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Compensatory heterogeneity in spatially explicit capture–recapture data

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Abstract. Spatially explicit capture–recapture methods, used widely to estimate the abundance of large carnivores, allow for movement within home ranges during sampling. Probability of detection is a decreasing function of distance from the home range center, with one parameter for magnitude and another for spatial scale. Sex-based and other differences in home range size potentially cause heterogeneity in individual detection and bias in estimates of density. The two parameters of detection have hitherto been treated as independent, but we suggest that an inverse relation is expected when detection probability depends on time spent near the detector. Variation in the spatial scale of detection is then compensated by reciprocal variation in the magnitude parameter. We define a net measure of detection ("single-detector sampling area," a_0), and show by simulation that its coefficient of variation (CV) is a better predictor of bias than the CV of either component or the sum of their squared CVs. In an example using the grizzly bear *Ursus arctos*, the estimated sex variation in a_0 was small despite large variation in each component. From the simulations, the relative bias of density estimates was generally negligible ($<5\%$) when $\mathrm{CV}(a_0) < 30\%$. Parameterization of the detection model in terms of a_0 and spatial scale can be more parsimonious and significantly aids the biological interpretation of detection parameters.

Key words: carnivores; density estimates; DNA; effective sampling area; grizzly bear; heterogeneity; home range; SECR; sex differences; single-detector sampling area; spatially explicit capture–recapture; Ursus arctos.

Introduction

There is widespread interest in spatially explicit capture–recapture (SECR) methods to assess populations of elusive and sparsely distributed animals, of which large carnivores are a prime example (e.g., Royle et al. 2009, Gardner et al. 2010, Obbard et al. 2010, Sollmann et al. 2011, Tobler et al. 2013). Sampling may use conventional traps, automatic cameras, or devices such as hair snares that passively sample DNA. A key advantage of SECR over conventional capture–recapture is that it models the differential exposure to detectors of animals whose home ranges are centered at different points in the habitat. A "detection function" is fitted to the latent (unobserved) distances between home range centers and detectors; the function uses at least one parameter σ to represent the scale of movements (home range size) and another (g_0 or λ_0) to represent the probability of detection by a detector notionally placed at the home range center. Individual exposure is heterogeneous, but because the effect is modeled, it does not cause bias in the density estimates. However, including spatial scale in the model introduces a new potential source of heterogeneity: variation in home range size among individuals.

All unmodeled individual heterogeneity is believed to cause bias in estimates of population size by conventional capture–recapture. The bias relates to the coefficient of variation (CV) of detection probability p among individuals (Cormack 1966, Carothers 1973, Lee and Chao 1994). For a simple model, Cormack (1966) predicted the relative bias to be $1/(1+\gamma^2) - 1$, where $\gamma = \mathrm{CV}(p)$, and we confirmed by simulation that this relationship holds for model M_0 of Otis et al. (1978) (Appendix A).

Mixture methods have been used in nonspatial models to allow for heterogeneity (Pledger 2000), and these methods have also been applied in SECR (Borchers and Efford 2008, Obbard et al. 2010, Efford 2013). However, results can be sensitive to the form of the model (Link 2003) and confidence intervals may be wide. In the context of Bayesian SECR, Royle et al. (2009) considered that "... researchers should make their own judgment as to whether individual heterogeneity should be fit [in SECR models] because this is a decision that cannot be made objectively in small samples." Researchers have little evidence to inform such a judgment,

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beyond the general assumption that heterogeneity is damaging.

This motivates our investigation of the robustness of SECR density estimators under realistic scenarios for heterogeneity of home range size. We focus first on sex differences in home range size as a tangible and general cause of heterogeneity. Home ranges differ strongly in size between the sexes in most species of solitary carnivore (Sandell 1989), and there is a prima facie case that SECR estimates of carnivore abundance will be negatively biased if the model does not include sex. This is supported by simulations such as those of Tobler and Powell (2013) for photo identification of jaguars (*Panthera onca*), and by empirical examples in which models allowing sex-related heterogeneity gave higher estimates of total density than null models (Gardner et al. 2010, Sollmann et al. 2011), although the effect may be small.

We first introduce SECR methods and analyze a grizzly bear *Ursus arctos* data set that throws up an apparently paradoxical result: despite clear sex differences in model parameters, a null model gives the same density estimate as one including sex as a covariate. We show that this result should be expected when the detection probability of an animal in different parts of its home range is directly proportional to the time it spends there. Simulations are used to quantify the relationship between various measures of heterogeneity and bias in density estimates. Compensatory heterogeneity lowers the bias in estimates of density, and we show by examples that the effect is sometimes large enough to reduce bias to negligible levels. We advocate distinguishing between variation in λ_0 that is a biologically trivial consequence of variation in home range size and variation that requires a specific behavioral explanation, and suggest a parameterization of the SECR model that makes explicit this distinction.

SECR methods

SECR methods have been described repeatedly (e.g., Efford 2004, Borchers and Efford 2008, Efford et al. 2009, Royle and Gardner 2011) and only relevant aspects will be summarized here. We define the detection model as a function $\lambda(d;\ \lambda_0, \sigma)$ whose value is the expected number of detections of an animal whose home range is centered at distance d from a detector (e.g., Royle and Gardner 2011). This is related to the alternative function $g(d)$ for the probability of at least one detection by $g(d) = 1 - \exp[-\lambda(d)]$, and $g(d) \approx \lambda(d)$ for small values of λ_0. Here we use the half-normal form: $\lambda(d;\ \lambda_0, \sigma) = \lambda_0 \exp\,[-d^2/(2\sigma^2)]$.

We maximize the likelihood conditional on n, the number of detected individuals (Borchers and Efford 2008). This is sufficient to fit the detection model when density does not vary over space. Density is estimated as a derived parameter using $\hat{D} = \sum_{i=1}^{n} \hat{a}_i^{-1}$, where $\hat{a}_i = a(\hat{\lambda}_{0i}, \hat{\sigma}_i)$ is the estimated effective sampling area for animal i. Effective sampling area here has the specific meaning given by Borchers and Efford (2008):

$$a(\lambda_{0i},\ \sigma_i) = \int_A p.(\mathbf{X}; \lambda_{0i}, \sigma_i)d\mathbf{X}, \qquad (1)$$

where $p.(\mathbf{X})$ represents the probability that an individual centered at $\mathbf{X}$ is detected at least once, and A is an appropriate area of integration. The form of $p.(\mathbf{X})$ depends on properties of the detectors; for "binary proximity detectors" (detectors that are independent, but can reliably record only presence vs. absence of an individual in any sampling interval), $p(\mathbf{X};\ \lambda_{0i}, \sigma_i) = 1 - \prod_{s=1}^{S} \prod_{k=1}^{K} [1 - g(\mathbf{X}; \lambda_{0i}, \sigma_i)]$, given sampling across S intervals with K detectors (Efford et al. 2009). For simplicity, we will assume that the detection function λ does not vary across sampling intervals (s) or detectors (k).

Inference for density via the conditional likelihood is directly analogous to the Huggins/Alho method in nonspatial capture–recapture (e.g., Chao and Huggins 2005) and yields estimates very similar or identical to those from maximizing the full likelihood (Borchers and Efford 2008) or from data augmentation and Markov chain Monte Carlo (MCMC; Royle and Gardner 2011). Detection parameters are allowed to depend on permanent individual covariates; these are not shown in the expression for $\hat{D}$, but are implied by the individual subscripts on a_i, λ_{0i}, and σ_i. Formulation in terms of the $\hat{a}_i$ allows insight into the effect of unmodeled individual heterogeneity, as we will describe.

The coefficient of variation is a summary of within-population variation in each detection parameter θ that, by analogy with nonspatial capture–recapture, may predict bias in density estimates. When variation results from m discrete classes with parameter values θ_i, standard formulae for the mean and variance of a discrete distribution lead to

$$\mathrm{CV}(\theta) = \sqrt{\sum_{i=1}^{m} p_i[\theta_i - \mu(\theta)]^2} / \mu(\theta) \qquad (2)$$

given probability mass p_i for the ith class and mean $\mu(\theta) = \sum_{i=1}^{m} p_i\theta_i$. In SECR, $p_i = w_i / \sum_{i=1}^{m} w_i$, where w_i is the density of the ith class.

Grizzly bear example

As a motivating example, we analyze a sex-specific grizzly bear *Ursos arctos* data set from the Flathead Valley of the southern Rocky Mountains of British Columbia, Canada. Bears were surveyed in 2007 using baited barbed-wire hair snares as in Mowat et al. (2005). One snare was located in each of 70 grid squares of 7×7 km; snares were checked after 14 days and moved to a new site within the grid square for a total of four sampling occasions. A total of 263 unique sites were sampled (some grid squares were sampled fewer than four times because of lack of bear habitat). Groups of hairs collected from the wire (see Plate 1) were assigned

TABLE 1. Sex-specific and combined-sex spatially explicit capture–recapture (SECR) analyses of grizzly bear abundance in Flathead Valley, British Columbia, Canada, in 2007.

Sex	n	$\hat{\lambda}_0$	$\hat{\sigma}$ (km)	$a(\hat{\lambda}_0, \hat{\sigma})$ (km^2)	$\hat{D}$ (no./km^2)
Male	34	0.049 (0.018)	7.13 (1.07)	2757 (482)	0.0123 (0.0030)
Female	50	0.477 (0.135)	2.39 (0.23)	2568 (231)	0.0195 (0.0033)
Combined	84	0.123 (0.026)	4.41 (0.35)	2548 (226)	0.0330 (0.0046)

Notes: DNA data are from hair snares operated asynchronously at 263 sites. Fitted half-normal detection parameters are: expected number of detections at center of home range λ_0 and spatial scale σ. Derived parameters are: effective sampling area $a(\hat{\lambda}_0, \hat{\sigma})$ and density $\hat{D} = n/a(\hat{\lambda}_0, \hat{\sigma})$, where n is the number of detected individuals. SE values are in parentheses.

individual identities based on their microsatellite genotype (Paetkau 2003), and sex was determined from the amelogenin gene (Ennis and Gallagher 1994). Each check potentially yielded hairs from multiple individuals, and multiple samples relating to one individual were treated as a single detection (i.e., these were binary proximity detectors).

SECR models were fitted by maximizing the conditional likelihood in secr version 2.6.1 (Efford 2013). The region of integration A (the extent of potential habitat) was based on a 30-km buffer around all hair-snare sites; the region was discretized as 13 190 1×1 km cells, and other settings followed the defaults in function secr.fit (Efford 2013). A null model was fitted separately for each sex. We also fitted a null model to the combined-sex data, discarding sex information and therefore not modeling that potential source of heterogeneity.

Sex-specific estimates of λ_0 differed by a factor of about 10 (female > male), and estimates of σ differed by a factor of about 3 (male > female); see Table 1. The sex ratio based on the estimated densities (Table 1) was 63% female. Applying Eq. 2 to estimate variation due to sex differences ($m = 2$), we get $\widehat{\mathrm{CV}}(\lambda_0) = 0.67$ and $\widehat{\mathrm{CV}}(\sigma) = 0.55$. Estimated sex-dependent variation in the effective sampling area was considerably less: $\widehat{\mathrm{CV}}(a(\lambda_0, \sigma)) = 0.03$. A combined-sex null model in which the data were highly heterogeneous might be expected to yield quite biased estimates, but the combined-sex $a(\hat{\lambda}_0, \hat{\sigma})$ was close to that from the sex-specific analyses, and the estimated density was close to the sum for the sexes separately (Table 1). We sought an explanation.

Space-use model for covariance of λ_0 and σ

We propose that the expected number of detections of an individual in part of its home range relates to the proportion of time spent there. Exceptions can easily be imagined, such as when detection relies on territorial marks or the response to traps varies with location, but a linear relationship between the intensity of use and the distribution of detections is a good starting point. Then $\lambda(\mathbf{X}) = a_0 f(\mathbf{X})$, where f is the bivariate probability density of activity and a_0 is a constant.

Simple and commonly used bivariate densities with center $\mathbf{x}$ and scale σ are the circular bivariate normal, $f(\mathbf{X}) = 1/(2\pi\sigma^2) \times \exp[-|\mathrm{X} - \mathrm{x}|^2/(2\sigma^2)]$, and the equivalent negative exponential, $f(\mathbf{X}) = 1/(2\pi\sigma^2) \times \exp(-|\mathrm{X} - \mathrm{x}|/\sigma)$. In both cases, $a_0 = 2\pi\sigma^2\lambda_0$. For an isolated detector on a single occasion, $p.(\mathbf{X}) = 1 - \exp[-\lambda(\mathbf{X})]$, which for small λ_0 implies $p.(\mathbf{X}) \approx \lambda(\mathbf{X})$ and $a_0 \approx a(\lambda_0, \sigma)$. We therefore call a_0 the "single-detector sampling area." While idealized, this case is instructive: σ^2 and λ_0 appear only as their product, and combinations with constant product will yield the same a_0. Thus we expect negative covariance between σ^2 and λ_0 across individuals ($\hat{\lambda}_0$ and $\hat{\sigma}$ also show negative sampling covariance, even when each is constant in the target population, but this is a separate issue).

If there are multiple sampling occasions, or multiple detectors with overlapping catchment areas, the effective sampling area $a(\lambda_0, \sigma)$ is a more complex nonlinear function of λ_0 and σ (Eq. 1). Placing detectors closer together reduces a, whereas increasing the number of sampling occasions or detectors increases a. Overlap of catchment areas shifts contours of $a_0(\lambda_0, \sigma)$ relative to contours of $a(\lambda_0, \sigma)$ when the value of either or both parameters is large, but their shape is not greatly

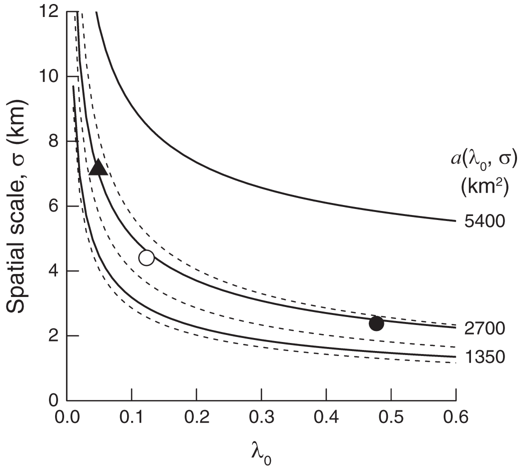

FIG. 1. Contours of effective sampling area a (solid lines, as labeled) as a function of half-normal detection parameters λ_0 (indicating the intercept, i.e., expected number of detections when the detector is at the home range center) and σ (spatial scale of the half-normal function). Sampling of grizzly bears (*Ursus arctos*) for one occasion on an array of 263 hair snares is shown. Dashed contours are for corresponding levels of the single-detector sampling area $a_0 = 2\pi\ \lambda_0\ \sigma^2$, scaled by the number of detectors (the contour for $a_0 = 5400$ km^2 is close to that for $a = 2700$ km^2). Flathead Valley grizzly bear estimates are plotted from female-only (solid circle), male-only (solid triangle), and combined-sex (open circle) models (Table 1). Within-population variation along a contour of a does not affect density estimates.

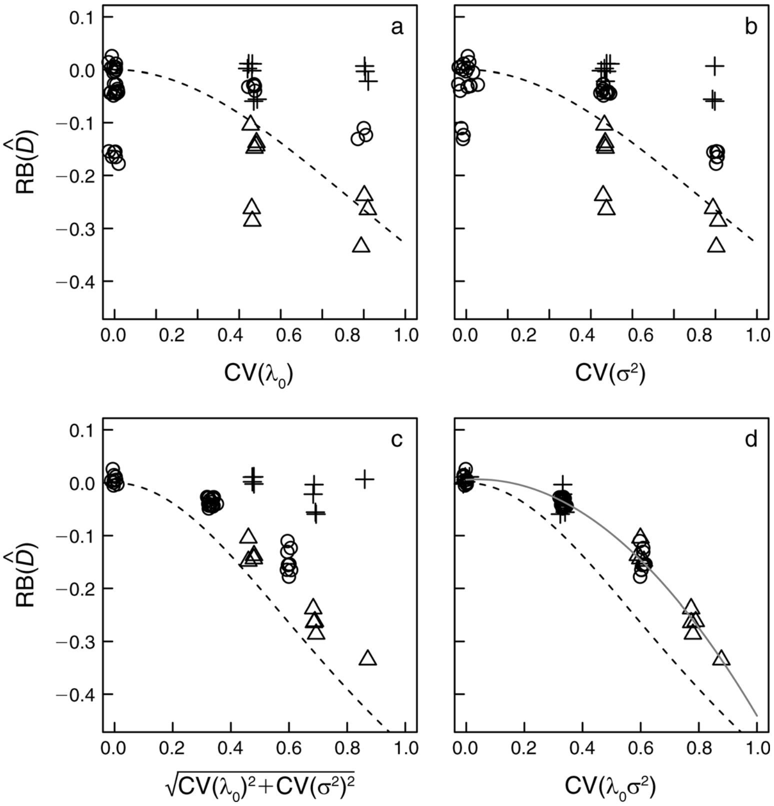

FIG. 2. Relative bias of estimated density, $\text{RB}(\hat{D})$, from the null spatially explicit capture–recapture (SECR) model applied to simulated data from populations with sex-dependent detection parameters λ_0 and σ. Shown are averages across 400 simulations for 54 scenarios, plotted in relation to (a, b) the separate CV of each parameter, (c) the pooled (square root of the sum of the squares) CV, and (d) the CV of the product $\lambda_0\sigma^2$. The dashed reference line indicates Cormack's (1966) predicted bias $1/(1+\gamma^2)-1$, where γ is the particular CV on the x-axis. The fitted quadratic in (d) has equation $y = 0.006 + 0.036x - 0.483x^2$. Symbols indicate whether between-sex variation in λ_0 and σ is compensatory (+ signs), reinforcing (open triangles), or neither (open circles). The 95% CI is obscured by symbols. Points are jittered slightly on the x-axis to reduce overlap.

affected (Fig. 1), and $a_0(\lambda_0, \sigma)$ is therefore a useful surrogate for $a(\lambda_0, \sigma)$. Whether a_0 is a nearly constant proportion of a for a given sampling design deserves further study.

Bias of density estimates when λ_0 and σ differ between sexes

In the preceding section, we established for a simple activity model that reciprocal variation in λ_0 and σ^2 results in near-constant $a(\lambda_0, \sigma)$: for example, sexes may differ in σ, yet have the same $a(\lambda_0, \sigma)$. It is not immediately obvious that fitting a SECR model in these conditions necessarily gives an unbiased estimate of $a(\lambda_0, \sigma)$, but our grizzly bear example raises this interesting possibility.

We therefore investigated the behavior of null SECR models fitted to simulated data in which two unobserved latent classes (nominally sexes) differed with respect to λ_0 and σ. Individuals of one sex shared the same combination of values for λ_0 and σ. Sex ratio was held constant at 1:1. Three levels of λ_0 (0.1, 0.2, 0.4) and three levels of σ (s, $\sqrt{2}s$, and $2s$, where s was the spacing of detectors on a 10×10 square grid) were used for each sex, giving a total of 54 unique scenarios (dropping scenarios that differed only in sex labeling). Simulated variation between the sexes resulted in parameter-specific heterogeneity measured by its CV (Eq. 2): $\text{CV}(\lambda_0)$ and $\text{CV}(\sigma^2)$ each took the values 0, 0.33, and 0.60. Of the 18 scenarios in which both λ_0 and σ differed between the sexes, the variation was in the same direction and reinforcing (positive covariance between λ_0 and σ) in one half, and compensatory (negative covariance) in the other half. The net effect of these patterns is reflected in the somewhat greater range of $\text{CV}(a_0)$ (from 0 to 0.88). Covariance was zero (and hence neither compensatory nor reinforcing) in the 36 scenarios with at least one parameter held constant. Further details are given in Appendix B, and R code is provided in the Supplement.

The relative bias of density estimated from the null model was small and probably negligible in scenarios in which neither λ_0 nor σ^2 varied among individuals (Fig. 2c). The magnitude of bias was predicted only weakly by either $\text{CV}(\lambda_0)$ (adjusted $R^2 = 0.08$) or $\text{CV}(\sigma^2)$ (adjusted $R^2 = 0.31$) used alone. Pooling the coefficients gave only a modest improvement in prediction (adjusted $R^2 =$

PLATE 1. Grizzly bear hairs on barbed wire surrounding a baited site in British Columbia. Individuals were identified from microsatellite DNA in the hair follicles. Photo credit: Douglas Heard.

0.42). These analyses ignored the covariance of λ_0 and σ^2, but it is clear from the spread of points in Fig. 2 that this was critical: scenarios with positive covariance showed large bias and those with negative covariance showed small or zero bias. Using CV(a_0) as the predictor captured this effect and greatly improved the prediction (adjusted $R^2 = 0.97$; Fig. 2d).

An alternative parameterization

We have proposed a model in which variation in σ^2 drives reciprocal variation in λ_0. The source of variation in σ may be observed individual-level covariates such as sex or unobserved membership of a latent class as in finite mixture models, and we use z to represent either source of heterogeneity. In order to represent dependence of λ_0 on σ, we require a new parameterization of the SECR model. We suggest replacing the conventional parameterization (λ_0, σ) with (a_0, σ), where $a_0 = 2\pi\lambda_0\sigma^2$. We prefer $a_0(\lambda_0, \sigma)$ to $a(\lambda_0, \sigma)$ because λ_0 may be inferred from a_0 without numerical root finding (since $\lambda_0 = a_0/(2\pi\sigma^2)$) and because a_0 is independent of the sampling design.

The new and old parameterizations overlap. In the absence of any modeled variation in σ, or when both λ_0 and σ vary, they are equivalent (i.e., have the same maximized likelihood) and yield identical estimates of D. The a_0 parameterization gains the ability to model compensatory heterogeneity, but lacks an equivalent of $\lambda_0 \sim 1$, $\sigma \sim z$.

The two parameterizations are compared for the grizzly bear data set in Table 2 using Akaike's Information Criterion (AIC). For this data set, models with constant a_0 and varying σ gave very similar fit and estimates to those under the conventional parameteri-

TABLE 2. Alternative models fitted to combined-sex grizzly bear data set, parameterized in terms of (λ_0, σ) or (a_0, σ), where $a_0 = 2\pi\lambda_0\sigma^2$.

Model	$\hat{a}_0$ (km^2)	$a(\hat{\lambda}_0, \hat{\sigma})$ (km^2)	$\hat{D}$ (no./km^2)	np	logLik	ΔAIC
$\lambda_0 \sim 1$, $\sigma \sim 1$		2548 (226)	0.0330 (0.0046)	2	−392.0	43.3
$\lambda_0 \sim 1$, $\sigma \sim$ sex		2297 (246)	0.0366 (0.0057)	3	−383.1	27.5
$\lambda_0 \sim$ sex, $\sigma \sim$ sex		2641 (231)	0.0318 (0.0044)	4	−369.3	1.9
$a_0 \sim 1$, $\sigma \sim$ sex	16.6 (2.4)	2658 (223)	0.0316 (0.0044)	3	−369.3	0.0

Notes: Here, "sex" refers to a two-level categorical individual covariate. ΔAIC was the difference in AIC between a particular model and the model with smallest AIC; np is the number of parameters, and logLik is log likelihood. SE values are in parentheses.

TABLE 3. Heterogeneity in detection parameters estimated by fitting a two-class finite mixture.

Data set	Scientific name	$\widehat{\text{CV}}(\lambda_0)$	$\widehat{\text{CV}}(\sigma_2)$	Comp	$\widehat{\text{CV}}(a_0)$	Test 1	Test 2	Predicted RB
Flat-tailed horned lizard	*Phrynosoma mcallii*	0.76	0.41	yes	0.13	0.002	0.678	+0.00
Deer mouse ESG	*Peromsycus maniculatus*	0.54	0.78	yes	0.10	0.001	0.558	+0.00
Deer mouse WSG	*Peromsycus maniculatus*	0.59	1.24	yes	0.07	<0.001	0.739	+0.01
House mouse	*Mus musculus*	0.43	1.32	yes	0.38	<0.001	0.006	−0.05
Speckled skink	*Oligosoma infrapunctatum*	0.19	1.33	yes	0.62	<0.001	0.001	−0.16
Spotted skink	*Oligosoma lineoocellatum*	0.52	1.04	yes	0.23	<0.001	<0.001	−0.01
Brushtail possum	*Trichosurus vulpecula*	0.46	0.96	yes	0.02	<0.001	0.899	+0.01
Ovenbird	*Seiurus aurocapilla*	0.14	0.50	no	0.73	0.201	0.194	−0.23

Notes: Variation is compensatory ("Comp") if the class with larger $\hat{\lambda}_0$ has the smaller $\hat{\sigma}$. For each latent class, $\hat{a}_0$ is computed from $\hat{a}_0 = 2\pi\hat{\lambda}_0\hat{\sigma}^2$. "Test 1" and "Test 2" are probability values for likelihood-ratio tests described in *An alternative parameterization* (variation in σ given compensatory variation in λ_0, and extra-compensatory variation in λ_0). "Predicted RB" refers to the relative bias of the null density estimator predicted from $\widehat{\text{CV}}(a_0)$ using the curve fitted to simulated data (Fig. 2d).

zation with varying λ_0 and σ, but with one less parameter and therefore slightly lower AIC (Table 2).

The new parameterization may be used to test for variation in σ while assuming that variation in λ_0 is compensatory, and to test for additional variation in λ_0 that cannot be explained as compensatory. The null model ($a_0 \sim 1$, $\sigma \sim 1$) allows for no variation in either detection parameter. If σ varies and variation in λ_0 is compensatory, we have the model ($a_0 \sim 1$, $\sigma \sim z$). If there is variation in λ_0 that cannot be explained by compensation, then the model is ($a_0 \sim z$, $\sigma \sim$ z). A likelihood-ratio test is appropriate because the models in each pair are nested: the difference in deviance is compared to a χ^2 distribution with degrees of freedom equal to the difference in number of fitted parameters (2 df and 1 df, respectively, when z refers to a two-class finite mixture, or 1 df for each test when z refers to sex). For the grizzly bear example, the first test is highly significant ($\chi^2 = 45.3$, 1 df, $P < 0.001$), but there is no evidence for extra-compensatory variation in λ_0 ($\chi^2 = 0.1$, 1 df, $P = 0.76$). Extra-compensatory variation in λ_0 may co-occur with compensatory variation, as we show in the next section.

There is another benefit of the a_0 parameterization when z is a covariate of interest (e.g., sex) and non-compensatory variation is found in λ_0. The coefficient corresponding to the effect $a_0 \sim z$ then may be useful for comparing the magnitude of z-dependent differences in behavior between studies while adjusting for direct effects of home range size.

Compensatory heterogeneity in other taxa

Heterogeneity in λ_0 tends to have a compensatory effect whenever λ_0 (or g_0) and σ covary negatively within a population. Our bear example was at the extreme of near-perfect compensation. We now present preliminary evidence on the prevalence and degree of compensation in other studies. Compensation may be assessed by fitting a two-class finite mixture model and examining the signs of the difference between latent classes for the two detection parameters, and the magnitude of $\widehat{\text{CV}}(a_0)$. We applied this approach, and the tests of the preceding section, to the capture–recapture data sets provided as examples in secr version 2.6.1 (Efford 2013), which span a variety of non-carnivore taxa (Table 3; Appendix C).

We fitted three models to each data set: a conventional null model ($\lambda_0 \sim 1$, $\sigma \sim 1$), a two-class finite mixture (heterogeneity) model (h2) in which σ varied and a_0 was held constant ($a_0 \sim 1$, $\sigma \sim$ h2), and a two-class finite mixture model in which both parameters were free to vary ($\lambda_0 \sim$ h2, $\sigma \sim$ h2). In the last model, individuals in a particular latent class shared the same combination of values for λ_0 and σ, and the single-detector sampling area ($a_0 = 2\pi\lambda_0\sigma^2$) was computed from the estimated detection parameters of each latent class. The CVs of each detection parameter and a_0 were computed using Eq. 2. Models were fitted by maximizing the full likelihood, with other settings appropriate to the study (Appendix C).

There was evidence for variation in σ in all data sets except Ovenbird (Table 3). For other species, the direction of variation in the two detection parameters λ_0 and σ was consistent with compensation. In consequence, $\widehat{\text{CV}}(a_0)$ was less than both $\widehat{\text{CV}}(\lambda_0)$ and $\widehat{\text{CV}}(\sigma^2)$, and the relative bias predicted from $\widehat{\text{CV}}(a_0)$ was generally small (range −0.16 to +0.01). Paradoxically, the data set for which there was least support for a heterogeneity model (Ovenbird) was the one predicted to show the greatest heterogeneity-induced relative bias in estimated density (−0.23). Extra-compensatory variation in λ_0 was detected only in the house mouse and skink studies.

DISCUSSION

Variation in home range size among individuals is an issue for density estimation by SECR, but perhaps not as big a problem as some have indicated. Variation in home range size is almost perfectly compensated by reciprocal variation in the magnitude of detection when detection is linear on the intensity of space use. This was apparently the case in our grizzly bear example. When compensation is imperfect or absent, the bias in $\hat{D}$ may be predicted from $\text{CV}(a_0)$, which itself may be estimated from a fitted two-class finite mixture model. If home range size (and hence σ) varies within a population, the biologically more appropriate null model will usually be constant a_0 (implying compensation) rather than constant λ_0 (implying independence of σ and λ_0). For realistic simulation of data from heterogeneity models, it is desirable to base the covariation of λ_0 and σ on a biologically plausible null model, and constant a_0 is a strong candidate; this is easy to achieve with finite mixtures, as we have shown (Appendix B).

Although it is usual for home range size to differ between the sexes in carnivores, and probably in most mammals, the inclusion of sex in SECR models is strictly necessary only when there is a large difference in overall detection probability, as measured by the effective sampling area or a_0. The relationship between the relative bias of estimated density and CV(a_0) was strongly nonlinear, as Cormack (1966) predicted for CV(p) in nonspatial capture–recapture models, but for SECR his curve was conservative: interpolating from our simulation results, the relative bias did not exceed 5% for CV(a_0) $< 30\%$ (Fig. 2d).

These findings extend our understanding of the robustness of SECR estimators and complement earlier assessments of the robustness of nonspatial estimators (Carothers 1973, Otis et al. 1978). They also highlight the potential value of parameterizing SECR models in terms of a_0. The parameterization is more parsimonious when detection depends directly on space use, but its key advantage is not parsimony per se. Rather, it allows users to distinguish variation in λ_0 that is a biologically trivial consequence of variation in home range size from variation that requires a specific behavioral explanation.

We contrast our grizzly bear example, in which males and females appeared to interact equally with detectors, once home range effects were implicitly removed, with the pattern of sex-based variation in two jaguar studies (Sollmann et al. 2011, Tobler et al. 2013). In the jaguar studies, both $\hat{\lambda}_0$ and $\hat{\sigma}$ were greater in males than females, which points to a difference in behavior toward detectors. M. Tobler (*personal communication*) suggests that this may be due to the greater speed and frequency with which males traverse their ranges, or their greater use of the human trails where cameras are often placed. In such cases, it is clearly a mistake not to model sex differences. There is a separate design consequence of large sex differences in home range size: a particular detector configuration may be adequate for one sex and inadequate for the other (e.g., Tobler and Powell 2013).

Compensatory variation in λ_0 and σ raises a more general point regarding model selection in capture–recapture. Models may differ radically by overall criteria such as AIC, while not differing materially with respect to the parameter of interest. Density estimation by SECR seems, fortuitously, to be robust to some misspecifications of the detection model. For example, failing to model the sex-specific σ of grizzly bears incurred a penalty of >40 AIC units while leaving the estimate of density essentially unchanged (Table 2). Focused information criteria (Claeskens and Hjort 2008) provide a formal mechanism for model selection when one parameter is of special interest, but we are not aware of any application to SECR.

Conclusion

Individual heterogeneity due to varying home range size is naturally compensatory when detection depends on the time an animal spends in each part of its home range. Sex differences in λ_0 and σ provide a convenient framework for discussing this idea because the biological basis is obvious and the heterogeneity inferred from SECR can be confirmed by observing sex differences in space use (e.g., by radiotelemetry). However, the idea extends also to cryptic variation in home range size within a population, and, approximately, to models parameterized in terms of g_0 rather than λ_0. The possibility that variation in λ_0 or g_0 compensates for variation in σ should also be considered when σ varies over time or between areas, rather than within a population at one time.

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SUPPLEMENTAL MATERIALS

Appendix A

Bias of population size estimated from model M_0 as function of CV(p) (*Ecological Archives* E095-115-A1).

Appendix B

Simulations of SECR with covariation of detection parameters (*Ecological Archives* E095-115-A2).

Appendix C

Compensatory detection inferred from SECR two-class finite mixture models applied to various data sets (*Ecological Archives* E095-115-A3).

Supplement

R code for simulation of heterogeneous detection (*Ecological Archives* E095-115-S1).