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Appendix C. Simulations to compare spatially explicit population estimates from signal-strength and binary detection models.

We simulated the detection of songbirds with a microphone array in a forest. Two microphone configurations were simulated: a single large array (10 x 10), and pooled data from 25 small arrays (2 x 2) operated independently. Microphones were 50 m apart. Home ranges (D = 2.0 ha^{-1}) were located at uniform random centers over a rectangular area A extending 60/–β_1 meters from the microphones[1]; the number of centers was Poisson-distributed with mean kDA where k refers to the number of arrays (1 or 25). A detection occurred when the strength of the signal received by a microphone exceeded an arbitrary threshold. Attenuation was assumed to be linear on the decibel scale. We set β_0 = 70 dB, β_1 = –0.3 dB/m, and simulated two levels of error standard deviation (σ_s = 2.5 dB, σ_s = 10 dB) and two thresholds for censoring ($c = \beta_0$–30, $c = \beta_0$–10 dB). The four combinations of σ_s and c resulted in varying numbers of detections as shown in Table C1.

We compared density estimates from the simulated acoustic data under two models; in the 'signal-strength' model the received signal strength above the detection threshold was modeled as a continuous variable, and in the 'binary' model detection was simply binomial. Both models used the same detection function in which the linear parameters β_0 and β_1 and the error standard deviation σ_s define the decline in detection probability

[1] For the most extreme error standard deviation (σ_s = 10 dB) this ensured that 99.9% of songs from birds at the edge of the rectangular area were attenuated by at least 30 dB before reaching a microphone.

with distance; the signal-strength model additionally modeled variation among the detected signals. The habitat mask was a square array of 4096 center points spaced evenly out to $60/–\beta_1$ meters from the microphones. We fitted models by minimizing the negative log likelihood with the 'L-BFGS-B' algorithm in function 'optim' of R 2.7.2 (R Development Core Team 2008).

The three detection parameters of the binary model are not independently estimable because of structural 'intrinsic' parameter redundancy (e.g., Gimenez et al. 2004) so we estimated only the composite parameters $(\beta_0–c)/\sigma_s$ and β_1/σ_s. With the 4-microphone configuration, some binary-model parameter combinations yielded a high proportion of numerically dubious estimates for the detection parameters (identified by extreme and implausible values, failure of asymptotic variance estimation, or estimated standard errors greater than the absolute value of the estimate). These estimates were excluded from the summary of results for the detection parameters, but not the corresponding density estimates (Table C2). We attribute the numerical problems to data-dependent 'extrinsic' parameter redundancy (Gimenez et al. 2004) in the binary model when the microphone array is small relative to the 'shoulder' of the detection function (e.g., main paper Fig. 2b). There appears to be little or no 'spillover' effect on the estimates of density, which remain nearly unbiased (Table C2).

If the asymptotic estimates of the sampling variance of $\hat{D}$ are reliable then we expect the computed standard errors to equal the standard deviation of $\hat{D}$ over a large sample of simulations. We assessed the asymptotic variance estimates by plotting the mean estimated standard error against the empirical standard deviation of $\hat{D}$. The sample size was 100 except for three trials in which only 96, 98 or 99 replicates yielded estimates of the sampling error. Empirical and asymptotic estimates were in agreement (Fig. C1).

Simulations may also be used to determine the coverage of confidence intervals based on the asymptotic standard errors, but many more replicates are needed and we have been able to assess coverage for only a subset of the detection scenarios (multiple 4-microphone arrays) and models (signal-strength only). Also, density in these trials was reduced to 0.5 ha^{-1} to assess performance when samples were smaller and to reduce computing time. Coverage was near the nominal level (95%) in three of the four trials (Table C3). Coverage dropped to 81% in the trial with a large error standard deviation and high signal threshold (σ_s = 10 dB, $c = \beta_0$–10 dB), but the relative standard error of the estimates was so large in this case (mean RSE = 95.8%) that the inadequacy of the estimates would be obvious.

Literature Cited

Gimenez, O., A. Viallefont, E. A. Catchpole, R. Choquet, and B. J. T. Morgan. 2004. Methods for investigating parameter redundancy. Animal Biodiversity and Conservation 27:561–572.

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Table C1. Number of individuals detected and total number of detections in simulated data for signal-strength models (SE over simulations in parentheses; n = 100)

Scenario	Individuals	Total detections
Multiple 4-microphone arrays		
$\sigma_s = 2.5$, $c = \beta_0 – 30$	273.0 (1.7)	636.1 (4.0)
$\sigma_s = 2.5$, $c = \beta_0 – 10$	62.3 (0.8)	74.7 (1.1)
$\sigma_s = 10$, $c = \beta_0 – 30$	337.9 (1.7)	699.6 (4.3)
$\sigma_s = 10$, $c = \beta_0 – 10$	98.2 (1.0)	134.0 (1.5)
Single 100-microphone array		
$\sigma_s = 2.5$, $c = \beta_0 – 30$	84.2 (0.9)	644.5 (7.8)
$\sigma_s = 2.5$, $c = \beta_0 – 10$	51.5 (0.7)	74.1 (1.1)
$\sigma_s = 10$, $c = \beta_0 – 30$	92.3 (0.9)	689.4 (8.7)
$\sigma_s = 10$, $c = \beta_0 – 10$	58.6 (0.7)	134.6 (1.9)

Table C2. Estimates from simulated acoustic detections with signal-strength or binary models (SE over simulations in parentheses). 'SE(estimate)' is the square root of the asymptotic sampling variance. n is the number of simulations that produced estimates, out of 100. In all simulations, $D = 2.0$ ha^{-1}, $\beta_0 = 70$ dB, and $\beta_1 = -0.30$ dB/m.

(a) Signal-strength model

Multiple 4-microphone arrays

	Parameter	Estimate		n	SE(estimate)		n
$\sigma_s = 2.5$, $c = \beta_0 - 30$							
	D	2.005	(0.014)	100	0.134	(0.001)	100
	β_0	69.994	(0.037)	100	0.367	(0.003)	100
	β_1	–0.300	(0.001)	100	0.006	(0.000)	100
	σs	2.492	(0.012)	100	0.123	(0.001)	100
$\sigma_s = 2.5$, $c = \beta_0 - 10$							
	D	2.061	(0.034)	100	0.340	(0.009)	100
	β_0	69.946	(0.124)	100	1.225	(0.039)	100
	β_1	–0.301	(0.004)	100	0.035	(0.001)	100
	σs	2.383	(0.068)	100	0.660	(0.022)	100
$\sigma_s = 10$, $c = \beta_0 - 30$							
	D	2.060	(0.032)	100	0.271	(0.002)	100
	β_0	69.905	(0.141)	100	1.307	(0.015)	100
	β_1	–0.303	(0.003)	100	0.023	(0.000)	100
	σs	9.941	(0.057)	100	0.490	(0.004)	100

$\sigma_s = 10$, $c = \beta_0 – 10$							
	D	1.926	(0.060)	100	0.604	(0.020)	98
	β_0	70.218	(0.313)	100	3.639	(0.097)	98
	β_1	–0.301	(0.008)	100	0.081	(0.002)	98
	σs	10.039	(0.129)	100	1.411	(0.027)	100

Single 100-microphone array

	Parameter	Estimate		n	SE(estimate)		n
$\sigma_s = 2.5$, $c = \beta_0 – 30$							
	D	2.017	(0.021)	100	0.220	(0.001)	100
	β_0	69.942	(0.028)	100	0.292	(0.002)	100
	β_1	–0.299	(0.000)	100	0.004	(0.000)	100
	σs	2.603	(0.007)	100	0.077	(0.001)	100
$\sigma_s = 2.5$, $c = \beta_0 – 10$							
	D	2.025	(0.028)	100	0.289	(0.002)	100
	β_0	70.013	(0.084)	100	0.954	(0.014)	100
	β_1	–0.302	(0.003)	100	0.030	(0.000)	100
	σs	2.432	(0.036)	100	0.378	(0.008)	100
$\sigma_s = 10$, $c = \beta_0 – 30$							
	D	1.966	(0.019)	100	0.206	(0.001)	100
	β_0	69.864	(0.076)	100	0.847	(0.006)	100
	β_1	–0.299	(0.001)	100	0.009	(0.000)	100

σs	10.032	(0.033)	100	0.301	(0.002)	100
$\sigma_s = 10$, $c = \beta_0 – 10$						
D	1.985	(0.023)	100	0.266	(0.002)	100
β_0	69.807	(0.163)	100	1.585	(0.020)	100
β_1	–0.295	(0.003)	100	0.027	(0.000)	100
σs	9.879	(0.087)	100	0.787	(0.011)	100

(b) Binary model (* indicates doubtful estimates – see text)

Multiple 4-microphone arrays

	Parameter	True	Estimate		n	SE(estimate)		n
$\sigma_s = 2.5$, $c = \beta_0 – 30$								
	D	2.0	1.977	(0.022)	100	0.242	(0.006)	96
	$(\beta_0 – c)/\sigma_s$	12.0	9.397*	(0.211)	57	3.756*	(0.281)	57
	β_1/σ_s	–0.12	–0.092*	(0.002)	57	0.042*	(0.003)	57
$\sigma_s = 2.5$, $c = \beta_0 – 10$								
	D	2.0	2.088	(0.037)	100	0.379	(0.018)	100
	$(\beta_0 – c)/\sigma_s$	4.0	3.277*	(0.150)	42	2.696*	(0.132)	42
	β_1/σ_s	–0.12	–0.099*	(0.004)	42	0.080*	(0.004)	42
$\sigma_s = 10$, $c = \beta_0 – 30$								
	D	2.0	2.077	(0.041)	100	0.380	(0.005)	100
	$(\beta_0 – c)/\sigma_s$	3.0	3.030	(0.035)	100	0.329	(0.004)	100
	β_1/σ_s	–0.03	–0.031	(0.001)	100	0.005	(0.000)	100
$\sigma_s = 10$, $c = \beta_0 – 10$								

Parameter	True	Estimate		n	SE(estimate)		n
D	2.0	1.924	(0.069)	96	0.718	(0.033)	96
$(\beta_0 – c)/\sigma_s$	1.0	1.246*	(0.074)	87	0.651*	(0.032)	87
β_1/σ_s	–0.03	–0.035*	(0.002)	87	0.016*	(0.001)	87

Single 100-microphone array

Parameter	True	Estimate		n	SE(estimate)		n
$\sigma_s = 2.5$, $c = \beta_0–30$							
D	2.0	2.019	(0.021)	100	0.221	(0.001)	100
$(\beta_0 – c)/\sigma_s$	12.0	12.344	(0.141)	100	1.231	(0.026)	100
β_1/σ_s	–0.12	–0.123	(0.001)	100	0.012	(0.000)	100
$\sigma_s = 2.5$, $c = \beta_0–10$							
D	2.0	2.064	(0.031)	100	0.316	(0.006)	100
$(\beta_0 – c)/\sigma_s$	4.0	4.984	(0.335)	100	2.646	(0.326)	99
β_1/σ_s	–0.12	–0.149	(0.009)	100	0.083	(0.013)	99
$\sigma_s = 10$, $c = \beta_0–30$							
D	2.0	1.968	(0.019)	99	0.206	(0.001)	99
$(\beta_0 – c)/\sigma_s$	3.0	2.991	(0.015)	99	0.141	(0.001)	99
β_1/σ_s	–0.03	–0.030	(0.000)	99	0.001	(0.000)	99
$\sigma_s = 10$, $c = \beta_0–10$							
D	2.0	1.985	(0.023)	100	0.267	(0.002)	100
$(\beta_0 – c)/\sigma_s$	1.0	0.998	(0.021)	100	0.199	(0.002)	100
β_1/σ_s	–0.03	–0.030	(0.000)	100	0.003	(0.000)	100

Table C3. Simulated coverage of 95% confidence intervals for the density of sound sources. Intervals back-transformed from ±1.96 times the estimated asymptotic standard error of D on the log scale. Signal-strength model fitted to simulated data from a population of $D = 0.5$ ha^{-1} sampled with 25 4-microphone arrays as in the main simulations ($\beta_0 = 70$ dB, and $\beta_1 = -0.30$ dB/m). 1000 replicates were simulated in each trial, but estimation was not possible when there were no 'recaptures' (number of individuals = total number of detections). Also shown are the number of individuals detected, the total number of detections, relative bias (RB), relative standard error (RSE) and the number of simulations that yielded estimates (*n*). SE in parentheses.

Scenario	Mean number of Individuals	Mean number of Detections	RB (%)	RSE (%)	Coverage (%)	*n*
$\sigma_s = 2.5$, $c = \beta_0-30$	68.3 (0.3)	158.8 (0.7)	–0.9 (0.4)	13.6 (0.03)	94.3	1000
$\sigma_s = 2.5$, $c = \beta_0-10$	15.6 (0.1)	18.9 (0.2)	–3.6 (1.4)	40.3 (2.6)	93.4	944
$\sigma_s = 10$, $c = \beta_0-30$	83.7 (0.3)	173.6 (0.7)	–0.6 (1.0)	30.0 (0.4)	91.3	1000
$\sigma_s = 10$, $c = \beta_0-10$	24.8 (0.2)	33.9 (0.2)	+5.1 (1.7)	95.8 (10.6)	81.4	994

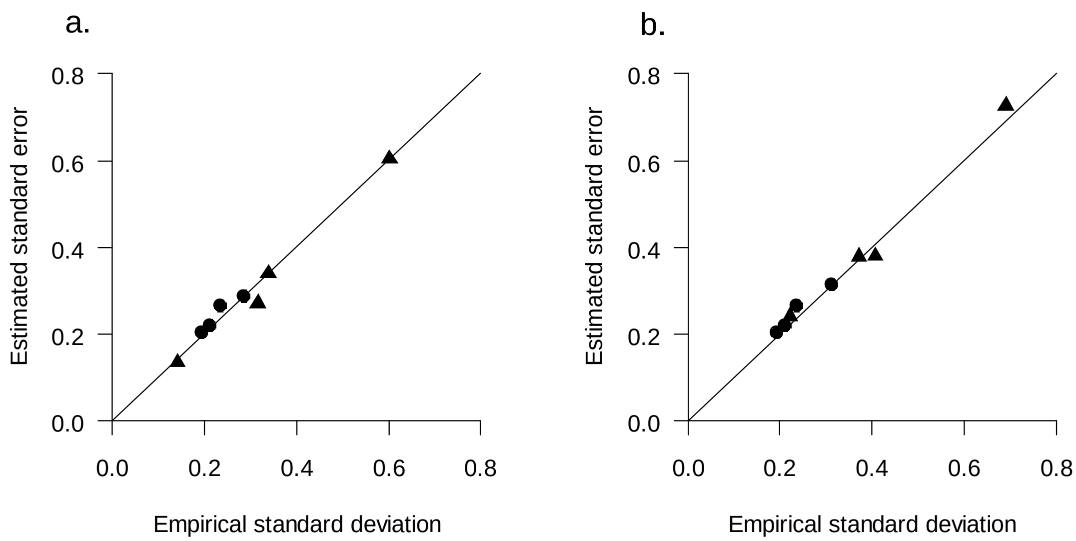

Fig. C1.

Asymptotic estimates of the precision of density estimates (ha^{-1}) from (a) signal strength model and (b) binary model, compared to empirical sampling standard deviation. Each point is for 100 simulations* with a particular combination of parameters (Table C2); ▲ multiple 4-microphone arrays, ● 100-microphone array. For large samples, unbiased and precise estimates of $SE(\hat{D})$ are expected to lie on the drawn line ($y = x$). * or slightly fewer in some cases – see text.