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Combining data from 43 standardized surveys to estimate densities of female American black bears by spatially explicit capture–recapture

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Abstract Spatially explicit capture–recapture (SECR) models are gaining popularity for estimating densities of mammalian carnivores. They use spatially explicit encounter histories of individual animals to estimate a detection probability function described by two parameters: magnitude (g_0), and spatial scale (σ). Carnivores exhibit heterogeneous detection probabilities and home range sizes, and exist at low densities, so g_0 and σ likely vary, but field surveys often yield inadequate data to detect and model the variation. We sampled American black bears (*Ursus americanus*) on 43 study areas in ON, Canada, 2006–2009. We detected 713 animals 1810 times; however, study area-specific samples were sometimes small (6–34 individuals detected 13–93 times). We compared AIC$_c$ values from SECR models fit to the complete data set to evaluate support for various forms of variation in g_0 and σ, and to identify a parsimonious model for aggregating data among study areas to estimate detection parameters more precisely. Models that aggregated data within broad habitat classes and years were supported over those with study area-specific g_0 and σ ($\Delta\text{AIC}_c \geq 30$), and precision was enhanced. Several other forms of variation in g_0 and σ, including individual heterogeneity, were also supported and affected density estimates. If study design cannot eliminate detection heterogeneity, it should ensure that samples are sufficient to detect and model it. Where this is not feasible, combing sparse data across multiple surveys could allow for improved inference.

Keywords Carnivore · Density estimation · Individual heterogeneity · Noninvasive sampling · Ontario · *Ursus americanus*

Introduction

Reliable information about population size is fundamental to the study of ecology and is necessary for effective conservation and management of wildlife populations. Bears and other large and medium-sized mammalian carnivores are notoriously difficult to enumerate because they range widely, occur at low densities, exhibit heterogeneous probabilities of detection and movement rates, and are often secretive or elusive (Garshelis 1992; Karanth 1995; Boulanger et al. 2004; MacKenzie et al. 2005; Kéry et al. 2011; Boitani and Powell 2012). Nevertheless, many carnivore populations are managed intensively because they pose conservation concerns, come into conflict with humans, or are subject to sport harvest. The potential to identify individuals from photographic or genetic detections has enabled researchers to collect sufficient capture–recapture (C–R) data to estimate population size from data collected over days or weeks, whereas multiple years of live-capture data were required previously (Karanth 1995; Woods et al. 1999). Estimates of population density are often preferred over estimates of population size because the former is independent of scale and comparable across

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studies. However, where occupied habitat extends beyond the study area, population size cannot be reliably converted to density because the area sampled is unknown (Dice 1938; White et al. 1982; Efford 2004). This is particularly problematic in studies of wide-ranging species including most mammalian carnivores (White et al. 1982; Garshelis 1992; Boulanger et al. 2002; Foster and Harmsen 2012).

Spatially explicit capture–recapture (SECR) is a recently-developed modeling framework for estimating animal density directly from spatially explicit C–R data collected on geographically open study areas, without estimating the area sampled (Efford 2004; Borchers and Efford 2008; Gardner et al. 2009). Density is estimated as the intensity of a spatial point process where the points are the unobserved central locations of home ranges, or "activity centers" (Efford 2004; Borchers and Efford 2008; Gardner et al. 2009). The models can accommodate different types of traps including live-traps, camera traps, and passive DNA sampling devices (Efford et al. 2009). They assume demographic closure, independence of captures or detections, and that individuals occupy home ranges, the central locations of which are independent and fixed during sampling (Efford 2004; Gardner et al. 2009). Probability of detection is modeled as a decreasing function of the distance between traps and the unobserved activity centers (Efford 2004; Gardner et al. 2009). The simplest model has two parameters: the magnitude (g_0) and spatial scale (σ) of a half-normal spatial detection probability function; g_0 may be thought of as the probability of detection where a trap is placed at an individual's activity center (i.e., at distance zero), and σ and the shape of the detection probability function describe how detection probability declines with increasing distance between home range center locations and traps (Efford 2004). By treating spatially variable exposure to traps explicitly, SECR models account for a major source of individual heterogeneity in the detection process (Garshelis 1992; Boulanger et al. 2004; Efford 2004; Royle et al. 2009). Furthermore, both g_0 and σ may be described as functions of covariates.

Several researchers recently concluded that SECR estimates of carnivore density were preferable to those obtained by dividing estimates of population size by estimates of the area sampled (Gardner et al. 2009; Royle et al. 2009, 2011; Obbard et al. 2010; Sollmann et al. 2011; Gerber et al. 2012; Noss et al. 2012). However, due to both the above-described characteristics of carnivores, and the fact that many factors and constraints influence study design, sample sizes and detection probabilities obtained from surveys of mammalian carnivores are frequently insufficient to detect and model variation in detection probabilities (McKelvey and Pearson 2001; Boulanger et al. 2002; Proctor et al. 2010; Doherty et al. 2012; Foster and Harmsen 2012; Gervasi et al. 2012; Sollmann et al. 2012). Consequently, most SECR studies published to date presented results from only one or a few simple models, often fit to sparse data (Gardner et al. 2009, 2010; Royle et al. 2009, 2011; Kéry et al. 2011; Kalle et al. 2011; O'Brien and Kinnaird 2011; Sollmann et al. 2011; Gray and Prum 2012; Noss et al. 2012). Therefore, the sensitivity of SECR density estimates to variation in the parameters of the detection probability function has not been adequately assessed using empirical data. This is problematic because large carnivores frequently exhibit heterogeneous detection probabilities, including among individuals, beyond what can be explained by variable exposure to traps (Noyce et al. 2001; Boulanger et al. 2004; Ebert et al. 2010; Gardner et al. 2010; Obbard et al. 2010; Sollmann et al. 2011). Furthermore, densities estimated from sparse data may not be sufficiently precise to inform management (Ebert et al. 2010; Foster and Harmsen 2012).

One approach to improving estimator performance where data from individual surveys are inadequate to estimate detection probabilities, but data from multiple surveys are available, is to combine the data and estimate those probabilities from all surveys simultaneously (Boulanger et al. 2002; MacKenzie et al. 2005; White 2005). This provides more power to detect and model variation among individuals and sampling occasions. Rather than assuming common detection probabilities across surveys, support for models representing different levels of aggregation may be compared using model selection criteria. One goal of model selection becomes the identification of a model of variation among surveys that describes the data reasonably well, but allows some aggregation to improve precision (Boulanger et al. 2002; MacKenzie et al. 2005; White 2005; Conn et al. 2006). With more aggregation, precision is enhanced at the expense of possible bias (White 2005).

We sampled female American black bears (*Ursus americanus*) on 43 study areas across ON, Canada (2006–2009), with the aim of providing local density estimates for management purposes. The main objective of the current study was to evaluate support for various forms of variation in the spatial detection probability function, and assess the effect of modeling them on density estimates. In particular, we sought a parsimonious model of variation among study areas that would allow us to estimate local densities more precisely by aggregating the data. We compared AIC_c values among candidate SECR models that allowed g_0 and σ to vary among study areas, individuals, sampling occasions, and in response to initial detection, to parameter-reduced models, including models which combined data across all study areas, or subsets of study areas in similar habitat, to estimate detection parameters. We expect these results to be of interest to those attempting to enumerate large carnivores because reliable estimates are required to inform management, but obtaining sample sizes necessary to detect and model heterogeneity in the detection function and yet estimate density with reasonable precision from individual C–R surveys of large carnivores is challenging, and not always feasible.

Methods

Field sampling

We conducted standardized noninvasive capture–recapture surveys of black bears on 43 study areas in the Boreal and Great Lakes-St. Lawrence (GLSL) forest regions (Rowe 1972) of ON, Canada (Fig. 1) during 2006–2009. Different study areas were sampled each year. During spring and early summer, black bears typically occupy stable home ranges and focus their activities within a smaller home range "core area"; however, they frequently make long-distance excursions from their breeding range when energy rich foods such as berries and nuts become available, typically beginning in mid-July (Rogers 1987; Powell et al. 1997; Schenk et al. 1998; Noyce and Garshelis 2011). We therefore sampled from late May through June (the latest any samples were collected was 06 July) in order to meet the SECR assumptions of demographic closure and static home range center locations (Efford 2004). Most study areas had been established previously for population monitoring by bait-station index lines in habitat representative of the respective management unit (McLaren et al. 2005). On each study area, we snagged bear hair at 20–25 barbed wire hair corrals (Woods et al. 1999), except on three study areas where 15, 17, and 18 corrals were used. Corrals were spaced approximately 2 km apart in curvilinear arrays along secondary roads, 20–200 m from the road itself. We baited corrals with 3 partially-opened tins of sardines in oil suspended from a board nailed 2.5 m high on a tree >2 m from any point along the wire. We collected samples and re-baited corrals one week later, and repeated this for a total of 5 sampling occasions on 36 study areas; bears were sampled on only 4 occasions on 4 study areas, and on six occasions on 3 other study areas. We air dried hair samples in paper envelopes and stored them at room temperature until DNA extraction.

DNA analysis

We did not attempt to extract DNA from samples with fewer than 5 guard hairs with visible roots; >90 % of samples were processed using 10–15 hairs to minimize technical artifacts from low template DNA. When the number of samples exceeded what we could analyze with available resources, we excluded samples collected from adjacent barbs at the same trap on the same occasion. Individuals were identified from their microsatellite genotypes at 10–15 polymorphic loci (Paetkau and Strobeck 1994; Paetkau et al. 1995; Taberlet et al. 1997; Kitahara et al. 2000), and sex was determined from amplification of a region of the Amelogenin gene (Ennis and Gallagher 1994). For more detailed DNA extraction, amplification, and profiling methods and criteria for ascribing samples to individuals see Obbard et al. (2010) and Pelletier et al. (2012).

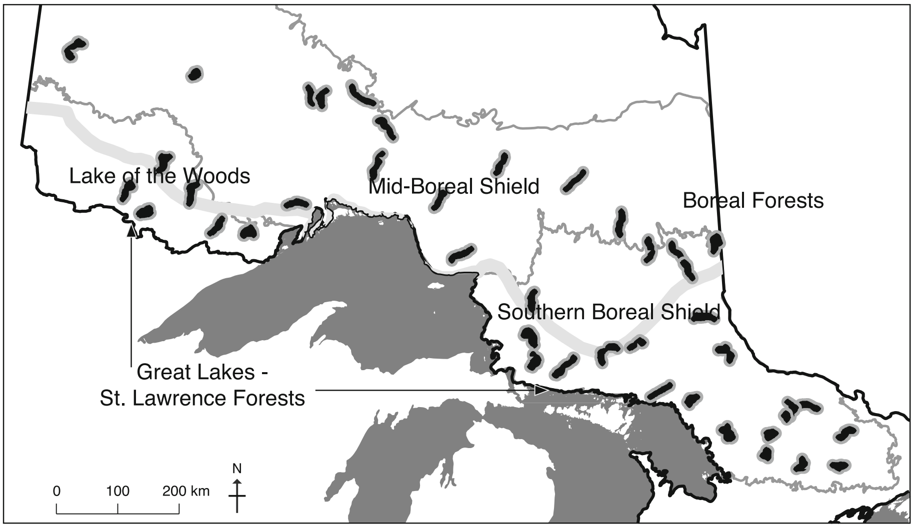

Fig. 1 Map of the greater study area in ON, Canada. The Great Lakes are *shaded dark grey*. Trap locations are marked with *black dots*; at this scale traps arrays appear as *thick black lines* surrounded by *gray shading* which depicts 10 km buffers around all traps within each study area. Rowe's (1972) Forest region boundary between Boreal and Great Lakes-St. Lawrence Forests is depicted as a *20 km-thick light grey line*. *Thinner*, *darker grey lines* show Ecoprovince boundaries between the Mid-Boreal Shield in the north, and each of the Lake of the Woods and Southern Boreal Shield to the south (Marshall et al. 1998)

Data analysis

We excluded males from statistical analyses because we were concerned that our study areas might be too small to estimate densities of male bears reliably as the size of their home ranges could approach or exceed that of our study areas (Alt et al. 1980; Koehler and Pierce 2003; Efford 2011; Marques et al. 2011). We assumed that the height of the barbed wire strand (~50 cm) would exclude cubs and yearlings from the sample (Woods et al. 1999).

We generated study area-specific integration meshes (see Borchers and Efford 2008, Efford et al. 2009) that extended 10 km around all traps on each study area and excluded points that would have fallen in lakes. Mesh points were spaced 0.8–1.0 km apart. We verified that the extent and resolution of our integration meshes were sufficient to avoid bias by fitting SECR models to data from two study areas with >25 recaptures and movement rate estimates near the minimum and maximum across study areas, while varying the extent of the mask and the spacing of mask points. Extents ranged from 5–15 km in increments of 2.5 km; the spacing of points ranged from 0.4–1.2 km in increments of 0.2 km. Density estimates and their coefficients of variation were insensitive to increases in the extent of the mesh beyond 10 km, or with reductions in point spacing below 1.0 km.

We analyzed data from all study areas simultaneously. In cases where study areas were <20 km apart, we verified that no individuals were detected on >1 study area. Study areas were modeled as groups or "sessions" in a multi-session analysis that allowed data to be pooled across study areas to estimate g_0 and σ (Efford et al. 2009). We assumed the total number of individuals was binomially-distributed on each study area. We estimated g_0 and σ by maximizing the conditional likelihood for proximity detectors, and estimated density as a derived parameter using a Horvitz–Thompson-like estimator (see Borchers and Efford 2008; Efford et al. 2009). We used the half-normal form of the detection function, which we suspected would reasonably approximate the above-described home range characteristics of female black bears.

We defined a set of candidate models of variation in g_0 and σ based on previously published information about the probabilities of detection, home ranges, and movements of black bears (Garshelis and Pelton 1980; Rogers 1987; Powell et al. 1997; Noyce et al. 2001; Koehler and Pierce 2003; Mowat et al. 2005; Obbard et al. 2010). We used the small-sample corrected version of Akaike's Information Criterion (AIC_c; Hurvitch and Tsai 1989) to identify the most parsimonious models in the candidate set. We assessed support for general and trap-specific responses to prior detection affecting g_0, (hereafter denoted *b* and *bk*, respectively) and differences in g_0 among individuals (*h*), years, and study areas. For σ, we considered differences among individuals, sampling occasions (*t*), years, study areas, and 4 different patterns of variation among habitat types. Individual heterogeneity was modeled using two-point finite mixture distributions (Pledger 2000; Borchers and Efford 2008). Three of the habitat type covariates used Rowe's (1972) Forest Regions to ascribe study areas to different habitat types; the fourth used Ecoprovince boundaries ("*ECOP*"; Marshall et al. 1998; see Fig. 1). Habitat productivity for black bears is superior in eastern GLSL than Boreal Forests (Rowe 1972; Kolenosky 1990; Obbard and Howe 2008). We hypothesized that σ would be smaller in GLSL than Boreal Forest Regions, and might also vary between eastern and western GLSL Forests, and that bears in the Lake of the Woods and Southern Boreal Shield Ecoprovinces might have lower σ than those in the Mid-Boreal Shield. The simplest habitat covariate (*FR2*) had two levels, and discriminated only between Boreal and GLSL Forests. *FR3* further separated eastern from western GLSL forests. *FR3I* combined eastern and western GLSL forests, but included a separate "intermediate" level for study areas that fell within 10 km of the Forest Region boundary. We fit a total of 76 models. The most constrained models in the candidate set were the null model and models with each form of variation in isolation. The most general model had 173 parameters and allowed for study area-specific g_0 and σ, and study area-specific differences among individuals (equivalent to fitting a model with *h* affecting g_0 and σ to each study area-specific data set). The most general additive model included differences in g_0 among individuals, after initial detection, and among study areas, and differences in σ among sampling occasions, individuals and study areas. Model fitting was prohibitively time-consuming on a stand-alone desktop computer. To reduce the total number of models, we initially emphasized the simplest habitat covariate, and later crossed other habitat covariates with the best-supported models of variation among individuals, years, sampling occasions, and in response to initial detection. We used the facilities of the high performance computing network "SHARCNET" (http://www.sharcnet.ca) to fit many models simultaneously. Integration meshes were generated using program DENSITY (version 4.4.5.1; Efford et al. 2004; Efford 2010); all other analyses were performed in the R programming environment version 2.15 (R Development Core Team 2012) using the "secr" package version 2.4.0 (Efford 2012).

Results

Field sampling and DNA analysis

The number of hair samples collected on each study area ranged from 104 to 860, from which we obtained 38 to 352 genetic detections (including multiple detections of the same individual at the same trap and occasion; Table 1). The number of unique females detected on each study area ranged from 6 to 34, and the total number of detections of females included in spatially explicit encounter histories (i.e., excluding multiple detections of the same individual at the same trap and occasion) ranged from 13 to 93 (Table 1). The mean of maximum distances moved among traps ranged from 881 to 5459 m, and the mean distance between successive detection locations ranged from 352 to 2677 m (Table 1).

Data analysis

Models of detection heterogeneity that minimized AIC$_c$ included a trap-specific response to initial detection and differences among individuals and years affecting g_0, and differences in σ among individuals, years, sampling occasions, and habitat types (Table 2). Model selection uncertainty was limited to whether σ differed among years, and which habitat type covariate best approximated variation in σ among study areas (Table 2). Models with study area specific g_0 and σ were not supported (Table 2). The top-ranked model that excluded *h* in either parameter (ΔAIC$_c = 108$) had the same structure otherwise as the top-ranked model. The most general model, with study area-specific g_0, σ, and effects of *h*, had ΔAIC$_c = 409$. Variance calculation failed when this model was fit, and parameter estimates for some study areas were not identifiable or were at a boundary. The null model ranked last (ΔAIC$_c = 439$).

Densities estimated from the top 8 AIC$_c$-ranked models ($\Sigma w_i = 1.00$) were similar in magnitude (mean $\hat{D}$ across study areas estimated from 1st–8th ranked models, respectively = 11.9, 12.2, 11.2, 11.0, 9.8, 9.4, 12.1, and 11.3), precision (mean CV across study areas = 0.27 from all 4 models that included differences in σ among years, and = 0.26 from models that did not), and the pattern of variation among study areas (Spearman's rank correlation coefficients from pairwise comparisons of $\hat{D}$ ranged from 0.903 to 0.986). Correlations among estimates from different models were strongest, ranging from 0.976 to 0.986, for the top 4 AIC$_c$-ranked models ($\Sigma w_i = 0.94$). $\hat{D}$ from supported models ranged from 3 to 30 females aged >1 year/100 km^2 and was generally higher in more productive habitat, but variable in eastern GLSL forests (Fig. 2).

Densities estimated from high-ranking models were similar because these models all had a similar structure. However, $\hat{D}$ varied when different forms of variation in g_0 and σ were modeled (Table 3). Individual heterogeneity increased $\hat{D}$ and reduced its precision, but the effect size was smaller where other forms of variation were also included in the estimating model (Table 3). Forest region and year effects altered the pattern of variation in $\hat{D}$ among study areas. For example, lower σ in GLSL Forests than in Boreal Forests was associated with higher $\hat{D}$ in the former (Tables 3, 4). Differences in g_0 among years reduced $\hat{D}$ on study areas sampled in all years other than 2006, and differences in σ among years increased $\hat{D}$ in 2006 relative to estimates from models without year effects (Table 3). Models with study area effects yielded density estimates which differed considerably from estimates from supported models in some cases (Table 3), and were relatively imprecise (mean CV across study areas from the highest-ranking model with study area effects on either parameter = 0.39). Effects of initial detection on g_0, and variation in σ among sampling occasions had little effect on $\hat{D}$ here (Table 3).

Parameter estimates from high-ranking models showed that g_0 increased in response to initial detection at the same trap (Table 4). Animals traveled farther to encounter traps in Boreal than GLSL forests; bears on study areas within 10 km of the forest region boundary had intermediate σ (Table 4). Parameter estimates from the highest-ranked models with ECOP and FR3 covariates indicated that σ was lower in the Lake of the Woods Ecoprovince than in the Southern Boreal Shield, and in Western than Eastern GLSL Forests (β SBS = 0.089, SE 0.061, β MBS = 0.335, SE 0.086; β GLSL E = −0.069, SE 0.063, β GLSL W = −0.187, SE 0.078). Bears also traveled farther on successive sampling occasions during the first 5 weeks of sampling (the estimate of σ on occasion 6 was based on data from only 3 study areas and was imprecisely estimated; Table 4). Models with differences in σ among years indicated that bears did not travel as far to encounter traps in 2006 as in other years (Table 4) Year effects indicated and that g_0 was highest in 2008 and lowest in 2006 (Table 3). Year effects were imprecise except in the case of lower g_0 in 2006 (Table 4).

Approximately 13 % of individuals were assigned to the 2nd mixture of individuals with higher g_0 and σ than other individuals (Table 4). Point estimates of g_0 from the top AIC$_c$-ranked model for the first mixture of individuals were 0.29 in 2008 and 0.10 in 2006, but increased to 0.52 and 0.23 respectively after initial detection (Table 4). Estimates of the same parameters for the second mixture of individuals were 0.64 in 2008 and 0.34 in 2006, and 0.82 and 0.56 after initial detection. Point estimates of σ on occasion 5 in 2008 for the first mixture of individuals were 1395 m in GLSL forests, 1876 m in Boreal forests, and 1539 m on study areas within 10 km of the Forest Region boundary; concurrent estimates for the second mixture were 2040, 2743, and 2250 m (Table 3).

Table 1 Summary of field sampling and DNA profiling of black bears in ON, Canada, 2006–2009, ordered by forest region and year of sampling, showing the number of barbed wire hair corrals (traps) set, the number of hair samples collected, the number of reliable individual genotypes obtained, the number of unique females detected, total detections (excluding multiple detections of the same individual at the same trap and occasion), the mean of the maximum distances moved by each individual (MMDM), and the mean distance between successive detection locations, pooled over individuals ($\bar{d}$)

Study area	Years	Forest region	Ecoprovince	Traps	Samples	Genotypes	Females	Detections	MMDM	$\bar{d}$
2	2006	Boreal	MBS	25	461	185	19	38	2149	1138
29	2006	Boreal	MBS	20	370	151	25	38	2887	769
18(1)	2006	Boreal	MBS	25	289	119	9	24	2297	1468
30	2007	Boreal	MBS	20	178	119	8	13	3298	1861
19	2008	Boreal	MBS	25	680	216	18	66	1493	1149
16C(1)	2008	Boreal	MBS	20	633	262	21	67	1357	1357
21A	2008	Boreal	MBS	25	413	142	11	35	2810	1041
28(1)	2008	Boreal	MBS	22	221	87	12	29	2343	916
28(2)	2008	Boreal	SBS	21	280	96	13	35	985	657
22	2009	Boreal	MBS	20	516	280	11	19	3232	743
23	2009	Boreal	MBS	20	293	143	15	31	2990	1495
33	2009	Boreal	MBS	23	495	192	15	43	1625	587
16B	2009	Boreal	MBS	17	329	176	13	46	1999	937
16C(2)	2009	Boreal	MBS	20	448	155	12	27	2187	1640
18(2)	2009	Boreal	MBS	25	366	183	19	43	2124	735
21B	2009	Boreal	MBS	20	530	311	29	93	1056	493
38	2006	Boreal*	SBS	20	235	92	10	20	3128	2677
12B	2006	Boreal*	LW	25	483	231	26	60	4001	1051
12A	2008	Boreal*	LW	25	636	243	22	57	2602	1293
28(3)	2008	Boreal*	SBS	23	383	131	20	50	2648	851
35(2)	2008	Boreal*	SBS	20	514	352	12	58	2647	894
13(2)	2009	Boreal*	MBS	20	457	268	34	84	2625	745
39	2006	GLSL E*	SBS	20	104	47	9	17	1997	880
40	2006	GLSL E	SBS	25	454	173	20	48	2792	1091
42	2006	GLSL E	SBS	20	124	53	15	23	3096	1098
47	2006	GLSL E	SBS	25	337	173	26	75	1723	559
49	2006	GLSL E	SBS	25	238	115	21	34	2984	1030
60	2006	GLSL E	SBS	20	192	94	14	30	2135	686
61	2006	GLSL E	SBS	18	320	146	17	41	3972	1173
52(1)	2006	GLSL E	SBS	20	167	83	12	27	3656	833
52(2)	2006	GLSL E	SBS	20	269	114	14	29	3477	1043
36	2007	GLSL E	SBS	23	227	157	16	50	4072	1372
37	2007	GLSL E	SBS	25	403	316	23	38	2362	1083
41	2007	GLSL E	SBS	22	399	235	21	55	5459	1608
56	2007	GLSL E	SBS	20	278	199	8	35	3192	761
54	2008	GLSL E	SBS	20	118	70	6	14	2539	1096
35(1)	2008	GLSL E	SBS	25	150	113	12	27	1916	877
52(3)	2008	GLSL E	SBS	15	242	161	13	43	1811	798
58	2009	GLSL E	SBS	20	143	38	7	16	2278	979
11B	2006	GLSL W	LW	20	410	199	23	49	4800	885
11A	2007	GLSL W	LW	25	213	151	9	22	1217	568
13(1)	2007	GLSL W	LW	20	543	260	29	84	881	352
9B	2008	GLSL W	LW	25	591	327	24	77	2921	1164

Table 1 continued

Study area	Years	Forest region	Ecoprovince	Traps	Samples	Genotypes	Females	Detections	MMDM	$\bar{d}$
Mean					352	171	17	42	2599	1033
SD					154	79	6.8	20	983	413

Study areas are designated by Wildlife Management Unit; numbers in parentheses appear where bears were sampled on more than one study area within a Unit. Forest regions were Boreal Forests and Great Lakes-St. Lawrence Forests in each of eastern and western ON (GLSL E and GLSL W) based on Rowe (1972). Ecoprovinces follow Marshall et al. (1998)

MBS mid-boreal shield, *SBS* southern-boreal shield, *LW* lake of the woods

* The study area was within 10 km of the Forest region boundary

Table 2 AIC$_c$ model selection criteria among the top 21-ranked models of variation in the spatial detection function for female black bears aged >1 year sampled on 43 study areas in ON, Canada, 2006–2009

Model	Parameters	LL	AIC$_c$	ΔAIC$_c$	w_i
$g_0(bk + h + yr)\sigma(t + h + yr + FR3I)$	19	−4962.1	9963.3	0.0	0.45
$g_0(bk + h + yr)\sigma(t + h + yr + ECOP)$	19	−4962.7	9964.5	1.1	0.25
$g_0(bk + h + yr)\sigma(t + h + FR3I)$	16	−4966.0	9964.9	1.5	0.21
$g_0(bk + h + yr)\sigma(t + h + ECOP)$	16	−4968.1	9969.1	5.7	0.03
$g_0(bk + h + yr)\sigma(t + h + yr + FR2)$	18	−4966.2	9969.3	6.0	0.02
$g_0(bk + h + yr)\sigma(t + h + FR2)$	15	−4969.4	9969.5	6.2	0.02
$g_0(bk + h + yr)\sigma(t + h + yr + FR3)$	19	−4965.6	9970.4	7.1	0.01
$g_0(bk + h + yr)\sigma(t + h + FR3)$	16	−4969.4	9971.5	8.2	0.01
$g_0(bk + h)\sigma(t + h + yr + FR2)$	15	−4976.0	9982.6	19.3	0.00
$g_0(bk + h)\sigma(t + h + FR2)$	12	−4981.9	9988.2	24.9	0.00
$g_0(bk + h + yr)\sigma(t + h + SA)$	56	−4935.7	9993.1	29.8	0.00
$g_0(bk + h)\sigma(t + h + SA)$	53	−4940.6	9995.9	32.5	0.00
$g_0(bk + h)\sigma(t + h)$	11	−4988.2	9998.7	35.4	0.00
$g_0(bk + h + SA)\sigma(t + h + FR2)$	54	−4942.4	10001.7	38.4	0.00
$g_0(bk + h + SA)\sigma(t + h + yr + FR2)$	57	−4941.1	10006.4	43.0	0.00
$g_0(b + h + yr)\sigma(t + h + yr + FR2)$	18	−4989.3	10015.6	52.3	0.00
$g_0(h + yr)\sigma(t + h + yr + FR2)$	17	−4990.6	10016.0	52.7	0.00
$g_0(bk + yr)\sigma(t + h + yr + FR2)$	17	−4992.6	10020.0	56.7	0.00
$g_0(bk + yr)\sigma(t + h + yr + FR2)$	17	−4992.6	10020.0	56.7	0.00
$g_0(bk + h)\sigma(h + FR2)$	7	−5004.6	10023.4	60.1	0.00
$g_0(bk + h + SA)\sigma(t + h + SA)$	95	−4903.3	10026.1	62.8	0.00

ECOP, *FR2*, *FR3*, and *FR3I* are categorical habitat covariates (see "Methods" and Fig. 1 for details)

LL log likelihood, w_i AIC$_c$ weight. In model names, *bk* a response to initial detection at the same trap, *h* individual heterogeneity, *yr* year of sampling, *t* differences among sampling occasions

Discussion

Capture–recapture surveys of mammalian carnivores frequently yield samples that provide insufficient information to select among candidate models or to estimate abundance precisely from models that allow for important forms of variation (Norris and Pollock 1995; Boulanger et al. 2002, 2004; Link 2004; Royle et al. 2009; Ebert et al. 2010; Kéry et al. 2011; Marucco et al. 2011; O'Brien and Kinnaird 2011; Sollmann et al. 2011; Doherty et al. 2012; Foster and Harmsen 2012; Gray and Prum 2012). Small samples are a consequence of both the biological characteristics of carnivores, and the fact that study designs and their ability to provide moderate to large samples are frequently constrained by factors such as habitat fragmentation, small population size, limited knowledge of the population under study, the need to place traps in specific habitats or along known travel corridors to maximize detection probabilities, conflicting research priorities, or limited funding (Boitani and Powell 2012). Sharing information across surveys increases power to detect heterogeneity and improves precision at the possible expense of bias (White 2005; Anderson 2008). Our results demonstrate empirically that by combining sparse data from multiple standardized

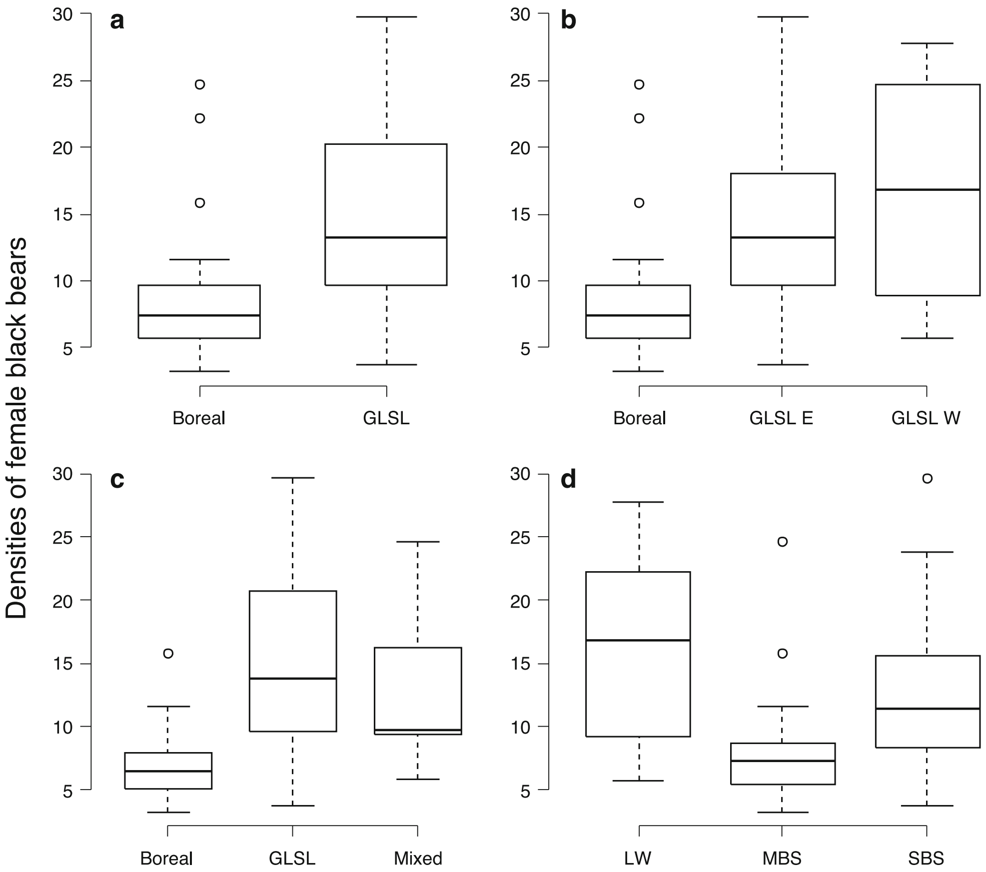

Fig. 2 Densities of female black bears aged >1 year (per 100 km^2) on 43 study areas in ON, Canada, 2006–2009, estimated from the top AIC$_c$-ranked spatially explicit capture–recapture model, within different habitat types (see Fig. 1). Study area-specific estimates were grouped into habitat types four ways (see Fig. 1): (1) Boreal and Great Lakes-St. Lawrence (GLSL) forests (**a**), (2) Boreal forests and GLSL forests in eastern and western ON (**b**), Boreal Forests, GLSL Forests, and study areas within 10 km of the Forest region boundary (**c**), and Southern Boreal Shield, Mid-Boreal Shield, and Lake of the Woods Ecoprovinces (**d**)

surveys, researchers may be able to detect and model forms of variation in SECR model parameters that are likely to be present in C–R data from carnivores, and yet estimate densities with reasonable precision.

Snagging hairs of American black bears on 5 occasions on our curvilinear arrays of 15–25 traps yielded samples that were insufficient to model heterogeneity or estimate density precisely enough to inform management on some study areas. Furthermore, we sometimes obtained few repeat detections of the same individuals at different traps, particularly nonadjacent traps, which may have rendered our estimates of σ prone to sampling error. The use of habitat and year covariates to describe variation in detection among study areas, and model selection using AIC$_c$, allowed us to identify a model that allowed for variation among study areas but also improved the precision of $\hat{D}$ by aggregating data to estimate some of the parameters of the detection function. Of course, there remains the potential for bias introduced by pooling the data across study areas. Different models of variation in detection probabilities among study areas, or more general combinations of the covariates we considered (e.g., including interactions) might have been supported had we considered them.

SECR represents an improvement over boundary strip methods for estimating carnivore density, especially where a conservation concerns exists because the latter are prone to overestimation (Gardner et al. 2009; Obbard et al. 2010; Sollmann et al. 2011; Gerber et al. 2012; Noss et al. 2012). However, considerable variation in $\hat{D}$ estimated from different models fit to the same data in our study demonstrates the potential to obtain biased density estimates by fitting an inappropriate SECR model. In particular, individual heterogeneity poses one of the greatest challenges to researchers attempting to estimate animal abundance from C–R data (Davis et al. 2003; Link 2004; Lukacs and Burnham 2005; Ebert et al. 2010; Marucco et al. 2011). SECR models represent an improvement in this regard because they treat heterogeneity associated with variable exposure to traps explicitly (Efford 2004; Royle et al. 2009). In our study, individual heterogeneity was still unambiguously supported even though we used a spatial detection model and limited the data set to females. Innate

Table 3 Densities (per 100 km^2) of female black bears aged >1 year on eight study areas in ON, Canada, with coefficients of variation in parentheses, estimated from spatially explicit capture–recapture models with different combinations of covariates of variation in the parameters of the spatial detection probability function

Model	Study area							
	Boreal				GLSL			
	2006 2	2007 30	2008 19	2009 21B	2006 49	2007 13(1)	2008 9B	2009 58
$g_0(bk + h + yr)\sigma(t + h + yr + FR3I)$	11.6 (0.25)	3.4 (0.35)	5.7 (0.21)	15.8 (0.21)	20.2 (0.24)	21.5 (0.21)	12.1 (0.20)	5.9 (0.39)
$g_0(bk + h + yr)\sigma(t + h + FR3I)$	10.4 (0.24)	3.6 (0.34)	6.1 (0.21)	14.6 (0.20)	17.4 (0.23)	21.9 (0.20)	12.6 (0.20)	5.3 (0.37)
$g_0(bk + h + yr)\sigma(t + h + SA)$	18.5 (0.37)	14.0 (0.68)	8.3 (0.31)	22.2 (0.27)	29.3 (0.42)	24.6 (0.28)	21.3 (0.29)	5.7 (0.49)
$g_0(h + yr)\sigma(h + yr + FR3I)$	11.1 (0.24)	3.5 (0.34)	5.9 (0.21)	16.7 (0.20)	19.2 (0.23)	21.7 (0.20)	12.3 (0.20)	6.2 (0.38)
$g_0(bk + h)\ \sigma(t + h)$	13.6 (0.27)	4.3 (0.36)	13.2 (0.27)	16.9 (0.21)	14.8 (0.26)	17.0 (0.21)	18.7 (0.25)	3.9 (0.37)
$g_0(h)\sigma(h)$	13.5 (0.24)	4.3 (0.35)	13.3 (0.24)	17.1 (0.19)	15.1 (0.23)	17.1 (0.19)	19.1 (0.22)	4.0 (0.37)
$g_0(bk + yr)\sigma(t + yr + FR3I)$	7.6 (0.22)	2.4 (0.32)	5.1 (0.20)	10.4 (0.17)	10.5 (0.21)	12.3 (0.18)	9.0 (0.19)	3.1 (0.35)
$g_0(SA)\sigma(SA)$	7.7 (0.25)	6.3 (0.51)	4.4 (0.22)	9.9 (0.19)	14.5 (0.32)	10.7 (0.18)	10.0 (0.20)	2.8 (0.43)
$g_0(.)\sigma(t)$	6.2 (0.20)	2.8 (0.31)	6.3 (0.20)	11.9 (0.16)	6.9 (0.19)	11.7 (0.16)	9.0 (0.17)	2.8 (0.33)
$g_0(bk)\sigma(.)$	6.6 (0.20)	3.0 (0.31)	6.6 (0.21)	12.3 (0.16)	7.3 (0.19)	12.2 (0.16)	9.3 (0.18)	3.0 (0.33)
$g_0(.)\sigma(.)$	6.3 (0.20)	2.9 (0.31)	6.4 (0.20)	12.0 (0.16)	7.0 (0.19)	11.8 (0.16)	9.1 (0.17)	2.9 (0.33)

All models used the half-normal form of the function. In model names "." indicates that the parameter was held constant

bk a response to initial detection at the same trap, *h* individual heterogeneity, *yr* year of sampling, *t* differences among sampling occasions, *FR3I* 3-level habitat type covariate, *SA* differences among study areas

differences in cautious behavior (DeBruyn 1999; Noyce et al. 2001) or differences among bears of different ages or social classes (Miller et al. 1997; Woods et al. 1999; Noyce et al. 2001; Boulanger et al. 2006) could have caused g_0 to vary among individuals independently of spatial effects. Home range sizes of female black bears also vary with age and social status (Alt et al. 1980; Rogers 1987; Wooding and Hardisky 1994; Costello 2008). Most previous SECR analyses of carnivore data did not attempt to model individual heterogeneity, except, in some cases, for differences between sexes (Gardner et al. 2009, 2010; Royle et al. 2009, 2011; Kalle et al. 2011; Kéry et al. 2011; Sollmann et al. 2011, 2012; Gray and Prum 2012; Noss et al. 2012). However, carnivores other than black bears also typically exhibit individual heterogeneity in detection probabilities and movement rates beyond what can be explained by spatial effects and sex, including differences among age and social classes (Boulanger et al. 2002, 2004, 2006; Cubaynes et al. 2010; Ebert et al. 2010; Marucco et al. 2011; Sollmann et al. 2012). O'Brien and Kinnaird (2011) attributed lack of support for individual heterogeneity in SECR data from four species of African carnivores to small sample size rather than a lack of differences among individuals, and Sollmann et al. (2012), in an SECR analysis of black bear data, noted that there was much residual variation in sex-specific SECR model parameters that may have been attributable to individual heterogeneity.

As age and social status cannot be inferred from genetic samples, we must rely on statistical approaches to correct for the associated variation. This requires larger samples to achieve similar precision (Pledger 2000; Dorazio and Royle 2003) and raises concerns about the sensitivity of density estimates to how individual heterogeneity is modeled (Dorazio and Royle 2003; Link 2004). These problems should not lead us to abandon models that correct for heterogeneity, because if it is present in the data, such models will generally yield more accurate estimates with better confidence interval coverage (Pledger 2000, 2005; Dorazio and Royle 2003; Boulanger et al. 2004; Link 2004; Cubaynes et al. 2010; Proctor et al. 2010). If a reduced-parameter model is selected a priori or because the power to detect variation is low, associated density estimates are not only potentially inaccurate, but also overstate precision (White et al. 1982; Boulanger et al. 2004). Proctor et al. (2010) and Ebert et al. (2010) recommended considering models that allow for individual heterogeneity for estimation purposes even when tests or model selection criteria do not detect it, because it is likely present in noninvasive data sets but power to detect it is often low. Statisticians might question the validity of such an approach, and in any case the parameters of SECR models that allow for individual heterogeneity may be inestimable when data are sparse (O'Brien and Kinnaird 2011; Sollmann et al. 2012; this study). Among the forms of variation we considered, individual heterogeneity had the greatest effect on $\hat{D}$ when modeled. Furthermore, variation among individuals was apparently overestimated, leading to even higher $\hat{D}$, when other forms of variation present in the data were not

Table 4 Parameter estimates (β) and their standard errors (SE), from spatially explicit capture–recapture models fit to data from female black bears on 43 study areas in ON, Canada, 2006–2009

Effect	Model			
	$g_0(bk + h + yr)\sigma(t + h + yr + FR3I)$		$g_0(bk + h + yr)\sigma(t + h + FR3I)$	
	β	SE	β	SE
g_0				
Intercept	−0.877	0.180	−0.904	0.187
Initial detection at the same trap	0.940	0.127	1.009	0.123
Member of 2nd group of individuals	1.470	0.191	1.465	0.195
$yr = 2009$	−0.763	0.258	−0.784	0.254
$yr = 2007$	−0.877	0.264	−0.812	0.260
$yr = 2006$	−1.281	0.240	−1.393	0.247
σ				
Intercept	7.311	0.077	7.267	0.073
Member of 2nd group of individuals	0.379	0.072	0.334	0.069
Occasion = 2	0.107	0.036	0.108	0.037
Occasion = 3	0.193	0.036	0.194	0.036
Occasion = 4	0.219	0.036	0.216	0.036
Occasion = 5	0.226	0.038	0.223	0.038
Occasion = 6	−0.004	0.121	−0.022	0.123
Forest region = GLSL	−0.294	0.074	−0.272	0.061
Forest region = Intermediate	−0.198	0.076	−0.178	0.072
$yr = 2009$	−0.113	0.080	n/a	n/a
$yr = 2007$	0.003	0.083	n/a	n/a
$yr = 2006$	−0.164	0.069	n/a	n/a
Probability of belonging to 2nd group of individuals				
	−1.863	0.197	−1.828	0.214

Estimates from the top AIC$_c$-ranked model appear at left, and from the 3rd AIC$_c$-ranked model (ΔAIC$_c$ = 1.5) at right. In model names, *bk* = a response to initial detection at the same trap, *h* = individual heterogeneity, *yr* = year sampled, *t* denotes a 6-level sampling occasion factor, and *FR3I* is denotes a 3-level habitat covariate separating Boreal Forests, Great Lakes-St. Lawrence (GLSL) Forests, and "intermediate" habitat within 10 km of the Forest region boundary. Link functions were the logit for g_0 and the probability of belonging to the 2nd group of individuals, and the log for σ

modeled explicitly. We agree with those who argued that if individual heterogeneity cannot be eliminated by study design or explained using covariates, then it is key to obtain sample sizes and detection probabilities sufficient to detect and model it (Boulanger et al. 2002; Lukacs and Burnham 2005; Marucco et al. 2011). More generally, we recommend treating variation in SECR model parameters as thoroughly as has become standard practice in conventional C–R studies. Where only sparse data from a single survey are available, SECR models that ignore individual heterogeneity could still be used to generate conservative estimates for management purposes because correcting for individual heterogeneity increases $\hat{D}$.

Although estimating abundance is the main goal of most C–R studies, identifying models of variation in g_0 and σ that minimize AIC$_c$ allows researchers to evaluate support for competing hypotheses about animal behavior (Kéry et al. 2011; Sollmann et al. 2011). For instance, comparisons of home range sizes of a species in different parts of its range or at different densities are of interest, but are often confounded by small samples of instrumented animals and differences in home range estimation methods among studies (Powell et al. 1997). In the case of American black bears, abundant prior research allows us to verify that our model selection results are consistent with independent information. For example, positive effects of initial detection were common where trap sites were baited (Boersen et al. 2003; Dreher et al. 2007; Immell and Anthony 2008; Gardner et al. 2010). The presence and magnitude of behavioral responses to detection at hair corrals may be related to the reliability and quantity of the food reward. Our baits (3 tins of sardines) provided a small food reward, were sometimes consumed by non-target species, and otherwise were likely consumed by the first bear to visit the trap; nevertheless, g_0 approximately doubled after initial detection. Responses to initial detection were not supported where the same bait was used but sampling occasions were separated by week-long intervals with no bait present (Obbard et al. 2010), or in two studies where a lure that provided little or no food reward was used (Belant et al. 2005; Sollmann et al. 2012). In one study where baits provided a larger food reward, the positive response was even stronger than that observed here (Wegan 2008; Gardner et al. 2010). A positive response to initial detection affecting g_0 had very slight effects on $\hat{D}$ here, but other studies suggest that failure to model such responses could cause underestimation (Borchers and Efford 2008; Gardner et al. 2010). We did not test for effects of initial detection on σ because we did not expect the small food reward to cause female black bears to deviate from their normal spring and early summer movement patterns, which are strongly influenced by social factors (Rogers 1987; Costello 2008; Castle 2010). However, the possibility that bears would move outside their normal home range in search of, or following the scent of, a baited trap after encountering one within it may warrant further investigation.

That σ increased during successive sampling occasions is consistent with telemetry studies that demonstrated increasing movement rates and home range sizes of black bears before and during the breeding season in early summer (Alt et al. 1980; Garshelis and Pelton 1980; Rogers 1987; Castle 2010). Black bears have also been shown to have smaller home ranges in higher quality habitat (Powell et al. 1997; Jones and Pelton 2003; Koehler and Pierce 2003). GLSL Forests provide more productive bear habitat than Boreal Forests (Rowe 1972; Kolenosky 1990; Obbard and Howe 2008) so higher σ in Boreal than GLSL forests was also expected. Possible explanations for the supported differences in g_0 and σ among years include differences in proportion of females accompanied by cubs if reproduction was synchronous, differences in food abundance during sampling or in the previous foraging season, differences in the timing of the onset of spring and associated bear behaviors, and effects of weather conditions on the rate of DNA degradation between the time samples were deposited and collected.

The patterns of variation in female bear density and home range size across ON described by our estimates are consistent with prior information indicating that both are related to habitat quality—the former directly and the latter inversely (Lindzey et al. 1986; Garshelis 1994; Powell et al. 1997; Koehler and Pierce 2003), though we note that our density estimates are partly a function of the way spatial variation in σ was modeled. Reproductive rates of black bears are generally higher in higher quality habitat (Garshelis 1994) but may also increase where densities are reduced by anthropogenic mortality (Czetwertynski et al. 2007; Obbard and Howe 2008); whether these latter increases are a consequence of increased home range size due to reduced competition for space or patchily-distributed food resources is not well-understood. That some of the lowest densities occurred in more southerly portions of the greater study area in eastern GLSL forests likely reflects greater habitat fragmentation and increased anthropogenic mortality near the southern limit of contiguous forests where human population density is higher and agricultural and urban development are more common. If black bears increase their home range size where densities are reduced, anthropogenic effects on bear density in the southeast may also explain why σ was larger on average in eastern than western GLSL forests.

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