i.e.* streams containing
103 anadromous fish). This provided a scenario for testing the targeted sampling approach (*Miller et*
104 *al., 1997; Hilderbrand et al., 1999; Boulanger et al., 2004b; Mowat et al., 2005*). Because
105 comparisons between designs would be nearly impossible to accomplish in the field, we
106 simulated all sampling in a geographical information system (GIS).

107 We began by determining the optimal dates to sample. Next, we evaluated if all bears were
108 available for capture during that period. For the targeted scenario, bears must be near streams
109 with anadromous fish. For grids, traps must occur within each bears home range. Therefore, we
110 compared brown bear home range sizes to grid cells of varying extent, to inform the cell sizes
111 used for sampling. For grid and targeted sampling, we sampled during the optimal periods, and
112 evaluated each design against seven criteria: bias, precision and accuracy in the population
113 estimates, effort required to obtain estimates (trap-nights) and encounter rates. We also evaluated
114 capture and recapture probabilities, since the best way to reduce capture heterogeneity is by
115 maximizing them (*Lukacs, 2009*).

116 When biologists estimate the abundance of animal populations, their sampling considerations
117 include logistics: the number of traps to deploy, how to place traps, and whether to move traps
118 between capture sessions. Their constraints are time and costs. Therefore, designs with fewer
119 traps and systematic placement are preferable, provided they produce unbiased abundance
120 estimates at the required precision. Similarly, since moving traps between capture sessions adds
121 considerable expense, it makes sense to move traps only if the improvements in accuracy
122 outweigh those costs. Hence, our sampling designs varied by trap amount, location (*i.e.* traps set
123 randomly, systematically or located by expert opinion), and traps stationary or moved between
124 capture sessions.

125 **METHODS**

126 **Study Area**

127 We studied brown bears on the Kenai Peninsula, of south-central Alaska, USA (23,310 km²). The
128 western third of the Peninsula consists of thickly forested plains (approximately sea level), while
129 ice fields and precipitous mountains dominate the remaining landscape. Mountains peak at
130 ≈2,000 m, and we never sampled areas covered by water or ice (Fig. 1). During summer, schools
131 of anadromous salmon (five species) leave the sea and spawn in the Kenai's freshwater
132 tributaries. These migrating salmon form a resource pulse for brown bears and other wildlife
133 (*Hilderbrand et al., 1999*).

134 **GPS Telemetry**

135 Data representing bear movements came from GPS telemetry of female brown bears acquired on
136 the Kenai Peninsula. During 1995 – 2003, the Alaska Department of Fish and Game captured
137 female brown bears throughout the entire Peninsula. Captures occurred in mid-Spring, before
138 deciduous trees leafed and salmon entered streams. Bear captures were geographically dispersed
139 (excluding glaciers) and each bear received a GPS collar. Only females were collared, since
140 males and cubs experience rapid weight gain throughout a season, making the collars either too
141 loose or tight, thereby increasing the risk of injuring (or killing) the bear. All field and capture
142 methods were approved by Alaska Department of Fish and Game, Animal Care and Use
143 Committee, Assurance No. 06-03. GPS collars recorded geographical location, and associated
144 date and time, at intervals ranging from 15 minutes to 13 hours. We only used data with 3-D

145 accuracy, and resampled these GPS data to 13 hours. Resampling kept the first GPS location for
146 each bear, and each 13-hour fix thereafter. Data for some bears spanned multiple years,
147 generating 51 bear/year combinations. Most data covered 1 June through 30 September of a
148 given year (period of most bear activity, after winter denning).

149 **Trapping Period**

150 CMR studies often use 4 to 5 sampling sessions (*Karanth & Nichols, 1998; Boulanger et al.,*
151 *2008a; Boulanger et al., 2008b; Sawaya et al., 2012*). We followed this practice, and simulated 5
152 sessions, each lasting 10 days (50 total days). We determined when to sample by identifying the
153 period between 1 June and 30 September that bears would most likely encounter traps.

154 We examined 3 approaches to identify the sample period for the grid-based designs. First, we
155 hypothesized that bears leaving dens would explore the landscape and encounter traps. For bears
156 in Alaska, this period began 1 June and ended 20 July. Next, we presumed that greater
157 movements would cause more trap encounters. Therefore, we found the contiguous window of
158 50 days, when the average movement rate for brown bears between successive GPS fixes was
159 maximized. Lastly, we examined long-range movements by identifying the contiguous window
160 of 50 days that maximized the average distances between the furthest-apart GPS fixes for each
161 bear.

162 To calculate the movement metrics, we divided the 1 June through 30 September period into 10-
163 day brackets. This generated 122 different intervals (day 1–10, day 2–11, etc.). We then
164 quantified the mean and standard error of brown bear movements in each of the intervals. We
165 retained the 5 contiguous intervals that maximized bear movements (50 contiguous days).

166 The targeted design hinged on salmon being an important food resource that attracted brown
167 bears to anadromous streams (*Hilderbrand et al., 1999; Beier, 2005*). Therefore, we used the
168 same 122, 10-day intervals to quantify the proportion of GPS fixes ≤ 500 m of an anadromous
169 stream for each bear. We chose the 5 contiguous 10-day intervals that maximized this proportion.
170 Targeted simulations occurred during those dates.

171 **Availability for Capture**

172 We quantified the sizes of brown bear home ranges, to inform the selection of appropriate cell
173 sizes for the grid-sampling frame. The objective was to ensure that all bears were available for
174 capture. Our method examined the relationships between grid-cell size (km), and the proportion
175 of bears with home range sizes below that cells area. We also calculated the number of traps
176 within each bears home range, to determine if it contained at least one trap. For each bear, home
177 range calculations used GPS data spanning 1 June through 20 July of a given year, to match when
178 grid sampling occurred (see Results). To estimate home range, we used 95% fixed-kernel and
179 least-squares cross-validation to calculate the smoothing parameter (*Hooge & Eichenlaub, 2000*).

180 Data represented home range sizes of different classes of bears (females without cubs, females
181 with cubs of the year, and females with cubs over one year old). In practice, biologists often do
182 not know in advance what classes, or numbers of individuals within those classes would be
183 trapped, so they usually rely on the average home range size to inform the area of the sampling
184 cell (*Boulanger et al., 2004a; Boulanger et al., 2006*). To test the notion of using an average
185 home range size to inform grid cell area, we averaged the sizes of all home ranges together ($n =$

186 42 bears with GPS data spanning the 1 June through 20 July period). We also reported the home
187 range size of just females with cubs (n = 29).

188 For targeted sampling, we also determined the proportion of bears available for capture. We
189 relied on the GPS data to evaluate if each bear was within 500 m of an anadromous stream during
190 the sampling period. We then examined the proportion of bears within this sampling frame, for
191 every year of GPS data. The sampling frame was about 3,500 km², or 22% of the grid-sampling
192 frame (≈16,000 km²).

193 **Sampling Designs**

194 For grids, we simulated traps in a GIS by dividing the peninsula into 3 sets of square cells, with
195 areas of 49, 81 and 121 km² (Table 1). These cell areas were informed by the home range
196 analysis, and similar cell sizes are often used to estimate brown and grizzly bear population sizes
197 (e.g. *Boulanger et al., 2002; Beier et al., 2005; Mowat et al., 2005; Boulanger et al., 2008b;*
198 *Kendall et al., 2008*). Traps were stationary between capture sessions and located using 3
199 different configurations: traps in cell centers, traps placed randomly in the cell, or traps placed by
200 expert opinion in each cell. Expert opinion relied on our knowledge of bear behavior to locate
201 traps (in the GIS) where bears would most likely intercept them, were the traps actually set on the
202 ground. This included locations along streams, ravines and similar topographical features that
203 can attract or funnel moving bears.

204 We simulated the targeted designs using two methods, each with effort (trap-nights) comparable
205 to or less than the grid configurations (Table 1). First, traps were systematically spaced in the

206 GIS, with 17 and 19 km spacing. Second, trap locations were identified in the field, by expert
207 opinion. We located these places by ground and plane reconnaissance, based on the
208 characteristics of shallow water or narrow reaches, since these attributes facilitate a bears' ability
209 to catch fish. Trap coordinates were input into the GIS. The traps placed by expert opinion had
210 two configurations that varied by effort.

211 Previous studies suggested that moving traps between captures sessions increases capture
212 probabilities and the number of individuals captured (*Boulanger et al., 2002; Boulanger et al.,*
213 *2004; Boulanger et al., 2006*). This should reduce bias and error in abundance estimates. We
214 tested this advice for brown bears using grid and targeted sampling designs, with traps placed by
215 expert opinion. For grids, we began by simulating 5 different sets of trap locations within each
216 cell. Trap locations were identified with aerial photography of the study area, and the coordinates
217 input into a GIS. We examined 30 scenarios of stationary traps (for each cell size). For five of
218 these scenarios, we held each of the trap sets (sets 1–5) constant across all capture sessions. For
219 the remaining 25 scenarios, we randomly picked a trap in each cell, and held this set constant
220 across all capture sessions (Table 1).

221 When traps were moved between capture sessions, a different trap set (1 of the 5) was used once
222 for each capture session. For example, trap set 3 in capture session 1, then trap set 4 in session 2,
223 etc. We randomly selected 30 of the 120 possible permutations of moved traps within each cell
224 (separately for grids of 49, 81, and 121 km²; Table 1).

225 For targeted scenarios, we iteratively picked every 5th trap from the set of expertly located traps,
226 to ensure a different trap was used each session (140 traps/session). A second configuration of

227 targeted sampling halved this number of traps (70 traps/session). Permutations of stationary and
228 moved traps followed the same procedure outlined above (Table 1).

229 Lastly, we generated a hybrid technique. This design had traps expertly placed along streams, and
230 traps in a grid formation at 9 km spacing, located ≥ 15 km from anadromous streams.

231 **Abundance estimation and evaluation**

232 For each sampling configuration, we recorded a capture when a bear's GPS location occurred
233 ≤ 500 m of a trap. All abundance estimates were then calculated with closed capture models in
234 the program MARK (version 6.2; *White & Burnham, 1999*). We fit 8 models under the "full
235 closed captures with heterogeneity" data type. The first model was M_o , which assumed no
236 variation in capture probability associated with individuals or occasions (only one capture
237 probability, p). Model M_t assumed variation in capture probability between sampling sessions,
238 but not among individuals within a session. Model M_h (heterogeneity) permits different capture
239 probabilities for individuals, which remains the same over all sampling occasions regardless of
240 the capture history (*Karanth et al., 2002*). The fourth model, M_b , allows bears to demonstrate
241 behavioral responses (*e.g.* trap happy or shyness), an effect which can exist in simulations
242 (*White, 2008*). The remaining models allowed for combinations of the previous models (M_{th} , M_{tb} ,
243 M_{bh} , M_{tbh}).

244 We used the program MARK to estimate abundance and the related metrics, based on the models
245 receiving the most parsimonious fit. We used second-order Akaike's Information Criterion
246 (AIC_c) for model selection and treated models with $\Delta AIC_c \leq 2$ as competitive (*Anderson &*

247 Burnham, 2002; Burnham & Anderson, 2002). We model averaged competitive models based on
248 model weights.

249 We evaluated abundance estimates for each grid and targeted sampling design against 7 criteria.
250 First, we calculated average bias (how close the population estimate was to the true abundance
251 value) as:

$$252 \text{Bias}(\hat{N}) = \frac{1}{n} \sum_{i=1}^n (\hat{N}_i - N)$$

253 with \hat{N} representing the abundance estimate, N the true abundance, and n the number of
254 simulations (30). We reported this as a relative score, by dividing bias by true abundance ($N =$
255 42). Next, we examined precision, the degree to which an individual estimate is repeatable or
256 reproducible. We reported coefficient of variation (CV) as a proportional measure of error in the
257 abundance estimates

$$258 \text{CV}(\hat{N}) = 100 * \frac{SD(\hat{N})}{\hat{N}}$$

259 Accuracy is a combination of these metrics (Williams et al., 2002), calculated as:

$$260 \text{RMSE}(\hat{N}) = \sqrt{\frac{1}{n} \sum_{i=1}^n (\hat{N}_i - N)^2}$$

261 $\text{RMSE}(\hat{N})$ was reported relatively, by dividing by true abundance ($N = 42$). We also reported
262 encounter rates, capture probabilities, and recapture probabilities. Encounter rates described the

263 number of GPS fixes considered captures, divided by the total number of GPS fixes (for each
264 bear). Capture probabilities were the number of bears caught divided by the total number of
265 known bears. Recapture probabilities were calculated as the number of bears caught more than
266 once, divided by the total number of bears captured. We used 2-sample *t*-tests to compare the
267 number of bears captured and recaptured between stationary and moved traps for each scenario
268 (Zar, 1999). If Levene's test for equality of variances indicated unequal variances, we used *t*-tests
269 where equal variances were not assumed (SPSS, 2010).

270 We also calculated the amount of effort (trap-nights) required to acquire population estimates as a
271 surrogate for cost. This value was the number of traps multiplied by the number of days sampled.

272 Lastly, we used program TRENDS to determine the number of survey years required to detect a
273 given population change or trend (Gerrodette, 1993). Parameters were $\alpha = 0.05$, $1-\beta$ (power) =
274 0.8 , $CV(\hat{N}) \propto \sqrt{\hat{N}}$, with a linear change over time. This exercise assisted with interpreting
275 the influence of $CV(\hat{N})$ on the effectiveness of each scenario for monitoring abundance
276 changes.

277 **RESULTS**

278 **Sampling Periods**

279 We analyzed data from 42 female brown bears to evaluate the grid and targeted sampling designs.
280 We based the grid simulations during the 1 Jun–20 Jul period, since the greatest number brown
281 bears encountered traps in spring. There was an average of 57.0 GPS fixes per bear (SD 11.0)
282 during this time. The targeted scenarios occurred between 10 July through 28 August, when

283 brown bears had most location fixes <500 m of anadromous streams. On average, there were 58.0
284 GPS fixes per bear (SD 20.1) during this sampling period.

285 **Availability for Capture**

286 For grid-based and targeted sampling to produce reliable population estimates, all individuals in
287 the population must have traps available to capture them. To accomplish this with grids,
288 practitioners recommend that cell area match the average home range size of the target species
289 (*Boulanger et al., 2004; Boulanger et al. 2006; Sawaya et al., 2012*). Therefore, we calculated
290 home range sizes for the brown bears we sampled. The mean value was 149.7 km² (SD 149.8
291 km²). When considering home range sizes of females with cubs, the mean home range size was
292 141.3 km² (SD 145.8 km²). A 12 x 12 km cell approximates either area (Fig. 2).

293 Sixty-seven percent of the bears had home range sizes below this value. A cell size of 25 km²
294 would miss <5% of bears yet the effort involved in employing such a grid is logistically
295 untenable (30,050 trap-nights) and would be exorbitantly costly for a study site this large. We
296 evaluated grids with edge lengths of 7, 9 and 11 km, and the following proportions of bears had
297 home range sizes below each of these areas, respectively: 26%, 49% and 63%.

298 However, traps (especially when expertly placed) may occur within the animals' home range,
299 even if it is smaller than the cell size employed. Therefore, for each grid scenario (expertly
300 placed traps) we determined if each bear had a trap within its home range. The average number
301 of bears without traps in their home range for stationary traps was 4.4 (SD 1.9; 49 km²), 9.5 (SD
302 3.2; 81 km²), and 14.8 (SD 2.1; 121 km²). Moving traps between capture sessions reduced these

303 values, whereby the following numbers of bears never had a trap within its home range 1 (49
304 km²), 1 (81 km²), and 3 (121 km²).

305 For targeted sampling, the sampling frame was the area within 500 m of an anadromous stream.
306 All bears were located within 500 m of anadromous streams during the sampling session, except
307 for 1997, when 2 bears were unavailable (although these bears were ≤ 500 m of streams after the
308 sampling session; Table 2).

309 Because one to three bears were always unavailable for capture, by definition, grid-based and
310 targeted sampling generated population indices, not estimates (hereafter termed indices). As
311 indicated, moving traps attenuates the problem of ensuring that all bears have equal opportunity
312 of encountering traps, but did not fix it.

313 **Evaluation of Sampling Configurations**

314 For each sampling configuration, we evaluated abundance indices, encounter rates, capture
315 probabilities, recapture probabilities, and the effort required to acquire them. For grids, the
316 configurations with traps in cell centers or randomly placed produced the lowest capture
317 probabilities, and generated abundance indices with high bias and error. Targeted sampling with
318 traps systematically placed also generated inaccurate abundance indices, and the hybrid
319 configuration provided results similar to targeted sampling alone. Therefore, we did not present
320 or consider these sampling designs further.

321 We focused on configurations with traps expertly placed in each cell (Table 3). Within each
322 configuration, sampling with traps moved between capture sessions always provided more
323 accurate population indices than sampling with stationary traps, mainly because moving traps
324 halved bias. Moving traps always increased precision for targeted sampling, but inconsistently for
325 grids (Table 3).

326 Sampling with traps moved between capture sessions using 49 km² cells and targeted sampling
327 generated the most accurate population indices (Table 3). The 49 km² grid had least bias (-
328 10.5%) and low precision (CV 21.2%), while targeted sampling had more bias (-17.3%) and most
329 precision (CV 12.3%). Their accuracy was nearly equivalent (RMSE = 21.7% and 20.0%
330 respectively; Table 3).

331 Grid-based sampling with moved traps in 81 km² cells and with stationary traps in 49 km² cells
332 also generated similar accuracy (RMSE = 26.5% and 25.6%). The 81 km² configuration had less
333 bias (-13.0), and more error (CV 26.6%), while stationary traps in the 49 km² grid had greater
334 bias (-21.5) and less error (CV 17.8%). Sampling in the 121 km² cells or with half the amount of
335 targeted traps (stationary) generated the most inaccurate indices, due to combinations of high bias
336 and imprecision (Table 3).

337 Usually, the techniques used to estimate or index abundance should be robust enough to identify
338 a specified level of change, be it the time necessary to quantify a given population trend, or the
339 time required to measure a set difference between individual surveys. For example, on the Kenai

340 Peninsula, this brown bear population has a growth rate (λ) of 1.04 (S. Farley, unpublished data).
341 At best, it would take ≥ 16 years to detect this trend with grid-based sampling (49 km² grids with
342 stationary traps). The targeted configuration required 12 years (moved traps; Table 4). A
343 doubling of population size is detectable in 19 or 28 years using a grid of 49 km² with traps
344 stationary or moved, respectively. Targeted sampling required 10 years (moved traps). Were a
345 population to halve in size, the same grid scenarios would require 6 and 7 years to detect it, while
346 targeted sampling would take 4 years (Table 4).

347 **Encounter rates, capture probabilities, recapture probabilities and effort**

348 Encounter rates within each grid and targeted configuration remained identical between traps
349 stationary or moved (moving traps reduced variability). Encounter rates for the targeted scenario
350 (moved traps) was 4 times greater than the best grid scenario (49 km²; Table 5).

351 Within each configuration, moving traps always resulted in higher capture probabilities than
352 stationary traps. The increases were between 10 and 33% (Table 6). Targeted sampling generated
353 the highest capture probabilities. With moved traps, capture probabilities were 11% higher than
354 sampling within the 49 km² grid ($t = -5.1$, $df = 52.2$, $p\text{-value} < 0.001$).

355 Within a given configuration, moving traps always reduced recapture probability. The result was
356 significant for every configuration except when sampling within 49 km² grids (Table 7). The
357 recapture probabilities declined with increasing cell size (49 km² and 81 km² grids), or with

358 fewer targeted traps. For grids, recapture probabilities were greater for 121 km² cells with
359 stationary traps, because the scenario caught fewer bears more often (Table 7). We found that
360 targeted sampling with moved traps had higher recapture probabilities than sampling in 49 km²
361 grids ($t = -13.2$, $df = 58$, $p\text{-value} < 0.001$).

362 Lastly, effort (measured by trap-nights) was highest for grid sampling with 49 and 81 km² cells,
363 as these scenarios expended 16,100 and 9,750 trap-nights each. Effort for the targeted
364 configuration was 57% less than the 49 km² grids and 28% less than 81 km² grids (7,000 trap-
365 nights; Table 1).

366 **DISCUSSION**

367 Establishing defensible and economical sampling methods to obtain species abundances will
368 inform conservation measures and management actions for many species inhabiting large, remote
369 or complicated landscapes. Therefore, we used a CMR framework and evaluated sampling
370 designs which varied by configuration, effort (trap amount) and complexity (stationary or
371 moved). The goal was to identify informative and affordable sampling designs that biologists
372 could use for estimating or indexing abundance.

373 For grid-based sampling, it is often recommended that cell size corresponds to the average area of
374 an animal's home range, or smaller, to reduce capture heterogeneity (*Boulanger et al., 2004*;
375 *Boulanger et al., 2006*; *Sawaya et al., 2012*). However, animal home ranges usually have much
376 variability, which can change within and across seasons based on resource pulses and their
377 distribution (*McNab, 1963*; *Boulanger et al., 2006*, *Nielsen et al., 2010*). Therefore, a value

378 describing the average home range size may not be biologically meaningful, making it risky to
379 justify grid resolution on this metric. In our case, cell sizes of 49, 81 and 121 km² seemed
380 appropriate since female brown bears had home range sizes averaging 149.6 km². Yet these cell
381 sizes were still too large for grid sampling to provide population estimates, since some bears were
382 not available for capture.

383 When grid configurations are used, justification for the cell size should not rely on the average
384 home range size of the target species. Instead, justification falls on making cell size as small as
385 project costs allow. However, to make studies affordable, the temptation is for fewer traps to be
386 employed, and therefore, increased cell size. Yet we found that as the grid cells became larger,
387 less numbers of traps caught fewer bears, which lowered encounter rates, capture and recapture
388 probabilities (Tables 5, 6 & 7). This produces results with more bias and imprecision (Table 3).
389 Given this information, how does one know when cell sizes are too large?

390 Unless preliminary work provides information for understanding a species use of the landscape,
391 then the cell size chosen will be a speculation. As a result, the abundance estimate generated may
392 indicate an estimate or an index, or be completely uninformative.

393 Previously, many projects that estimated brown bear abundance operated in places spanning
394 ~2,000 - 8,000 km² (e.g. *Poole et al., 2001; Boulanger et al., 2002; Mowat et al., 2005;*
395 *Boulanger et al., 2006, Kendall et al., 2008*). Our site spanned 16,000 km². For areas of this
396 size, small grids grow prohibitively expensive to use. In our case, cell size should be <49 km²,
397 requiring > 322 traps and >16,100 trap-nights (>0.02 traps/km²). Checking these traps in remote
398 locations usually requires the use of helicopters, which often exceed \$700.00 per flight hour.

399 Project costs can easily approach \$1,000,000.00 in such large areas, when sampling in grids at or
400 below this resolution. In any event, grid sampling places many traps in low density, to sample
401 low densities of animals across an expansive area. It seems costly and inefficient.

402 For the targeted design, species biology informed the sampling frame, as anadromous streams
403 attracted bears from the wider landscape. The technique was more efficient, by operating 140
404 traps in a 3,500 km² area (0.04 traps/ km²). It sampled higher densities of animals in a smaller
405 area with less traps, generating the highest capture and recapture probabilities (Tables 6 & 7). Its
406 accuracy was equivalent to the grid index (49 km²; Table 3).

407 For brown bears in Alaska, the targeted configuration is easier and cheaper to operate in the field
408 for at least three reasons. First, it required half the effort of the 49km² grids. Second, since traps
409 occur along streams, they are more accessible by walking or rafting. Third, the lure (fish) is
410 provided naturally, reducing time, expense and costs for trap set-up, and concerns that the target
411 species may lose interest in the trap over time (*Boulanger et al. 2004a; Boulanger et al. 2008b*).

412 The conventional assumption is that moving traps raises capture probabilities, by increasing the
413 proportion of bears captured, and therefore reducing bias (*Boulanger et al., 2002; Boulanger et*
414 *al., 2004a; Boulanger et al., 2006*). Our simulation confirmed this assumption for grid and
415 targeted sampling, as moving traps always increased capture probabilities. Moving traps between
416 capture sessions raised capture probabilities, because moving traps to new areas increased their
417 availability to more bears that would otherwise not have the opportunity to encounter them.
418 However, moving traps also caused a decline in recapture probabilities. This makes sense, as
419 moving traps takes them from a location where they already sampled bears, and places them

420 someplace new. Then, it becomes more difficult to recapture those same bears already caught, as
421 the trap is more likely to be moved to a spot where they do not occur. The 49 km² grid had most
422 traps, which may explain why the effects of relocating traps was not as marked.

423 For indexing species abundances, the most accurate results occurred with traps moved between
424 capture sessions, and traps placed by expert opinion. Moving traps reduced capture heterogeneity,
425 by increasing the number of animals in the sampling frame with a nonzero probability of
426 encountering a trap (*Williams et al., 2002; Lukacs 2009*). Unfortunately, moving traps did not
427 ensure trap availability to all bears, and therefore did not completely alleviate the sampling bias
428 caused by using too large a cell, or sampling at anadromous streams. All individuals in the
429 population must visit the sampling area to generate valid estimates of abundance. Hence, the final
430 abundances generated from both sampling designs represented population indices. Providing
431 population estimates would require smaller grid cells, or more traps in the targeted design.

432 **Sampling synopsis**

433 The most accurate configurations, targeted and grid-based sampling with 49 km² cells, had
434 tradeoffs in bias, precision and effort (costs). Targeted sampling was more biased and precise
435 while the 49 km² grid was less biased and less precise. Because abundances gained from grid
436 sampling tend to be imprecise, some projects incorporate ancillary information (*i.e.* covariates) to
437 increase precision, or data from captures gained elsewhere (*Boulanger et al., 2008b; Kendall et*
438 *al., 2009; Sawaya et al., 2012*). Many applications to index abundance for bears and other
439 species will not have such ancillary data available, and therefore we did not include covariates in
440 our analyses.

441 Often, management applications center on evaluating trends in abundances over time. Because
442 this exercise requires high precision, most wildlife surveys aim for a $CV \leq 20\%$ (*Boulanger et*
443 *al., 2002; Williams et al., 2002*). Otherwise, it takes unacceptably long to measure population
444 changes and trends in time for managers to act. The most accurate targeted scenario met the
445 criteria, by generating a CV of 12%, while the most accurate 49 km² grid did not.

446 When using the program MARK, the most competitive models for grids (moved traps) typically
447 contained M_o models (80% 49 km², 86% 81 km²), and rarely M_h based models. This outcome is
448 indicative of grid sampling reducing heterogeneity between capture sessions. However, M_o based
449 models are sensitive to violations in the underlying model assumption of homogenous capture
450 probabilities (*Otis et al., 1978*). For the targeted approaches, we anticipated variation in capture
451 probability among individuals, and found that all targeted configurations (moved traps) used M_h
452 based models. The M_h models are robust to violations in underlying model assumptions,
453 providing greater confidence in those abundance estimates (*Burnham & Overton, 1978; Otis et*
454 *al., 1978; Karanth et al., 2002*).

455 Given this synopsis, targeted sampling provides results with accuracy comparable to grid
456 sampling, only more affordably. Hence, targeted sampling opens opportunities for indexing
457 abundances of animal populations for many conservation and management projects, provided that
458 the species are attracted to resource concentrations. Often, these projects are cost limited, large in
459 geographical size, focus on rare and sparsely distributed species, and cover locations with
460 challenging access. The abundance indices gained would contribute toward understanding
461 population changes between periods and measuring the trajectory of populations over time, for
462 many species whose current information is deficient.

463 **Encounter distance and use of lure**

464 The effective distance that a bear would be attracted to a scent or visual lure is unknown. The
465 distance depends on the type of lure used, amount of elapsed time since lure deployment (more
466 time dilutes lure effectiveness), topography, weather (*e.g.* aridity, precipitation), wind speed and
467 direction, bear gender, experience and behavior (*i.e.* waning interest in lure; *Boulanger et al.,*
468 *2004a; Boulanger et al., 2008b; Sawaya et al., 2012*). Potentially, future studies aimed at
469 quantifying this distance could leverage off projects that estimate population sizes of lions
470 (*Panthera leo*) and hyenas (*Crocuta crocuta*) using call playbacks as lure (*Mills et al., 2001;*
471 *Kiffner et al., 2008*).

472 Our simulation considered distances between a bears GPS location and hypothetical trap < 500 m
473 as encounters. The actual distance used is essentially irrelevant for the simulation. What matters
474 is bear density in a given area. Areas with high bear density will get more captures than a place
475 with low density, regardless of the distance between bear and trap. In our example, targeted
476 sampling occurred in a confined area, defined as places within 500 m of anadaramous streams.
477 Since all bears visit this relatively small area – about 88% smaller than the grid area – then traps
478 placed here catch more bears more often. The wider landscape has lower density of bears, so
479 traps placed there catch fewer bears less often. Preliminary work with a 100 m encounter
480 distance generated similar outcomes to those presented here, only with less encounters and
481 captures (G. Harris, unpublished data). Seemingly, by considering larger encounter distances, it
482 would generate more encounters and captures.

483 Because our effort is a simulation, it did not account for baiting traps, a common practice to
484 attract bears when field sampling (*e.g. Woods et al., 1999; Boulanger et al. 2002; Sawaya et al.*
485 *2012*). Were a field study to occur, with traps baited, then we would expect encounter
486 probabilities to increase, for grid and targeted sampling alike. Both sampling designs can have
487 lure associated with them (*Sawaya et al., 2012*). Therefore, in the simulation, since data are
488 handled identically, there is no more attraction for a bear to visit a targeted snare any more so
489 than a grid snare. Additionally, the behavioral responses measured in the modeling can reflect
490 survey configuration (*White, 2008*).

491 As above, what differs is bear density in an area. The targeted sampling frame matched species
492 biology by relying on animals' attraction to resource concentrations (*Karanth et al., 2004*). This
493 outcome enabled targeted sampling to provide accurate abundance indices. The targeted approach
494 is not new, and has been used elsewhere to provide abundance data with informative results, be it
495 rub trees to collect bear hair (*e.g. Mowat et al., 2005; Kendall et al., 2008; Kendall et al., 2009;*
496 *Sawaya et al., 2012*) or to gain photographs of tigers along trails (*Karanth & Nichols, 1998*).

497 **Spatial capture-recapture models**

498 We relied on closed capture models in the program MARK (*White & Burnham, 1999*) to quantify
499 abundances, instead of other approaches such as spatially explicit capture-recapture models
500 (SECR; *Efford et al., 2009; Efford, 2011; Royle et al., 2011*). While the SECR approach can
501 apply to grid sampling, and we applaud the innovation, there are five reasons why we employed
502 MARK. First, MARK is a proven method and appropriate for estimating animal abundances.
503 Second, this project is a simulation, with all bears completely within the study frame, and the
504 population closed (based on the GPS location data). This eliminated any ambiguity over the

505 effective sampling area, which the SECR models rigorously address for the purposes of density
506 estimation. Third, when grid cells exceed home range size – as encountered herein – then not all
507 individuals are available for capture. SECR models do not solve this bias. Fourth, the SECR
508 models rely on information describing where and when a given animal is trapped (session
509 number) to identify each individual animals "activity center". The probability of detection for
510 each trap is modeled as a function of the distance from the activity center to traps in the array. If
511 the method relies on animal movements to estimate home range centers (*Royle et al., 2009*), then
512 SECR requires multiple captures. Yet, over one-third of these bears had only one capture (each,
513 for 49 km² and 81 km² grid cells with moved traps). This renders the SECR technique less
514 effective. Fifth, some SECR models assume that activity centers are uniform and symmetric
515 (*Efford et al., 2009; Efford, 2011; Royle et al., 2011*). Unfortunately, this assumption is untenable
516 for brown bears inhabiting the Kenai Peninsula. Home range sizes varied widely in area (Fig. 2),
517 and spatially, as bears often moved linearly within mountain valleys and through passes, thereby
518 defying the notion of a symmetrical home range (G. Harris and S. Farley, unpublished data).

519 Unfortunately, SECR models are not yet designed for data gained by a targeted approach (J. A.
520 Royle, pers. comm. 2013). If activity centers were built for bears trapped at streams, it would
521 imply that bears only occurred there. This would severely bias the true distribution of bear's
522 activity centers across the landscape. In reality, bear movements follow a general pattern
523 whereby they periodically visit streams as they wander throughout the wider landscape (G. Harris
524 & S. Farley, unpublished data). Therefore, by using MARK to compute abundance indexes, it
525 ensured that each of the scenarios contained similar sampling and quantitative assumptions.

526 **Density estimation**

527 An important part of abundance estimation is defining the sampling area, and determining if that
528 area is open or closed to species movement. For targeted sampling, defining the study area
529 requires knowing the “attraction distance” of the species to the resource concentrations (where
530 sampling occurs). We do not know the attraction distance of brown bears to anadromous streams.
531 However, in our study, all bears spanning the peninsula visited anadromous streams. Because the
532 attraction distance was not exceeded for these bears, a targeted sampling design actually
533 conducted on the Kenai Peninsula could estimate density. Obviously, this is not the case for
534 many other species and locations. For them, additional work will probably be required to
535 determine the attraction distance, which would in turn define the sampling frame. Fortunately,
536 there is precedence for such efforts, as biologists on the African continent estimate abundance of
537 lions and hyenas based on their attraction to vocalization lures. Biologists quantified the
538 attraction distance of these carnivores to the lure, to estimate species density (*Ogutu & Dublin,*
539 *1998*).

540 **CONCLUSIONS**

541 When sampling cryptic animals inhabiting thickly vegetated and expansive areas, with DNA,
542 camera traps or other CMR methodology, it can challenge abilities to produce accurate and
543 affordable abundance indices. Yet targeted sampling met these criteria, by sampling where
544 individuals gathered in smaller areas, at biologically important places and times. It generated
545 encounter rates four times higher than grid sampling, capture probabilities 11% higher, and 60%
546 higher recapture probabilities. This reduced capture heterogeneity (*Williams et al., 2002; Lukacs,*
547 *2009*). By generating a CV of 12%, targeted sampling was precise. Better precision enables
548 measuring changes in abundances quicker, with trends more likely to reflect true changes in the

549 population and not sampling or biological artifacts. Lastly, targeted sampling was more
550 economical, as it used half the effort of the grid.

551 Since our simulation had a known number of bears, it enabled us to evaluate the veracity of the
552 grid and targeted designs. Hence, our simulation provided insight into sampling approaches and
553 assumptions for grid and targeted sampling that would be difficult to provide with field studies.
554 However, conducting field studies to test and verify our findings, or refine methodologies, forms
555 a logical next step. Fortunately, for targeted sampling, some field studies already provide insight.
556 For instance, Saway et al. (2012) found that collecting hair from bear rubs generated higher
557 detection rates and capture probabilities than traps in grids, for all classes of bears. Kendall et al.
558 (2009) also relied on collecting hair on bear rubs and from physical captures to improve capture
559 probabilities, as samples gained from grid traps alone provided inaccurate results.

560 Grids blanket entire study areas under the guise of ensuring equal probability of capture. This
561 approach should work, provided the cells are small enough to encapsulate home ranges of all
562 individuals. This requires home range data, which can be expensive and laborious to procure. If
563 the average home range size is used, or were cell size based on home range data gained
564 elsewhere, or home range sizes changed between surveys, then cell sizes may be too large. Then,
565 users of grid sampling may assume that their techniques meet the sampling assumptions required
566 to estimate population abundance, when in actuality, not all individuals are available for capture.
567 Worryingly, many studies have not confirmed that the cell sizes they employ are appropriate (e.g.
568 *Woods et al., 1999; Boulanger et al., 2004; Mowat et al., 2005; Boulanger et al., 2006;*
569 *Boulanger et al., 2008; Kendall et al., 2008; Sawaya et al., 2012*). Therefore, their results may
570 represent estimates or indices, and if the latter, how the index relates to the estimate is unknown.

571 Criticism of the targeted approach centers on subjective or convenience sampling, largely
572 regarded as poor practice. As with grids, to ensure that subjective sampling does not occur,
573 studies should demonstrate that individuals have a nonzero probability of capture (to produce
574 estimates). Unfortunately, other studies using targeted sampling have not justified if all
575 individuals in the sampling frame have a nonzero probability of capture, so whether these studies
576 meet this assumption also remains unknown (*Karanth et al., 1998; Kendall et al., 2009; Sawaya*
577 *et al., 2012*).

578 We found that grid and targeted sampling of brown bears on the Kenai Peninsula had a few
579 individuals with zero probability of capture, and therefore did not meet this assumption. The
580 extent that serious problems in wildlife management or conservation stem from studies sampling
581 with grids or targeted designs and presenting estimates that could represent indices remains
582 uncertain. However, in keeping with our results, the biases are likely to be negative, thereby
583 erring conservatively. Although, the trends for grids would likely be less informative than the
584 trends reported from targeted designs, because the grid designs were more imprecise, which
585 could mask population changes when they occur.

586 The targeted approach relied on identifying biologically important resource concentrations, and
587 sampling at those sites. For bears, salmon runs may change in timing between periods, so bears
588 could visit them outside the sampling period. Or, some resource concentrations may be unknown,
589 and therefore not sampled. If so, the cost of inadequately covering all resource concentrations is
590 larger bias. However, population indices from the targeted design maintained precision,
591 rendering them useful for evaluating trend (provided traps were moved between sessions).
592 Therefore, the outcome of heterogeneity in animal captures for trend analyses manifests in grid

593 sampling losing utility as trap density declines (via larger grid cells), while trends from targeted
594 sampling remained useful.

595 Biologists must weigh the theoretical robustness of sampling and modeling procedures with the
596 logistical constraints of a given sampling design. Clearly, both grid and targeted sampling have
597 benefits and flaws. Before employing these designs, practitioners should evaluate their sampling
598 assumptions, the methodological drawbacks, and the utility of the results generated. The grid and
599 targeted designs are not appropriate for all species in every situation. Neither approach is a
600 panacea.

601 Targeted sampling could assist with indexing abundance of other species that concentrate at
602 biological resources – be it trails, water holes, mineral licks, or animal latrines (*Karanth et al.,*
603 *2004*). For example, travel routes and trail intersections draw tigers (*Karanth & Nichols, 1998*).
604 The thick lowland forests of the Southwestern Amazon contain sparsely distributed macaws.
605 Macaws gather by the hundreds to take clay from exposed riverbanks (*Diamond, 1999*).
606 Similarly, burned patches in lowland Nepal attract axis deer (*Axis axis*) from forests (*Moe &*
607 *Wege, 1997*), while alpine ibex (*Capra ibex*) and bighorn sheep (*Ovis canadensis*) vacate rugged
608 terrain to frequent natural and anthropogenic sources of salt and minerals (*Schmidt et al., 1978;*
609 *Watts & Schemnitz, 1985; Bassano et al., 2003*). Walruses (*Odobenus rosmarus*) aggregate at
610 terrestrial haul-out sites (*Lydersen et al., 2008*) and elephants congregate at water sources (*Harris*
611 *et al., 2008*).

612 Globally, many species inhabit expansive and inaccessible areas, and have sparse distributions
613 within them. Because these species are difficult to sample, data describing their abundances are
614 often deficient. Many of these animals are of high conservation concern. Biologists require

615 methods to sample these animals effectively and economically, for indexing abundance and
616 reporting trends, to subsequently conserve and manage their populations. In extensive areas
617 where animals concentrate in confined locations, targeted sampling could provide such an
618 approach.

619 **ACKNOWLEDGEMENTS**

620 We thank the Alaska Department of Fish and Game for continuing to support telemetry of brown
621 bears. Pilots J. DeCreft, R. Ernst, and M. Litzen ensured safe captures and data collection. M.
622 Conroy, T. Debruyne, J. Morton and J. Sanderson were generous with time, knowledge and ideas.
623 A. Jacobson, D.H. Johnson and other anonymous reviewers provided helpful comments to
624 strengthen this manuscript. The findings and conclusions in this article are those of the author(s)
625 and do not necessarily represent the views of the U.S. Fish and Wildlife Service. The use of trade,
626 firm, or product names is for descriptive purposes only and does not imply endorsement by the
627 U.S. Government.

628 **REFERENCES**

- 629 Anderson DR, Burnham KP. 2002. Avoiding pitfalls when using information-theoretic methods.
630 The Journal of Wildlife Management 66:912–918.
- 631 Bassano B, von Hardenberg A, Pelletier F, Gobbi G. 2003. A method to weigh free-ranging
632 ungulates without handling. Wildlife Society Bulletin 31:1205–1209.

- 633 Beier LR, Lewis SB, Flynn RW, Pendleton G, Schumacher TV. 2005. A single-catch snare to
634 collect brown bear hair for genetic mark-recapture studies. *Wildlife Society Bulletin* 33: 766-
635 773.
- 636 Boulanger J, White GC, McLellan BN, Woods J, Proctor M, Himmer S. 2002. A meta-analysis of
637 grizzly bear DNA mark-recapture projects in British Columbia, Canada: Invited paper. *Ursus*
638 13: 137-152.
- 639 Boulanger J, Himmer S, Swan C. 2004a. Monitoring of grizzly bear population trends and
640 demography using DNA mark-recapture methods in the Owikeno Lake area of British
641 Columbia. *Canadian Journal of Zoology* 82: 1267-1277.
- 642 Boulanger J, Stenhouse G, Munro R. 2004b. Sources of heterogeneity bias when DNA mark-
643 recapture sampling methods are applied to grizzly bear (*Ursus arctos*) populations. *Journal of*
644 *Mammalogy* 85: 618-624.
- 645 Boulanger J, Proctor M, Himmer S, Stenhouse G, Paetkau D, Cranston J. 2006. An empirical test
646 of DNA mark-recapture sampling strategies for grizzly bears. *Ursus* 17: 149-158.
- 647 Boulanger J, Kendall KC, Stetz JB, Roon DA, Waits LP, Paetkau D. 2008a. Multiple data sources
648 improve DNA-based mark-recapture population estimates of grizzly bears. *Ecological*
649 *Applications* 18: 577-589.
- 650 Boulanger J, White GC, Proctor M, Stenhouse G, Machutchon G, Himmer S. 2008b. Use of
651 Occupancy Models to Estimate the Influence of Previous Live Captures on DNA-Based
652 Detection Probabilities of Grizzly Bears. *The Journal of Wildlife Management* 72: 589-595.
- 653 Burnham KP, Overton WS. 1978. Estimation of the size of a closed population when capture
654 probabilities vary among animals. *Biometrika* 65: 625-633.

- 655 Burnham KP, Anderson DR. 2002. Model selection and multmodel inference: a practical
656 information-theoretic approach. New York: Springer-Verlag.
- 657 Diamond JM. 1999. Evolutionary biology: Dirty eating for healthy living. *Nature* 400: 120-121.
- 658 Efford MG, Dawson DK, Borchers DL. 2009. Population density estimated from location of
659 individuals on a passive detector array. *Ecology* 90:2676-2682.
- 660 Efford MG. 2011. Estimation of population density by spatially explicit capture-recapture
661 analysis of data from area searches. *Ecology* 92: 2202-2207.
- 662 Fuller TK. 1995. An international review of large carnivore conservation status. In: Bissonette
663 JA, Krausman PR, eds. Integrating people and wildlife for a sustainable future. Bethesda: The
664 Wildlife Society. 410-412.
- 665 Gerrodette T. 1993. Trends: software for a power analysis of linear regression. *Wildlife Society*
666 *Bulletin* 21:515–516.
- 667 Harris GM, Russell GJ, van Aarde RJ, Pimm SL. 2008. Rules of habitat use by elephants
668 *Loxodonta africana* in southern Africa: insights for regional management. *Oryx* 42: 66-75.
- 669 Harris RB, Winnie Jr J, Amish SJ, Beja-Pereira A, Godinho R, Costa V, Luikart G. 2010. Argali
670 abundance in the Afgan pamir using capture-recapture modeling from fecal DNA. *Journal of*
671 *Wildlife Management* 74: 668-677.
- 672 Hilderbrand GV, Schwartz CC, Robbins CT, Jacoby ME, Hanley TA, Arthur SM, Servheen C.
673 1999. The importance of meat, particularly salmon, to body size, population productivity, and
674 conservation of North American brown bears. *Canadian Journal of Zoology* 77: 132-138.

- 675 Hooge PN, Eichenlaub B. 2000. Animal movement extension to Arcview. ver. 2.0. Anchorage:
676 Alaska Science Center - Biological Science Office, U.S. Geological Survey.
- 677 Karanth KU, Nichols JD. 1998. Estimation of tiger densities in India using photographic captures
678 and recaptures. *Ecology* 79: 2852-2862.
- 679 Karanth KU, NS Kumar, Nichols JD. 2002. Field Surveys: Estimating absolute densities of tigers
680 using capture-recapture sampling. In: Karanth KU, Nichols JD, eds. *Monitoring tigers and
681 their prey: A manual for researchers, managers and conservationists in tropical Asia.*
682 Bangalore: Centre for Wildlife Studies. 139-152.
- 683 Karanth KU, Nichols JD, Kumar NS. 2004. Photographic sampling of elusive mammals in
684 tropical forests. In: Thompson WT, ed. *Sampling Rare or Elusive Species: Concepts, designs,
685 and techniques for estimating population parameters.* Washington D.C.: Island Press. 229-
686 247.
- 687 Kendall, KC, Stetz JB, Roon DA, Waits LP, Boulanger JB, Paetkau, D. 2008. Grizzly bear
688 density in Glacier National Park, Montana. *The Journal of Wildlife Management* 72: 1693-
689 1705.
- 690 Kendall KC, Stetz JB, Boulanger J, Macleod AC, Paetkau D, White GC. 2009. Demography and
691 genetic structure of a recovering grizzly bear population. *The Journal of Wildlife
692 Management* 73: 3-16.
- 693 Kindberg J, Swenson JE, Ericsson G, Bellemain E, Miquel C, Taberlet P. 2011. Estimating
694 population size and trends of the Swedish brown bear *Ursus arctos* population. *Wildlife
695 Biology* 17: 114-123.

- 696 Kiffner C, Waltert M, Meyer B, Mühlenberg M. 2008. Response of lions (*Panthera leo*
697 LINNAEUS 1758) and spotted hyaenas (*Crocuta crocuta* ERXLEBEN 1777) to sound
698 playbacks. African Journal of Ecology 46: 223-226.
- 699 Lukacs P. 2009. Closed population capture-recapture models. In Cooch E, White G. eds. Program
700 MARK: a gentle introduction. Available: <http://www.phidot.org/software/mark/docs/book/>.
701 July 2009. pp. 14-1–14-26.
- 702 Lydersen C, Aars J, Kovacs KM. 2008. Estimating the number of walruses in Svalbard from
703 aerial surveys and behavioural data from satellite telemetry. Arctic 61: 119-128.
- 704 MacArthur RH. 1972. Geographical Ecology: Patterns in the distribution of species. Princeton:
705 Princeton University Press.
- 706 McNab BK. 1963. Bioenergetics and the determination of home range size. The American
707 Naturalist 97:133-140.
- 708 Miller SD, White GC, Sellers RA, Reynolds HV, Schoen JW, Titus K, Barnes VG Jr, Smith RB,
709 Nelson RR, Ballard WB, Schwartz CC. 1997. Brown and black bear density estimation in
710 Alaska using radiotelemetry and replicated mark-resight techniques. Wildlife Monographs
711 133.
- 712 Mills MGL, Juritz JM, Zucchini W. 2001. Estimating the size of spotted hyaena (*Crocuta*
713 *crocuta*) populations through playback recordings allowing for non-response. Animal
714 Conservation, 4(4), 335-343.
- 715 Moe SR, Wegge P. 1997. The effects of cutting and burning on grass quality and axis deer .Axis
716 axis. use of grassland in lowland Nepal. Journal of Tropical Ecology 13: 279-292.

- 717 Mowat G, Heard DC, Seip DR, Poole KG, Stenhouse G, Paetkau DW. 2005. Grizzly *Ursus arctos*
718 and black bear *U. americanus* densities in the interior mountains of North America. *Wildlife*
719 *Biology* 11: 31-48
- 720 Nichols JD, Karanth KU. 2002. Statistical concepts: Estimating absolute densities of tigers using
721 capture-recapture sampling. In Karanth KU, Nichols JD, eds. *Monitoring tigers and their*
722 *prey: A manual for researchers, managers and conservationists in tropical Asia*. Bangalore:
723 Centre for Wildlife Studies. 121-137.
- 724 Nielsen SE, McDermid G, Stenhouse GB, Boyce MS. 2010. Dynamic wildlife habitat models:
725 seasonal foods and mortality risk predict occupancy-abundance and habitat selection in
726 grizzly bears. *Biological Conservation* 143: 1623-1634.
- 727 Ogutu JO, Dublin HT. 1998. The response of lions and spotted hyaenas to sound playbacks as a
728 technique for estimating population size. *African Journal of Ecology* 36: 83–95. doi:
729 10.1046/j.1365-2028.1998.113-89113.x
- 730 Otis DL, Burnham KP, White GC, Anderson DR. 1978. Statistical inference from capture data on
731 closed animal populations. *Wildlife monographs* 62: 3-135.
- 732 Poole KG, Mowat G, Fear DA. 2001. DNA-based population estimate for grizzly bears *Ursus*
733 *arctos* in northeastern British Columbia, Canada. *Wildlife Biology* 7:105-115.
- 734 Powell RA. 2000. Animal home ranges and territories and home range estimators. In Boitaini L,
735 Fuller TK, eds. *Research techniques in animal ecology: controversies and consequences*. New
736 York: Columbia University Press. 65-110.

- 737 Royle JA, Magoun AJ, Gardner B, Valkenburg P, Lowell RE. 2011. Density estimation in a
738 wolverine population using spatial capture–recapture models. *The Journal of Wildlife*
739 *Management* 75: 604-611.
- 740 Royle JA, Karanth KU, Gopaldaswamy AM, Kumar NS. 2009. Bayesian inference in camera
741 trapping studies for a class of spatial capture-recapture models. *Ecology* 90: 3233-3244.
- 742 Sawaya MA, Stetz JB, Clevenger AP, Gibeau ML, Kalinowski ST. 2012.. Estimating grizzly and
743 black bear population abundance and trend in Banff National Park using noninvasive genetic
744 sampling. *PloS one* 7 e34777.
- 745 Schmidt RL, Rutherford WH, Bodenham FM. 1978. Colorado bighorn sheep-trapping
746 techniques. *Wildlife Society Bulletin* 6: 159-163.
- 747 Shackleton DM (Ed.). 1997. Wild sheep and goats and their relatives: status survey and
748 conservation action plan for *Caprinae* (Vol. 33). IUCN.
- 749 SPSS.2010. IBM® SPSS® statistics 19.0. SPSS Inc., Armonk, New York, USA.
- 750 Watts TJ, Schemnitz SD. 1985. Mineral lick use and movement in a remnant desert bighorn sheep
751 population. *The Journal of wildlife management* 49: 994-996.
- 752 Weber W, Rabinowitz A. 1996. A global perspective on large carnivore conservation.
753 *Conservation Biology* 10: 1046-1054.
- 754 White GC. 2008. Closed population estimation models and their extensions in Program MARK.
755 *Environmental and Ecological Statistics* 15: 89-99.
- 756 White GC, Burnham KP. 1999. Program MARK: Survival estimation from populations of
757 marked animals. *Bird Study* 46 Supplement: 120-138.

- 758 Williams BK, Nichols JD, Conroy M. 2002. Analysis and management of animal populations.
759 San Diego: Academic Press.
- 760 Woods JG, Paetkau D, Lewis D, McLellan BN, Proctor M, Strobeck C. 1999. Genetic tagging of
761 free-ranging black and brown bears. *Wildlife Society Bulletin* 27: 616-627.
- 762 Zar JH.1999. Biostatistical analysis. Second edition. Upper Saddle River: Prentice Hall.

Table 1 (on next page)

Sampling configurations.

Characteristics of the sampling configurations used to simulate capture-mark-recapture of brown bears on the Kenai Peninsula, south-central Alaska, USA. Attributes included the timing of the simulation (period), position of traps (placement), whether traps were stationary or moved between capture sessions, cell area (km²) or trap spacing apart (km), the number of traps in each of 5 capture sessions, and effort (trap-nights).

Table 1

Sampling Configuration	Period	Placement	Stationary (S) or Moved (M)	Cell Area or Spacing	No. Traps per Capture Session	Total Effort (Trap-Nights)	
Grid	6/1–7/20	Cell Center	S	49, 81, 121	322, 195, 135	16,100, 9,750, 6,750	
Grid	6/1–7/20	Random	S	49, 81, 121	322, 195, 135	16,100, 9,750, 6,750	
Grid ^a	6/1–7/20	Expert opinion	S	49, 81, 121	322, 195, 135	16,100, 9,750, 6,750	
Grid ^a	6/1–7/20	Expert opinion	M	49, 81, 121	322, 195, 135	16,100, 9,750, 6,750	
Targeted	7/10–8/28	Systematic	S	17, 19	324, 312	16,200, 15,600	
Targeted ^a	7/10–8/28	Expert opinion	S	N/A	140, 70	7,000, 3,500	
		Targeted ^a	7/10–8/28	Expert opinion	M	N/A	140, 70
	7,000, 3,500						

^a These configurations were analyzed and compared (each configuration had 30 simulations). The other configurations produced inaccurate abundances.

Table 2(on next page)

Availability for capture.

The total number of bears on the Kenai Peninsula during the sampling period for the targeted scenario, along with the number of bears present within the sampling frame (< 500m of an anadromous stream) during that period, for each year of sampling.

Table 2

Year	Total No. Bears In Sampling Period	No. Bears Within Sampling Frame
1996	2.0	2.0
1997	14.0	12.0
1998	4.0	4.0
1999	8.0	8.0
2000	6.0	6.0
2003	5.0	5.0
2004	3.0	3.0

Table 3(on next page)

Comparison of sampling configurations.

Results describing the bias, precision and accuracy of abundance estimates generated from the grid and targeted sampling configurations, with trap placement stationary or moved between capture sessions ($N = 42$ for each configuration).

Table 3

Configuration	Placement	n^a	\hat{N}^b	SD	\hat{N}^c	% Bias^d	% RMSE^e CV	\hat{N}^f
Grid 7km	Stationary	30	32.98	5.88	-21.48	25.63	17.82	
	Moved	30	37.59	7.98	-10.51	21.70	21.22	
Grid 9km	Stationary	30	29.96	10.57	-28.67	38.16	35.30	
	Moved	30	36.56	9.72	-12.95	26.51	26.58	
Grid 11km	Stationary	30	19.49	9.76	-53.60	58.42	50.10	
	Moved	30	32.21	17.45	-23.31	47.63	54.16	
Targeted	Stationary	30	28.23	4.22	-32.77	34.28	14.94	
	Moved	30	34.75	4.26	-17.27	20.02	12.26	
Targeted(1/2)	Stationary	30	20.36	5.00	-51.51	52.87	24.56	
	Moved	30	27.42	4.32	-34.71	36.20	15.75	

^a Sample size

^b Mean estimated abundance

^c Standard deviation of mean estimated abundance.

^d Percent relative bias

^e Percent relative root mean squared error (accuracy)

^f Coefficient of variation (precision)

Table 4(on next page)

Time required to measure population change.

Time (years) required to measure a lambda of 1.04, and a doubling or halving of overall population size, from 5 different sampling configurations with traps stationary (S) or moved (M) between capture sessions. Calculations relied on CVs reported in Table 3.

Table 4

Sampling Configuration	T_{λ}^a	T_d^b	T_h^c
Grid 7km (S)	16	19	6
Grid 7km (M)	19	28	7
Grid 9km (S)	34	61	17
Grid 9km (M)	23	43	11
Grid 11km (S)	48	82	36
Grid 11km (M)	54	106	41
Targeted (S)	14	13	4
Targeted (M)	12	10	4
Targeted(1/2) (S)	21	36	9
Targeted(1/2) (M)	15	16	5

^a Number of years required to detect a yearly growth rate (λ) of 1.04.

^b Number of years required to detect a doubling of the overall population size

^c Number of years required to detect a halving of the overall population size

Table 5(on next page)

Encounter rates.

Mean and standard deviation of encounter rates (number of GPS locations considered captures / total number of GPS locations) for all bears in the sampling period, for 5 grid and targeted sampling configurations, with traps stationary or moved between capture sessions ($N= 42$ bears, with 30 simulations for each configuration).

Table 5

Configuration	Stationary		Moved	
	\bar{X}_a	SD	\bar{X}_a	SD
49 km ² grid	0.03	0.01	0.03	0.00
81 km ² grid	0.02	0.01	0.02	0.00
121 km ² grid	0.01	0.01	0.01	0.00
Targeted	0.12	0.03	0.12	0.01
Targeted (1/2)	0.06	0.02	0.06	0.01

^a Encounter rates

Table 6(on next page)

Comparison of capture probabilities.

Mean and standard deviation of capture probabilities for 5 sampling configurations. We used a *t*-test to compare capture probabilities.

Table 6

Configuration	Stationary Traps		Moved Traps		Levene's Test		t-test		
	\hat{p}^a	SD(\hat{p}^a)	\hat{p}^a	$\sigma(p)$	F		p-value	tdf	
49 km ² grid	0.60	0.08	0.66	0.07	2.82	0.099	-2.92	58.0	0.005
81 km ² grid	0.44	0.09	0.52	0.06	2.56	0.115	-3.95	58.0	0.000
121 km ² grid	0.32	0.07	0.38	0.07	0.20	0.656	-3.31	58.0	0.002
Targeted	0.61	0.07	0.73	0.05	2.74	0.103	-8.16	58.0	0.000
Targeted(1/2)	0.43	0.10	0.57	0.05	10.61	0.002	-7.008	44.78	0.000

^a Capture probability

Table 7 (on next page)

Comparison of recapture probabilities.

Mean and standard deviation of recapture probabilities for 5 sampling configurations. We used a *t*-test to compare recapture probabilities.

Table 7

Configuration	Stationary		Moved		Levene's Test			t-test
	\hat{c}^a	\bar{c}_R	SD(\hat{c})		\hat{c}^a	SD(\hat{c})	F	p-value
	t	df	p-value					
49 km ² grid	0.47 0.241	0.13	0.43	0.08	4.05	0.049	1.19	49.17
81 km ² grid	0.42 0.007	0.12	0.34	0.10	0.11	0.747	2.79	58.0
121 km ² grid	0.48 0.000	0.10	0.29	0.10	0.01	0.934	7.36	58.0
Targeted	0.75 0.000	0.08	0.69	0.06	1.48	0.230	3.73	58.0
Targeted(1/2)	0.70 0.000	0.09	0.53	0.08	0.17	0.678	7.52	58.0

^a Recapture probability

Figure 1

Study Location.

We simulated and compared capture-mark-recapture using grid-based and targeted sampling designs for brown bears (*Ursus arctos*) inhabiting the Kenai Peninsula (center, with elevation shaded from low [light gray] to high [black]), south-central Alaska, USA (inset). The grid-based design used cells with an area of 49 km², 81 km² (pictured in gray), and 121 km². The targeted design sampled places where important biological resources concentrated the target species (*i.e.* bear's attraction to anadromous streams; black lines).

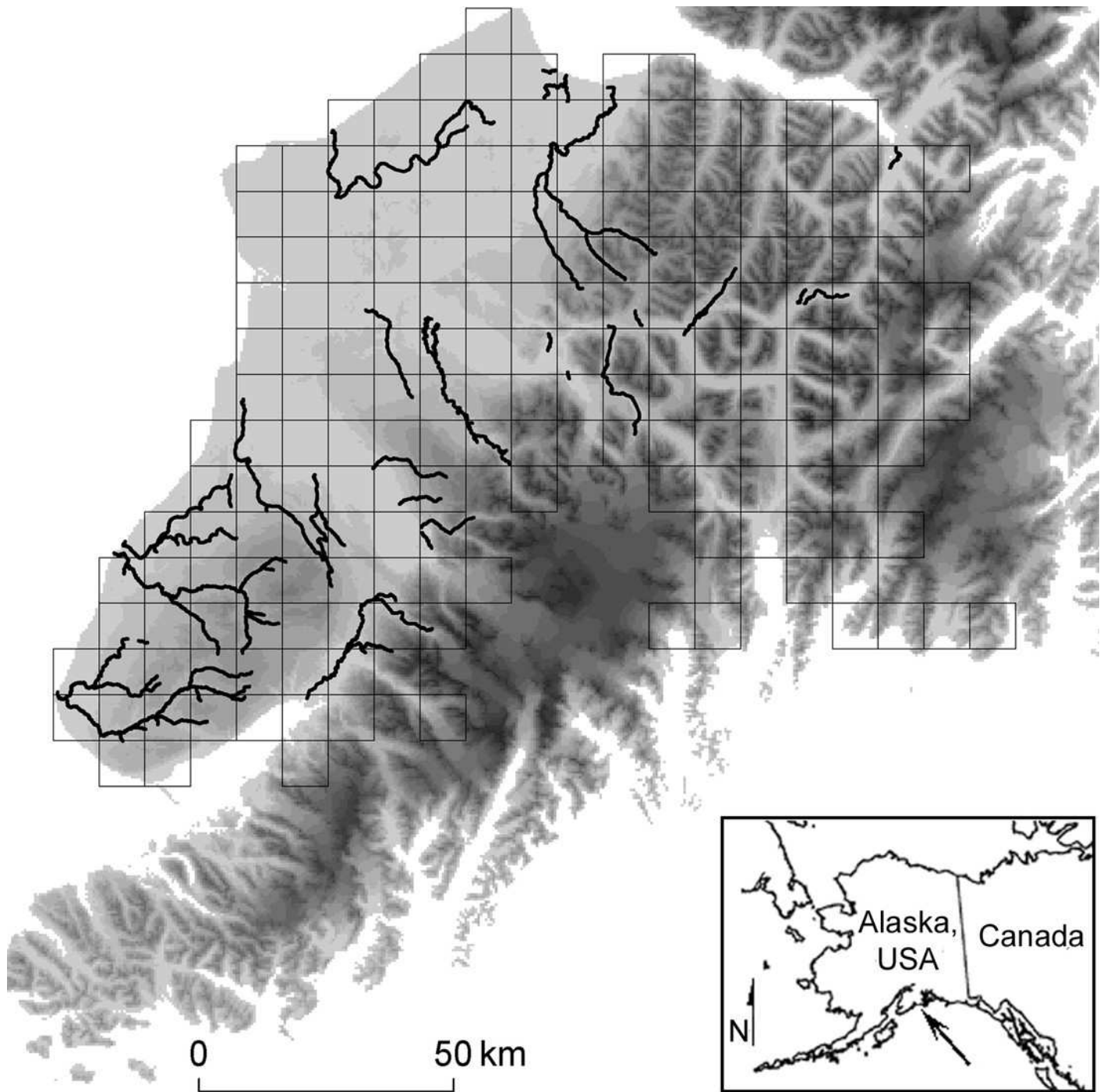


Figure 2

Brown bear home range sizes.

Distribution of home range sizes of brown bears ($n = 42$) during 1 June through 20 July on the Kenai Peninsula, south-central Alaska, USA. Mean home range size (M) was 149.6 km^2 ($\text{SD} = 149.7 \text{ km}^2$). Sixty-seven percent of bears had home ranges smaller than the mean.

