A field test of two methods for density estimation

Murray G. Efford, Bruce Warburton, Morgan C. Coleman, and Richard J. Barker

Abstract Density of wildlife populations is a key variable for management, yet reliable estimation is elusive. We tested one established method (trapping webs and distance analysis) and one novel method (inverse prediction from capture–recapture data) on a population of brushtail possums (*Trichosurus vulpecula*) whose density also could be determined by exhaustive removal. The study area was approximately 315 ha of coastal plantation forest surrounded on 3 sides by sand and water. We placed 4 lines of 9 cage traps at 20-m spacing in a square to form a "hollow grid." We set 5 hollow grids, each comprising 36 traps, for 5 days; we tagged and released possums. We later set 5 trapping webs of 50 traps each at the same sites; we caught possums and removed them over 4 days. Wide-area removal used a combination of acute poisoning and leghold trapping. The estimate of density by inverse prediction (1.88/ha, SE = 0.26) was consistent with the removal estimate (2.27/ha), whereas estimates from trapping webs were positively biased (6.5 to 8.0/ha, depending on method of analysis). The inverse prediction method frees capture–recapture from the straitjacket of conventional grids and should allow accurate landscape-scale estimation of density once the requisite trapping effort is identified.

Key words brushtail possum, capture–recapture, density estimation, inverse prediction, trapping web, *Trichosurus vulpecula*

Density of wildlife populations is a key variable for management. Live-trapping is the standard field method for species that are cryptic and mobile, but the analysis of such data to give unbiased estimates of density is problematic (Otis et al. 1978, Williams et al. 2002, Parmenter et al. 2003). In particular, the movement of animals on and off a trapping grid creates an unknown "edge effect." Attempts to estimate the edge effect and obtain unbiased estimates of density ($\hat{D} = \hat{N}/A_W$ where $\hat{N}$ is an estimate of population size and A_W is the "effective" trapping area obtained by adding a boundary strip) generally have failed. For example, estimates by the "nested subgrid" method of MacLulich (1951) and Otis et al. (1978) remain biased except when grids are large and capture rates high (Wilson and Anderson 1985*a*, Efford 2004).

Difficulties with grid trapping have inspired a search for alternatives. Foremost among these is the trapping web of Anderson et al. (1983). The radial distribution of first captures on a trapping web may be analyzed by distance methods (Buckland et al. 2001) or a geometric analysis (Link and Barker 1994) to estimate absolute density. The performance of trapping webs for estimating density of small mammals has been assessed by simulation (Wilson and Anderson 1985*b*, Lukacs 2002), by comparing grid-based and trapping-web estimates (Jett and Nichols 1987, Corn and Conroy 1998), and by comparing trapping-web estimates to estimates from enumeration of enclosed populations (Parmenter et al. 2003). The most critical field test (Parmenter et al. 2003) indicated that webs sometimes provide acceptable estimates with real data

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from rodent populations, but the results depended heavily on details of the analysis. Experts often selected methods of distance analysis that gave poor estimates of density.

Another class of methods for estimating density from capture–recapture data has been developed recently (Efford 2004, Efford et al. 2004). These methods fit a simple spatial model of animal trapping. The probability that an animal is caught in a trap at a given distance r from its home-range center is assumed to follow a 2-parameter spatial detection function $g(r)$ (e.g., half normal with parameters g_0 [detection probability when $r = 0$] and σ [spatial scale]), when there is no competition from other animals. Range centers are assumed to be Poisson-distributed with density D. The problem is to estimate D, g_0, and σ jointly from the trapping data. The locations of home-range centers are unknown, so trapping does not provide a sample of distances r (the basis for conventional distance analyses; e.g., Buckland et al. 2001). However, the mean distance between recaptures of marked individuals (d) does contain information on the scale of movements (σ), and information on D and g_0 is contained in conventional capture–recapture statistics (summarized as estimates of population size N and capture probability p). This enables us to use an indirect strategy for estimation: simulate trapped samples with varying, but known, D, g_0 and σ, and match the statistics calculated from these samples ($\hat{N}$, $\hat{p}$, $\bar{d}$) to those from our field data. "Matching" is done by simulating on a factorial design in parameter space and fitting a multivariate linear model to the simulated capture data to map the parameter space into the statistic space. The inverted linear model may then be used to "predict" the parameter values that correspond to the field data (hence "inverse prediction"; Pledger and Efford 1998, Efford 2004, Efford et al. 2004). Simulations use a queuing algorithm to allow for competition between animals for traps (Efford 2004). In addition to the usual assumptions of closed-population analysis regarding lack of population turnover and accurate reporting of marks (Otis et al. 1978), the method assumes that the animals occupy stable home ranges and that capture does not affect the probability of recapture at the same or different locations.

We tested inverse-prediction and trapping-web estimates of density for a population of brushtail possums (*Trichosurus vulpecula*) living in the North Island of New Zealand. The brushtail possum is a nocturnal, 2–4-kg, introduced conservation pest and the major wildlife reservoir of bovine tuberculosis in New Zealand (Cowan 1990). We compared the results from each method with an estimate of average density over a wide area relatively unaffected by edge effects. The inverse-prediction method does not rely on a particular trap configuration (simulations are performed with virtual traps arranged identically to the actual traps). For inverse prediction, we therefore arranged live traps in a novel "hollow grid" pattern that was easy to set up and operate.

Study area

We selected an area of exotic plantation forest at Waitarere (40°30′S, 175°14′E) on the southwest coast of the North Island. The study area was bounded to the west by the sea and to the north and east by the Manawatu River, leaving a single edge across which possums moved freely. The nominal southern limit of the study area was set by a dirt road. The study area comprised 294 ha of habitat (excluding open sand and nonwoody vegetation). This was 80% 10-year-old *Pinus radiata* plantation with a ground cover of grasses and pine needles and occasional bushes of gorse (*Pinus radiata* and coastal plantings for sand retention (especially *Acacia longifolia*).

Methods

Capture–recapture

We selected at random the centers of 5 trapping sites from within the 294-ha area. At each site we first set 36 cage traps at 20-m spacing in a square around the edge of a "hollow grid" (Figure 1). Each hollow grid was 180 m on a side. We baited traps with a piece of apple lured with flour and aniseed and locked them open for a week before trapping started. Capture–recapture occurred over 5 days (21–25 April 2002). We checked traps each morning. We identified possums individually with a numbered monel tag (National Band & Tag Company, Newport, Ky.) in each ear and released them where they were caught.

To determine the southern limit of the effective trapping area, we also live-trapped on a line 150 m outside and mostly parallel to the nominal southern boundary. We set 108 cage traps 20 m apart for 5 days. We tagged possums and released them as on the hollow grids.

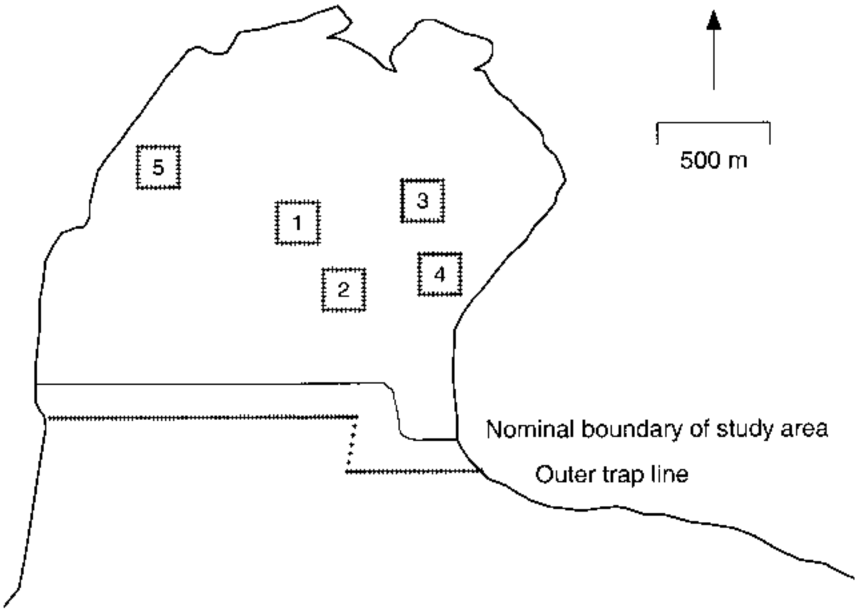

Figure 1. Study area used to compare methods of density estimation at Waitarere, southwest North Island, New Zealand, April–June 2002. Heavy line marks the vegetated area of a coastal peninsula. Brushtail possums were live-trapped, tagged, and released on the hollow grids and on the outer line ('+' indicates trap site). Trapping webs (not shown) were centered within the squares and used the same numbering. Intensive poisoning and removal trapping were conducted within the "nominal boundary" line to estimate wide-area density.

Trapping webs

Following live-trapping, we established a trapping web of 50 leghold traps (Victor No. 1, Woodstream Corp., Lititz, Pa.) at each site. Each web comprised 10 radial lines of 5 traps spaced 20 m apart, with the first trap on each line 20 m from the center. This design had been determined by simulation to minimize the sampling variance of density estimated by the geometric analysis of Link and Barker (1994) (simulations used a half-normal detection function). We lured traps with a mixture of flour and powdered sugar. We ran each trapping web for 4 consecutive nights, starting on 6 May (webs 2, 4 and 5), 7 May (web 3), or 8 May (web 1). We killed all animals humanely with a blow to the head.

Residual population

The residual population of the study area was poisoned and trapped. In the first phase, we set cyanide paste baits approximately every 4 m on lines 100 m apart throughout the area and oriented nearly north–south. We set further poison lines along the southern boundary and 50 m, 100 m, and 150 m inside the boundary and parallel to it. We used leghold traps along the seashore to reduce the risk to the public. We lured sites with a mixture of flour and powdered sugar 3 to 7 days before we laid baits on 20–23 May 2002. We recovered tagged and untagged dead animals by searching intensively along each line 3–5 days after baits were laid. Animals usually died within 2 m of the bait. Rain on 21–23 May probably reduced the effectiveness of poisoning.

We ran 10 randomly sited standard monitoring lines of 10 leghold traps at 20-m spacing (National Possum Control Agencies 2002) on the nights of 29–30 May. These showed a significant residual population (13 possum captures in 200 trap-nights). We therefore followed up with intensive leghold trapping on a 100-m × 100-m grid across the area. Due to limited manpower, we did not initiate trapping simultaneously across the entire area. We divided the area into 7 arbitrary blocks and trapped each block for 6 consecutive nights starting on different dates in the period 18 June 2002 to 26 June 2002. We killed possums humanely as before.

Data analysis

We estimated local density by simulation and inverse prediction from the capture–recapture data on each of the hollow grids using version 3 of program DENSITY (Efford et al. 2004; http://www.landcareresearch.co.nz/services/software/density/). DENSITY simulated trapping at known parameter values on a 2^3 factorial design (±20% of central values of each parameter) with 3 center points, and collected statistics ($\hat{N}$, $\hat{p}$, $\bar{d}$; definitions follow) as output from each simulation. Enough replicates were simulated to ensure that the coefficient of variation of the mean of each statistic was less than 1%. A multivariate linear model was fitted, inverted, and used to infer the density and detection function that best matched statistics from the field. For the closed population estimate $\hat{N}$ we chose Chao's second coverage estimator for Model M_{th} (Otis et al. 1978, Lee and Chao 1994), for its robustness to temporal variation in capture rates (possum activity is known to vary between nights) and to individual heterogeneity (we expected sex- and age-related variation in trappability). We also computed estimates from the pooled data for all grids with the maximum likelihood estimators for models M_0, M_t and M_b (Otis et al. 1978), and with several alternative estimators for models M_h and M_{th} (Burnham and Overton 1978, Chao 1987, Lee and Chao 1994, Pledger 2000, Dorazio and Royle 2003). Simulations assumed an even dispersion of animals at the scale of individual trap lines and a Poisson distribution for the pooled analyses. Daily capture probability $\hat{p}$ was estimated as $n/(k\hat{N})$ where n was the total number of captures and k was the number of occasions ($k = 5$). Mean recapture distance $\bar{d}$ was pooled across individuals.

Too few animals were caught on each trapping web for separate analyses (Table 1), so we pooled the counts on each ring of traps. Point transect analysis was performed in DISTANCE 4 (Thomas et al. 2002). Counts were related to 5 radial intervals (0–30 m, 30–50 m, 50–70 m, 70–90 m, 90–110 m). We fitted the default detection function (half-normal) and also a uniform detection function, both with cosine adjustment, as these methods were found by Parmenter et al. (2003) to provide the best estimates with their rodent data. We also applied Link and Barker's (1994) geometric method modified for a half-normal detection function.

We obtained a Petersen estimate of the residual population at the start of the first phase of removal from recaptures of tagged animals during that phase (including monitoring trapping), using Chapman's adjustment for small sample bias (Seber 1982). The residual population at the start of the second phase of removal was estimated by the generalized removal method for model M_{bh} of Otis et al. (1978). For removal analysis, we aligned data from blocks trapped asynchronously (i.e., sample day was relative to the start date for each block). We estimated the total population at the start of web trapping as the sum of animals killed when caught on the webs, monitoring lines, and cyanide baits in the first wide area removal phase, plus the generalized removal estimate from the second removal phase.

Table 1. Removal trapping of brushtail possums on concentric rings of 5 trapping webs at Waitarere, North Island, New Zealand, May 2002.

	Number caught on ring					
Web	1	2	3	4	5	Total
1	1	3	3	7	6	20
2	2	0	2	6	10	20
3	1	3	2	8	7	21
4	0	3	5	6	7	21
5	5	6	5	14	12	42
Total	9	15	17	41	42	124

Our estimate of the effective trapping area was subject to error because of possum movements across the southern boundary. We assessed this by the appearance during the removal phases of animals tagged on the external line, and by recalculating the density with different effective trapping areas.

Results

Density estimates

Density estimates by inverse prediction for each of the hollow grids ranged from 0.85/ha (SE = 0.42) to 2.30/ha (SE = 0.72) (Table 2). The mean of these values (1.49/ha, SE = 0.34) was close to the inverse prediction estimate (1.88/ha, SE = 0.26) for the pooled data (Table 2). The detection function fitted by inverse prediction to the pooled data had parameters $\hat{g}_0 = 0.229$ (SE = 0.033) and $\hat{\sigma} = 48.6$ m (SE =

Table 2. Live-trapping of brushtail possums on 5 randomly placed hollow grids at Waitarere, North Island, New Zealand, April 2002. M_{t+1} total number of individuals, Σm number of recaptures, $\hat{N}$ population estimate, $\bar{d}$ mean recapture distance (m), $\hat{D}$ density estimated by inverse prediction (/ha).[a]

Grid	M_{t+1}	Σm	$\hat{N}$	SE	$\bar{d}$	SE	$\hat{D}$	SE	95% CI
1	17	25	16.8	0.7	69.5	9.2	0.85	0.42	0.02–1.69
2	17	39	18.9	2.3	56.5	9.0	0.86	0.43	0.01–1.71
3	26	36	29.8	3.6	53.3	6.9	1.13	0.52	0.09–2.17
4	27	50	31.6	3.8	52.5	6.2	2.30	0.72	0.86–3.75
5	27	43	36.6	6.4	59.2	7.4	2.30	0.65	1.00–3.60
Pooled	112[a]	195[a]	128.5	7.2	59.4	4.0	1.88	0.26	1.37–2.39

[a] Pooled values are not the sum of the respective columns because 2 animals were each caught on 2 grids.

Table 3. Effect of estimator for closed-population size $\hat{N}$ on inverse-prediction estimates of density $\hat{D}$(/ha) and the parameters of a half-normal detection function ($\hat{g}_0$, $\hat{\sigma}$). Pooled data for brushtail possums trapped on 5 hollow grids at Waitarere, North Island, New Zealand, April 2002.

Model	Estimator	$\hat{N}$	SE	$\hat{D}$	SE	$\hat{g}_0$	SE	$\hat{\sigma}$	SE
None	M_{t+1}	112	—	1.77	0.22	0.254	0.026	48.7	2.6
M_0	ML[a]	114	1.7	1.76	0.21	0.255	0.030	48.6	2.7
M_t	ML[a]	114	1.6	1.76	0.21	0.253	0.032	48.6	2.6
M_b	ML[a]	119	4.2	1.93	0.26	0.167	0.037	48.3	3.1
M_h	Jackknife[b]	144.1	11.2	1.88	0.35	0.228	0.040	48.5	3.5
M_h	Chao N_h[c]	136.4	11.3	1.88	0.30	0.230	0.042	48.4	2.9
M_h	ML (2-part mixture)[d]	126.5	8.4	1.67	0.44	0.263	0.059	48.7	3.3
M_h	ML (Beta)[e]	169.1	43.3	2.45	0.44	0.158	0.029	47.9	2.9
M_{th}	Coverage 1[f]	135.1	8.2	1.85	0.24	0.234	0.032	48.6	2.8
M_{th}	Coverage 2[f]	128.5	7.2	1.88	0.26	0.229	0.033	48.6	2.7

[a] Otis et al. (1978).

[b] Burnham and Overton (1978).

[c] Chao (1987).

[d] Pledger (2000). Some simulations produced extreme values for $\hat{N}$ with this estimator; we rejected simulations for which $\hat{N} > 10M_{t+1}$.

[e] Dorazio and Royle (2003).

[f] Lee and Chao (1994).

2.7). Density estimates obtained with different closed population estimators ranged from 1.67 to 2.45/ha, but all 95% confidence intervals (±2 SE) included the initial estimate (Table 3). The inverse prediction estimate using data from the first 3 days of trapping ($\hat{D}_3$ = 1.74/ha, SE = 0.30) was similar to that from 5 days ($\hat{D}_5$ = 1.88/ha, SE = 0.26), suggesting that a usable estimate could have been obtained with less effort.

We also caught and tagged 40 animals on the boundary line, with 20 recaptures on that line. From these data, we obtained a further inverse prediction estimate ($\hat{D}$ = 1.39/ha, SE = 0.59; $\hat{g}_0$ = 0.032, SE = 0.010; $\hat{\sigma}$ = 63.2 m, SE = 11.6).

Estimates from the pooled trapping webs varied with the method of analysis (Table 4) but were consistently higher than those by capture–recapture and inverse prediction. The precision of trapping-web estimates (CV($\hat{D}$) 0.14–0.24) was similar to that of pooled estimates by inverse prediction (CV($\hat{D}$) 0.11–0.27).

Table 4. Density estimates $\hat{D}$ (/ ha) from pooled trapping web data. Waitarere, North Island, New Zealand, May 2002.

Analysis method	$\hat{D}$(SE)	95% CI	CV($\hat{D}$)
Distance–half-normal	6.53 (1.54)	3.95–10.79	0.237
Distance–uniform	6.53 (1.13)	4.04–10.53	0.174
Geometric	8.03 (1.16)	5.71–10.35	0.144

Wide-area density

All but 17 of the 112 animals tagged and released on the live-trapping squares were killed in the web-removal trapping. Eleven of the survivors from the web trapping were among the 354 animals killed in the first wide-area removal and monitoring, and another possum was recovered in the second removal phase. These data yield a Petersen estimate of 532 (SE = 84) possums.

The total population estimate, including data from the second removal phase, was 716 (SE = 7) (Table 5). The shore and the southernmost cyanide poison line enclosed an area of 294 ha. The "naïve" density in this area was therefore 2.44/ha. However, 10 of 40 individuals tagged on the trap line 150 m outside the nominal boundary of the study area also were caught in the wide-area removal, indicating a significant flux of animals across the boundary. We inferred by linear interpolation that 50% of animals tagged on a line 100 m outside the nominal boundary would have been caught in the wide-area removals. The area enclosed by the shore and such a line was 315 ha. From this adjusted estimate of the effective trapping area, we calculated a density of 2.27/ha.

Discussion

To estimate density we selected a closed-population estimator (Chao's second coverage estimator) a priori, rather than on the basis of the data. Capture–recapture data are often inadequate to distinguish between models of heterogeneity in capture probability (beta, finite mixture, etc.), and 2 models can each provide good fits to the observed data yet yield different estimates of N (Coull and Agresti 1999, Link 2003). Choice of the "wrong" model causes bias in $\hat{N}$, but it does not follow that $\hat{D}$ by inverse prediction also is biased. True population size is infinite in our spatial model, and $\hat{N}$ enters the inverse prediction algorithm only as an ad hoc correlate of local density (Efford et al.

Table 5. Total possum population estimated from successive phases of removal trapping at Waitarere, North Island, New Zealand, May–June 2002.

Category	Number of animals
Killed on trapping webs	124
Phase 1 removal (cyanide poisoning)	341
Killed on monitoring lines	13
Phase 2 removal (widespread leghold trapping)	
Day 1	67
Day 2	44
Day 3	54
Day 4	32
Day 5	16
Day 6	12
Subtotal	225
Phase 2 generalized removal estimate	238 (SE = 7)
Total	716 (SE = 7)

2004). Inverse prediction is insensitive to bias that occurs equally in the simulated and field data (Pledger and Efford 1998). When we compared $\hat{D}$ computed with different estimators for N (Table 3), most values were clustered within a narrow range of $\hat{D}$ with the pre-selected N estimator (–6% to +3%). This cluster included $\hat{D}$ based on the number of animals caught, M_{t+1}, despite M_{t+1} being a clearly biased estimator of N. Two $\hat{D}$ based on different maximum likelihood estimators for model M_h had large standard errors and fell outside the cluster of other estimates. Estimates of the spatial parameter σ were stable and unaffected by the N-estimator (range –1.4% to +0.2% of the value with the pre-selected estimator). Further work is needed to define the properties of a good N-estimator in this context, but low variance is certainly one.

Our removal estimate of the true density across the wide area was subject to bias caused by edge effects on the southern boundary and possibly also by net immigration of more distant animals during the removal phases. We evaluated likely edge effects by considering the width of a strip that should be added to the southern boundary to give the effective trapping area. The effective trapping area includes a number of "inside" animals missed by trapping that exactly balances the number of "outside" animals trapped. If the proportion of animals counted during wide-area removal declined linearly from 100% at the nominal edge of the study area to 25% on the outer (150-m) trap line, we estimate that 50% would be caught at 100 m. We used this as our estimate of strip width. A calculation of the 95% daily home-range radius from the detection function fitted by inverse prediction gives a similar figure ($2.45\sigma = 118$ m; Jennrich and Turner 1969). Hypothetically increasing the boundary strip width by 50% to 150 m increased the effective trapping area by only 3.4%, giving a density estimate of 2.20/ha rather than 2.27/ha. These effects are small compared to other errors. Similarly, negligible uncertainty was introduced by our reliance on a removal estimate of the wide-area population ($\mathrm{CV}(\hat{N}) \approx 1\%$) rather than complete enumeration.

Recruitment of long-distance migrants during the 10 weeks of our study is a further possible source of positive bias in the wide-area density. However, the study was done at a time of year (late autumn and early winter) after the main annual pulse of recruitment and dispersal (Cowan 1990, Efford 1998), and immigration was likely to have been minimal. Turnover generally is slow in populations of the brushtail possum (annual disappearance is on the order of 10–20%; e.g., Efford 1998), and there was no meteorological or other reason to expect an abrupt decline in the period of our study. It is reasonable to consider the population approximately constant across the 3 surveys.

Our best estimate of the true density (2.27/ha) was within the 95% confidence interval of the estimate by inverse prediction from the pooled capture–recapture data. The confidence intervals of trapping-web estimates did not include the estimated true density. Further adjustments for the potential positive bias in wide-area density due to immigration or edge effects would reduce the estimate of wide-area density and favor the inverse prediction estimates.

Simulations with a range of values suggested that trapping webs frequently produce density estimates with large positive bias (M. Efford, unpublished data). The capture locations of mobile animals on a web tend to be displaced from their actual home-range center toward the web center where the trap density is greatest. This increases the average slope of the detection function and causes positive bias (Borchers et al. 2002). Small webs also suffer from an edge effect analogous to that of trapping grids: the sample caught on the web includes peripheral animals whose ranges are centered outside the web.

The failure of trapping webs in this study may be due to their small size relative to possum movements. To check this we simulated removal trapping on webs in program DENSITY using detection parameter values from the pooled hollow grids (g_0 = 0.23, σ = 48 m) and a density of 2/ha. We first simulated trapping on the design used in the field: 5 50-trap webs (radius 100 m) operated for 4 days; home-range centers were Poisson-distributed, and detection followed a half-normal function of radial distance. Analyses were conducted on pooled data using a half-normal detection function with cosine adjustment as for the field study. Distance estimates of density (8.12/ha, SE = 0.10) were strongly biased (relative bias +306%, SE = 5; average of 1,000 simulations). The corresponding trapping-web estimate from the field (6.5/ ha) was close to the median of the simulated values (6.6/ha). The trapping-web estimates plausibly may have resulted from a true density of 2/ha. When corrected for bias the estimates were therefore consistent with the capture–recapture and wide-area removal estimates. When we simulated similar webs with twice the number of traps per line and a radius of 200 m, the relative bias was lower but still unacceptably large in our view (+64%, SE = 1). Conditions for the successful estimation of density with trapping webs remain to be defined.

Our initial choice of web design was an attempt to maximize precision for fixed total effort (R. J. Barker, unpublished data). Direct comparison of relative precision between the webs and hollow grids was problematic because the field costs differed. Webs were more difficult to survey than hollow grids and required more traps, but cage traps were more expensive and difficult to carry than leghold traps. Nevertheless the precision of estimates from the pooled hollow grids compared favorably with estimates from the trapping webs.

We have shown that capture–recapture is a viable field method for estimating the absolute density of wildlife populations when coupled with simulation and inverse prediction. Conventionally, live traps are placed in dense grids to minimize edge effects (e.g., Otis et al. 1978, Williams et al. 2002). This has the undesirable side effect that landscape coverage is often low and unrepresentative. Edge effects are not a consideration in the design of a live-trap layout to estimate density by inverse prediction, although the layout must include some intertrap distances on the scale of animal home ranges in order to sample animal movements. In particular, traps in scattered clusters such as hollow grids appear to provide largely unbiased density estimates both in simulations (Efford 2004; unpublished data) and in the field (this study). A hollow grid is preferable to a straight line because it samples animal movement in multiple directions rather than just 1, and it is often convenient to finish at the starting point. Lack of edge effect has the advantage that sampling effort may be subdivided into smaller units and distributed widely to obtain a more representative sample. Data or estimates from widely separated hollow grids (and, by extension, from trap clusters with other geometries) may be combined to estimate average density at landscape scales. At these scales there will often be substantial spatial variance in animal density, and it is desirable to randomize the placement of trap clusters to allow for this, possibly also stratifying by habitat. The optimal distribution of trapping effort is a subject for further investigation.

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