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SMALL-MAMMAL DENSITY ESTIMATION: A FIELD COMPARISON OF GRID-BASED VS. WEB-BASED DENSITY ESTIMATORS

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Abstract. Statistical models for estimating absolute densities of field populations of animals have been widely used over the last century in both scientific studies and wildlife management programs. To date, two general classes of density estimation models have been developed: models that use data sets from capture–recapture or removal sampling techniques (often derived from trapping grids) from which separate estimates of population size (\hat{N}) and effective sampling area (\hat{A}) are used to calculate density ($\hat{D} = \hat{N}/\hat{A}$); and models applicable to sampling regimes using distance-sampling theory (typically transect lines or trapping webs) to estimate detection functions and densities directly from the distance data. However, few studies have evaluated these respective models for accuracy, precision, and bias on known field populations, and no studies have been conducted that compare the two approaches under controlled field conditions. In this study, we evaluated both classes of density estimators on known densities of enclosed rodent populations. Test data sets ($n = 11$) were developed using nine rodent species from capture–recapture live-trapping on both trapping grids and trapping webs in four replicate 4.2-ha enclosures on the Sevilleta National Wildlife Refuge in central New Mexico, USA. Additional “saturation” trapping efforts resulted in an enumeration of the rodent populations in each enclosure, allowing the computation of true densities. Density estimates (\hat{D}) were calculated using program CAPTURE for the grid data sets and program DISTANCE for the web data sets, and these results were compared to the known true densities (D) to evaluate each model’s relative mean square error, accuracy, precision, and bias. In addition, we evaluated a variety of approaches to each data set’s analysis by having a group of independent expert analysts calculate their best density estimates without a priori knowledge of the true densities; this “blind” test allowed us to evaluate the influence of expertise and experience in calculating density estimates in comparison to simply using default values in programs CAPTURE and DISTANCE. While the rodent sample sizes were considerably smaller than the recommended minimum for good model results, we found that several models performed well empirically, including the web-based uniform and half-normal models in program DISTANCE, and the grid-based models M_h and M_{bh} in program CAPTURE (with \hat{A} adjusted by species-specific full mean maximum distance moved (MMDM) values). These models produced accurate \hat{D} values (with 95% confidence intervals that included the true D values) and exhibited acceptable bias but poor precision. However, in linear regression analyses comparing each model’s \hat{D} values to the true D values over the range of observed test densities, only the web-based uniform model exhibited a regression slope near 1.0; all other models showed substantial slope deviations, indicating biased estimates at higher or lower density values. In addition, the grid-based \hat{D} analyses using full MMDM values for \hat{W} area adjustments required a number of theoretical assumptions of uncertain validity, and we therefore viewed their empirical successes with caution. Finally, density estimates from the independent analysts were highly variable, but estimates from web-based approaches had smaller mean square errors and better achieved confidence-interval coverage of D than did grid-based

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approaches. Our results support the contention that web-based approaches for density estimation of small-mammal populations are both theoretically and empirically superior to grid-based approaches, even when sample size is far less than often recommended. In view of the increasing need for standardized environmental measures for comparisons among ecosystems and through time, analytical models based on distance sampling appear to offer accurate density estimation approaches for research studies involving small-mammal abundances.

Key words: capture–recapture; density estimation: accuracy, precision, and bias; distance-sampling theory; rodent density; small mammals; trapping grids, accuracy of density estimates; trapping webs, accuracy of density estimates.

INTRODUCTION

A fundamental requirement for many research studies and management operations involving animals is the accurate assessment of a species' density in its natural habitat. A few conspicuous animal species are conducive to complete enumeration for assessing population size (N) within well-defined areas (A), making density calculations relatively simple ($D = N/A$). However, many animal species are difficult to observe, and must be sampled using various direct observational procedures, capture–recapture techniques, or removal/harvest methods. A large number of statistical models have been derived to produce estimates of population sizes (\hat{N}), sampling areas (\hat{A}), and densities (\hat{D}) for animal species whose numbers and movement patterns cannot be enumerated in the field (see reviews in Seber 1982, 1986, 1992, Seber and Schwarz 1999).

In recent years, two general classes of estimators have emerged that rely on different configurations of field sampling designs. The oldest, and hence most commonly used, is a group of models that produce populations size estimates (\hat{N}) based on capture–recapture or removal techniques, and rely on separate sampling-areas estimates (\hat{A}) to calculate a density estimate (\hat{D}). These models have been particularly popular in estimating densities of terrestrial small mammals, usually with data from trapping grids. Early estimation models were often encumbered with a number of unrealistic assumptions regarding capture probabilities for calculating \hat{N} , until Otis et al. (1978) and White et al. (1982) synthesized a suite of models incorporating realistic variability in capture probabilities. These models were assembled in the computer program CAPTURE (White et al. 1978, 1982, Rexstad and Burnham 1991), which has been widely used in estimating N in small-mammal research studies. The measurement of the effective sampling area (A) has usually been derived through the summation of the trapping-grid area and an additional area outside of the grid from which some of the sampled animals have come (i.e., an estimated boundary strip of width \hat{W}). The size of this boundary strip has been estimated from inter-trap distances, the animals' home-range sizes, average animal movements among traps, mean maximum distance movements among traps, nested grids, or assessment lines (see Otis et al. [1978] and references therein).

The second class of models was developed using distance-sampling theory (Burnham et al. 1980, Buckland et al. 1993, 2001) and is applicable to data sets derived from line transects (Burnham et al. 1980), point transects (e.g., variable circular plots [Buckland 1987]), and trapping webs (Anderson et al. 1983). These models have relatively few assumptions, and these generally can be met during field sampling efforts. Computer software programs, such as TRANSECT (Laake et al. 1979), DISTANCE (Laake et al. 1993), and DISTANCE 3.5 (Thomas et al. 1998), were developed to analyze such data sets. These models and sampling designs have been incorporated into a number of studies, including small-mammal studies at a number of sites within the U.S. Long Term Ecological Research network (LTER), monitoring programs for rodent-borne zoonotic diseases conducted by public health agencies in the United States (Parmenter et al. 1999), and global-change/biodiversity programs around the world.

As with any analytical procedure, the accuracy of the method is critical to proper interpretation of results. Unfortunately, tests of density-estimator accuracy, precision, and bias under field conditions have been relatively few in number, and have yielded mixed results (Table 1). A number of estimator evaluations using capture–recapture methods on populations with known abundances (\hat{N} vs. N) have found that abundance has been generally underestimated because of individual heterogeneity (e.g., Buck and Thoits 1965, Carothers 1973, Greenwood et al. 1985, Manning et al. 1995). These studies demonstrated that estimators with heterogeneity and behavior components generally perform best, a finding that has been typical of such empirical evaluations of closed-model estimators of population size (Manning et al. 1995). Note also that in many of these studies, estimates were limited to population sizes, not densities; i.e., no attempts were made to estimate the effective sampling area of the populations.

Transect and web-based methods, using distance-sampling theory, have been field tested on known population densities with better results (Table 1). Methods using perpendicular distances on transect lines or trapping webs often produced acceptable results on large mammals (Robinette et al. 1974, Hone 1988, White et al. 1989, Southwell 1994), birds (Bollinger et al. 1988), ground-dwelling beetles (Parmenter et al. 1989), and a

TABLE 1. Summary of literature findings of density-estimator performances on known populations, by parameter used.

Taxa or object type	Location	Estimators†	Reported results	Citation
Population size estimate, \hat{N}				
Perch, bass, bluegills Percidae, Centrarchidae	Illinois, USA	Petersen (1896)	\hat{N} underestimated	Buck and Thoits (1965)
Cottontail rabbit (<i>Sylvilagus floridanus</i>)	Ohio, USA	Schnabel (1938), Schumacher and Eschmeyer (1943), and geometric regressions	\hat{N} underestimated, but one geometric estimator proved accurate	Edwards and Eberhardt (1967)
Taxicabs	Edinburgh, Scotland	Chapman (1951), Leslie (1952), Carothers (1973)	\hat{N} underestimated	Carothers (1973)
Striped skunk (<i>Mephitis mephitis</i>)	North Dakota, USA	Program CAPTURE and others	\hat{N} underestimated; Jackknife most accurate	Greenwood et al. (1985)
Gray-tailed voles (<i>Microtus canadensis</i>)	Oregon, USA	Program CAPTURE	Most underestimated \hat{N} ; heterogeneity models and Jackknife most accurate	Manning et al. (1995)
Density estimate, \hat{D}				
Elephant (<i>Loxodonta africana</i>)	Africa	Variety of strip census methods and transect analyses	Two belt-transect methods and one sighting-distance analysis method gave accurate results	Robinette et al. (1974)
Wooden blocks, sacks, and deer carcasses	Colorado, USA, and Utah, USA			
Pig carcasses (<i>Sus scrofa</i>)	Australia	Program TRANSECT	Fourier series most accurate; other models also accurate	Hone (1988)
Bobolinks (<i>Dolichonyx oryzivorus</i>)	New York, USA	Program TRANSECT, using transect and circular plot data	Transects better than circular plots; some \hat{D} values overestimated	Bollinger et al. (1988)
Bricks	Lake Huron	Program DISTANCE	Accurate \hat{D} computed	Bergstedt and Anderson (1990)
Mule deer (<i>Odocoileus hemionus</i>)	Colorado, USA	Program TRANSECT	Accurate \hat{D} values using negative exponential and exponential polynomial models	White et al. (1989)
Kangaroos (<i>Macropus</i> spp.)	Australia	16 radial and perpendicular transect estimators	Five estimators accurate, with <5% bias	Southwell (1994)
Darkling beetles (<i>Eleodes</i> spp.)	Wyoming, USA	Program TRANSECT	Accurate \hat{D} values using negative exponential, exponential, and Fourier series	Parmenter et al. (1989)
"Model" desert tortoises (<i>Gopherus agassizii</i>)	Nevada, USA	Program DISTANCE	Accurate \hat{D} values using transect analyses; <-4% bias for "adult" models; -20% bias for "juveniles"	Anderson et al. (2001)

† For the computer program CAPTURE (grid-based estimators), see White et al. (1978, 1982) and Rexstad and Burnham (1991); for TRANSECT, see Laake et al. (1979); for DISTANCE (web-based estimators), see Laake et al. (1993).

variety of inanimate objects (Robinette et al. 1974, Bergstedt and Anderson 1990, Otto and Pollock 1990, Anderson et al. 2001).

While no attempt has been made to directly compare grid-based and web-based density estimation models using known population densities, two studies have reported on field comparisons of the methods on wild (unknown) populations. Corn and Conroy (1998) compared two density estimators using a single data set from a mongoose population (*Herpestes javanicus*) in

Antigua, West Indies. They found large discrepancies in density estimates, with DISTANCE producing $\hat{D} = 9.5 \pm 2.9$ mongooses/ha (mean ± 1 SE), and CAPTURE producing $\hat{D} = 1.8 \pm 0.1$ mongooses/ha; however, because the true density was not known, the more accurate estimate could not be determined. Similarly, Jett and Nichols (1987) compared the density estimates obtained from a single web and grid data set on meadow voles (*Microtus pennsylvanicus*) in Pennsylvania (USA), and obtained values of 112 ± 14.6 voles/ha

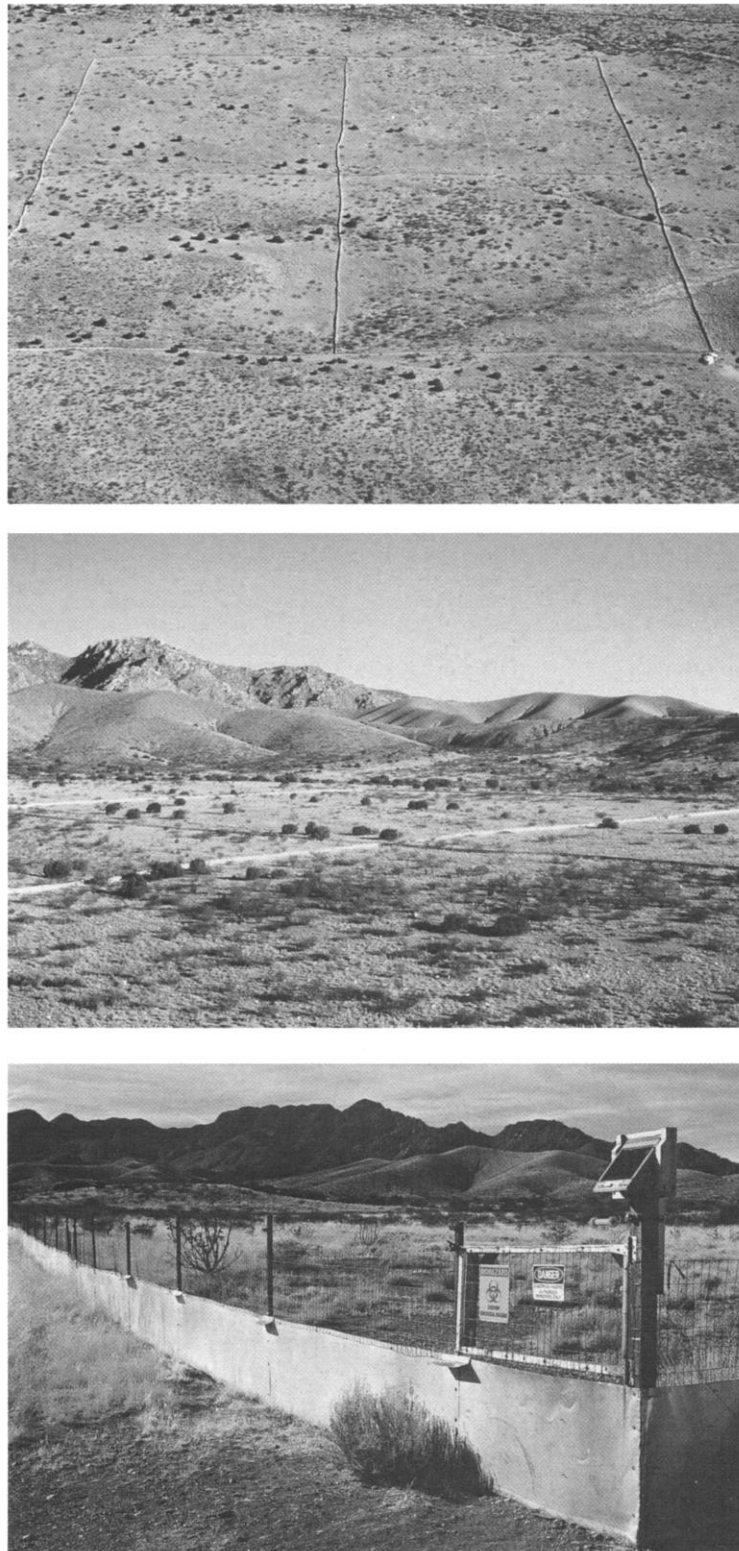


FIG. 1. (Top) Aerial photograph of study area, looking northward and showing the four 4.2-ha enclosures on the Sevilleta National Wildlife Refuge, New Mexico, USA. (Middle) Oblique angle aerial photograph looking northwest, showing habitat within the enclosures. (Bottom) Photo looking west-northwest; section of enclosure wall showing steel rodent-proof wall section topped with anti-predator electric wire and fencing.

from the web and 99 ± 15.8 voles/ha from the grid; again, the true density was unknown.

In our present study we assessed the mean relative mean square error, accuracy, precision, and bias of these two classes of density estimators on a series of 11 data sets compiled from field capture–recapture studies of rodents. The rodent populations were sampled in four 4.2-ha enclosures, in which the absolute rodent densities were known. We compared the density estimates calculated from grid-based estimators (CAPTURE) and web-based estimators (DISTANCE) with the known density values of each data set. We also evaluated each model's assumptions within the context of the experimental design and the observed data.

In addition to understanding the overall performance characteristics of density estimation models, a second important component in evaluating either class of density estimation models is how well each model performs with typical, realistic field sample sizes. For many of the density estimation models, theoretical considerations have led to recommended sample sizes in the range of ~80–100 individuals per taxon (Otis et al. 1978, Burnham et al. 1980, Buckland et al. 1993, 2001). Sample sizes of this magnitude are often difficult to obtain; hence, this study focused on the performance of the methods on data sets where the sample size, while realistic, was substantially smaller than the recommended standards.

Finally, in view of the wide variety of approaches and data manipulations used by researchers in estimating small-mammal densities, we conducted a “blind” evaluation of density estimation techniques using 11 independent researchers experienced in population estimation methods. In this part of the study, each researcher calculated density estimates for each grid- and web-based data set without knowing either the true density values or which data-set pairs (grid and web) were from the same enclosures. We then compared the results of the researchers’ “blind” density estimates with the true densities to evaluate the various approaches taken and to assess the variation among analysts; we also compared the analysts’ results to those of each individual model in programs CAPTURE and DISTANCE.

STUDY AREA

Site description

The field experiment was conducted in the foothills of the Sierra Ladrone, on the Sevilleta National Wildlife Refuge, Socorro County, in central New Mexico, USA (latitude $34^{\circ}24'29''$ N, longitude $107^{\circ}00'05''$ W, elevation 1690 m). The study site was in a valley with a slight slope (<5%) and easterly aspect (Fig. 1). The vegetation on the site was a mix of creosotebush (*Larrea tridentata*), shadscale (*Atriplex confertifolia*), honey mesquite (*Prosopis glandulosa*), one-seed juniper

(*Juniperus monosperma*), and a variety of grasses, including galleta grass (*Pleuraphis jamesii*), black grama (*Bouteloua eriopoda*), and several species of sacaton (*Sporobolus* spp.); plant nomenclature follows Kartesz (1994). Twelve rodent species inhabited the area, including Ord's kangaroo rat (*Dipodomys ordii*), Merriam's kangaroo rat (*D. merriami*), the banner-tailed kangaroo rat (*D. spectabilis*), silky pocket mouse (*Perognathus flavus*), deer mouse (*Peromyscus maniculatus*), brush mouse (*P. boylii*), white-footed mouse (*P. leucopus*), northern grasshopper mouse (*Onychomys leucogaster*), Texas grasshopper mouse (*O. arenicola*), western harvest mouse (*Reithrodontomys megalotis*), plains woodrat (*Neotoma micropus*), and the white-throated woodrat (*N. albigula*); rodent nomenclature follows Wilson and Reeder (1993). Annual precipitation averaged 285 mm (Sevilleta Long Term Ecological Research [LTER] Red Tank Meteorological Station, 1990–1999), of which ~60% fell during the summer monsoon months of June through September. Mean monthly temperatures ranged from 8.9°C in December to 31.4°C in July. Soils on the site were deep, well-drained alluvium, classified as fine-loamy, mixed, thermic Typic Haploargids (Berino-Dona Ana association) (Johnson 1988).

Rodent enclosures

Four rodent enclosures were constructed in 1997 (Fig. 2). Each square enclosure was ~4.2 ha in size (~205 m on a side). Some terrain features (hills and arroyos) caused small shifts in wall alignments, but all walls were mapped with global positioning system (GPS) units using post-processed, differentially corrected GPS data (accuracy of ~70 cm). These data were then used to derive accurate enclosure area estimates. The four enclosures were arranged in a 2×2 array, sharing interior walls with adjacent enclosures (Fig. 2). The enclosure walls were made of smooth sheet steel, buried ~60 cm into the soil and extending ~60 cm above the ground (Fig. 1). A predator-exclosure fence and electric wire extended above the top of the metal fence to exclude coyotes, foxes, bobcats, weasels, and snakes; owls and hawks could still potentially gain entry to the study site (although none were observed during this study).

Each enclosure had a surveyed trapping grid and trapping web established in the enclosure's center, with permanently marked and labeled stakes at each trap location. Trapping grids were composed of 144 traps in a 12×12 arrangement (Fig. 2). Trap intervals were 10 m, so the grid size was 110 m square, or 1.21 ha. While this grid size is obviously smaller than the size of the web (see below), we elected to maintain a comparable number of traps (web = 148; grid = 144) in each sampling scheme rather than try to maintain equal trapping areas. The edge of each trapping grid was ~50 m from the enclosure wall.

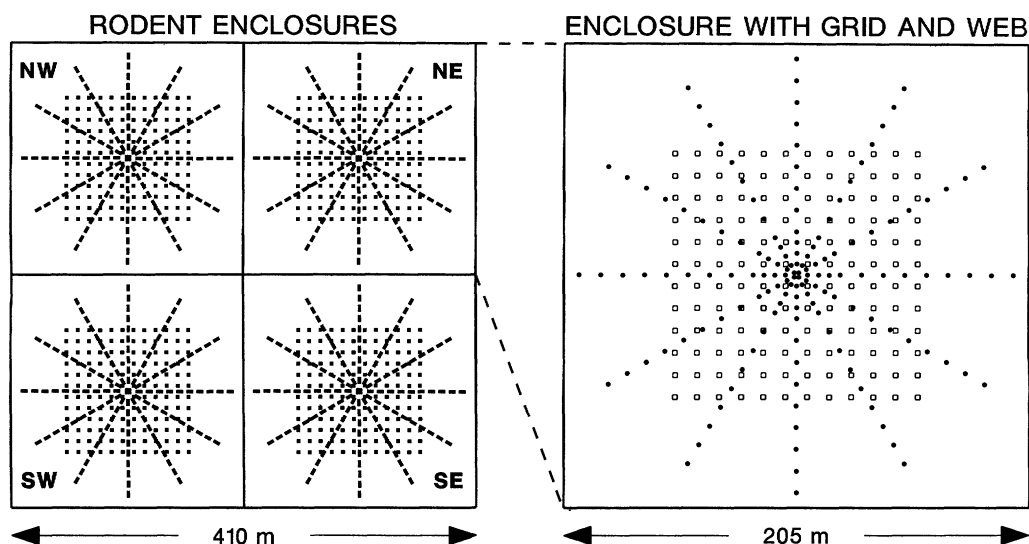


FIG. 2. (Left) Schematic diagram of the four enclosures (identified by compass-direction abbreviations; see top panel of Fig. 1), showing the locations of trapping webs and trapping grids. (Right) Enlargement of single enclosure showing trap locations on web (●) and grid (□).

The trapping webs each consisted of twelve radial lines of 100 m each (Fig. 2). Each trapping line had 12 trap stations; the first 4 trap stations were at 5-m intervals from the center (5, 10, 15, and 20 m), and the next 8 trap stations were at 10-m intervals (30, 40, 50, 60, 70, 80, 90, and 100 m). We placed an additional four traps at the web center; thus, the total number per web was 148 traps. The circular area of each web was 3.14 ha, and the edge of the web's perimeter varied from ~5 m (at mid-wall) to ~50 m (at the corners) from the enclosure wall.

METHODS

Field rodent trapping

The field trapping of rodent populations in the enclosures consisted of two parts. First, we conducted sequential web and grid trapping sessions in each enclosure to generate the data sets for the evaluation of the density estimators. Next, we conducted "saturation trapping" to completely enumerate the rodent populations within the enclosure walls; these efforts allowed an appropriate census of rodent numbers as a basis for comparison.

To generate the test data sets, we trapped all four enclosures simultaneously for two periods of five consecutive nights, 28 June–2 July and 5–9 July 1998. During the first trapping session, the northwest and southeast enclosures were sampled as grids, while the other two enclosures were sampled as webs (Fig. 2). Between trapping sessions, the trap arrangement (grid or web) in each enclosure was switched, and then sampled again for five nights. Thus, each cell was subjected to both web and grid sampling during the first part of the study.

Traps were Sherman live traps (H. B. Sherman, Tallahassee, Florida, USA), and were baited every evening with a seed mixture coated with molasses. Traps were checked each morning between 0530 and 0800 hours. Traps were closed during the day, and reopened each evening. Rodents were identified to species (using body measurements in the case of murids), and marked with both PIT tags (MUSICC Chip Identification System, Avid Identification Systems, Norco, California, USA) and ear tags (except for *Perognathus flavus*, which was too small for ear tags; for this species, we used unique toe clips for identification). The multiple tags ensured high accuracy of individual identifications, and reduced the possibilities of tag losses. Other data recorded included trap location, sex, body mass at each capture event, reproductive condition, and any evidence of wounds. Data on all recaptured rodents were checked against previously recorded data to ensure accuracy. Rodents were then returned to their point of capture and released shortly after processing (usually by 0830 hours). All field personnel used standard safety procedures (Mills et al. 1995) to prevent zoonotic disease transmission.

As part of an ongoing hantavirus research program, on the first capture of every cricetine rodent, we collected a blood sample to test for Sin Nombre Hantavirus using procedures described in Parmenter et al. (1998). Previous research (Parmenter et al. 1998) showed that these procedures had extremely minimal effects on murid rodent recapture probabilities; in a sample of 1000 murid rodents in New Mexico, the recapture percentage of "control" (=non-bled) rodents was 50.0%, while the recapture percentage of bled rodents was 50.1%.

We attempted to census the actual total number of rodents inhabiting each enclosure, to serve as a basis

to compare estimates of density to true density. Following the two five-night trapping periods, we established a "saturation" grid of live traps that extended from wall to wall in each enclosure. These grids were 22×22 trap stations (484 traps per enclosure) at 10-m intervals. Traps were opened and baited on 13 July, and run for four consecutive nights as described above. After a weekend break, we resumed trapping during 20–24 July. Each enclosure cell was trapped until we found no "new" (=unmarked) animals, after which we terminated trapping efforts in that cell. We did not count obvious juvenile animals as "new" during these last two weeks of trapping, as they would not have been at risk of being sampled during the previous two weeks of the study. The criterion of no new animals was met after five additional nights of trapping in one cell, and required six, seven, and eight additional nights in the other three enclosures, respectively. The "true densities" of each species were calculated as the number of individuals within a particular enclosure divided by the actual area of that enclosure.

Density estimation

Density estimates were obtained using program CAPTURE (Rexstad and Burnham 1991) for the grid-based data sets and DISTANCE (Laake et al. 1993) for the web-based data sets. (Note: other approaches for web-based data sets exist [e.g., Link and Barker 1994], but require equidistant trap spacing along web trap lines, which was not the case with the enclosure webs; program MARK [White and Burnham 1999] also analyzes grid-based data, and was used by several of the independent researchers in the second phase of analyses.) We took two approaches to the evaluation of the different estimators. First, a subset of the authors (R. R. Parmenter and C. A. Parmenter) calculated the density estimates for the rodent populations using each estimator in the two computer programs. For these analyses, each data set was used in its entirety (i.e., no data truncation or pooling was performed). In program CAPTURE, data were provided in "xy-reduced" format (all capture locations for all rodents), and CAPTURE was instructed to run all available population estimators; nested grid analyses were conducted using four grids, defined by the outermost four rings of traps (grid sizes = 9×9 , 10×10 , 11×11 , 12×12). For the grid-based data sets, population size estimates (\hat{N}) were computed, along with several sampling area (\hat{A}) estimates: (1) grid area (A_{grid}) plus a boundary strip (\hat{W}) equal to one-half of a trap interval; (2) grid area (A_{grid}) plus a boundary strip (\hat{W}) equal to one-half of the estimated mean maximum distance moved (MMDM) of each rodent population, where "maximum distance moved" was the distance between the two farthest capture locations for each individual rodent; (3) grid area (A_{grid}) plus a boundary strip (\hat{W}) equal to the full estimated MMDM of each rodent population; and (4) nested grids (an analysis procedure featured in CAP-

TURE). From these estimates, density estimates (\hat{D}) were derived in all combinations of \hat{N} and \hat{A} .

For the web-based data sets, using program DISTANCE, data were entered as interval data (using first-capture locations for each individual rodent, with intervals defined as the midpoints between trap rings; i.e., 0, 2.5, 7.5, 12.5, 17.5, 25, 35, . . . , 105 m). DISTANCE was instructed to run all estimators with all adjustment terms, using sequential model selection, selection criterion set to "AIC," and model monotonicity set to "weak."

For the grid-based data sets, sampling variance estimates for \hat{D} were derived from \hat{N} variances calculated by program CAPTURE for methods (1) and (4) above; for methods (2) and (3) using one-half or full MMDM boundary-strip estimates, sampling variances of \hat{D} (incorporating variances for both \hat{N} and \hat{A} using the Delta method [Seber 1982]) were derived from the equation

$$\text{Var}(\hat{D}) = \frac{\text{Var}(\hat{N})}{\hat{A}^2} + \frac{N^2 \text{Var}(\hat{A})}{\hat{A}^4}$$

where $\text{Var}(\hat{N})$ was computed by program CAPTURE, and the estimated area (\hat{A}) was calculated as

$$\hat{A} = L^2 + 4L\hat{W} + \pi\hat{W}^2$$

where L = length of grid side (110 m), and \hat{W} = species-specific mean maximum distance moved (MMDM). This latter equation represents the sum of the grid area (L^2) and the extended "effective trapping area" boundary zone composed of four rectangles ($L \times \hat{W}$) on the sides of the grid plus the combined four quarter-circle areas outside the grid corners ($\pi\hat{W}^2$). For one-half MMDM areas, \hat{W} was divided in half. The variance of \hat{A} was computed using the Delta method (Seber 1982) as

$$\text{Var}(\hat{A}) = (4L + 2\pi\hat{W})^2 \text{Var}(\hat{W}).$$

For the web-based data sets, density estimates and sampling variances from program DISTANCE were calculated in all possible combinations of models and adjustment functions. The models for detection functions included the uniform, negative exponential, half-normal, and hazard models; three adjustment functions were used with each model, including the cosine, Hermite, and polynomial. The estimated density values were then compared to the true density values obtained from the saturation-trapping effort, and evaluated for confidence-interval coverage, mean relative mean square error, accuracy, precision, and bias.

Both computer programs (CAPTURE and DISTANCE) included a selection routine that indicated which estimator model best fit the individual data set being analyzed (see Otis et al. 1978, Buckland et al. 1993, 2001, Burnham and Anderson 1998); therefore, we noted which model was selected as the most "appropriate" for each rodent data set. Estimates from these best models were compared to the true densities to assess their performance.

In the second approach, another subset of co-authors (D. R. Anderson, K. P. Burnham, A. B. Franklin, B. Lubow, M. Miller, G. S. Olson, J. Pollard, E. Rexstad, T. M. Shenk, T. R. Stanley, and G. C. White) conducted a “blind” analysis of densities without knowing either the true densities or which grid- and web-data sets were from the same enclosure. The purpose of this exercise was to evaluate confidence-interval coverage, relative mean square error, accuracy, precision, and bias for a range of approaches by a number of researchers who have training and expertise in estimating population densities, and to determine if the “experts” could produce more-accurate estimates than the default values available in programs DISTANCE or CAPTURE. Five of the people (D. R. Anderson, K. P. Burnham, E. Rexstad, T. R. Stanley, and G. C. White) had been active in developing statistical theory and computer software for distance sampling or capture–recapture surveys and could be considered experts in these areas. The remaining six people had intensive training and extensive experience in the use of these models and could be expected to be working at the state-of-the-science level in this area. Similar tests have been conducted with line-transect data sets by Anderson and Southwell (1995).

In this part of the study, we provided each analyst with a detailed description of the study area, the trap arrangements, the methods, the species, and the raw trapping data. The analysts were first given all the grid-based data sets (labeled consecutively with data set numbers, but without reference as to which enclosure or sampling period they represented), and were asked to calculate their best density estimate using any technique they deemed appropriate. After returning their grid-based density estimates, they were given the web-based data sets for density calculations (with different data set numbers so that web-based and grid-based data sets could not be paired). The results of the two approaches were then compared to the true densities to evaluate confidence-interval coverage, relative mean square error, accuracy, precision, and bias.

Evaluation of assumptions

The models included in programs CAPTURE and DISTANCE require that certain assumptions be met in order to expect accurate results. For the capture–recapture estimators using the grid-based data, the models assumed that the rodent study populations were geographically and demographically closed (i.e., no immigration or emigration, and no births or deaths, respectively), and that rodent capture probabilities varied according to the specific models being evaluated. In regard to population closure, the enclosure walls ensured geographic closure by preventing animals from entering or leaving the enclosure cells (see *Results: Estimator assumptions*, below); demographic closure was controlled by excluding obvious juvenile animals (recent births) from the data set, and reducing predation

by erecting the predator fences (Fig. 1) to exclude coyotes, foxes, weasels, badgers, and snakes. We have assumed that mortality from other sources (e.g., owls, diseases, or parasites) was minimal during the short period of study.

The various estimators in program CAPTURE assumed different sources of variation in rodent capture probabilities. The estimators included: (1) the null model (M_0 [Otis et al. 1978]) that assumed equal capture probabilities among individuals; (2) two heterogeneity models (M_h [Otis et al. 1978] and M_{h-Chao} [Chao 1988]) that assumed capture probabilities varied independently among individuals (i.e., based on sex, age, social status, health, etc.); (3) the behavior model (M_b [Otis et al. 1978]) that assumed capture probabilities varied with trap experience (i.e., “trap happy” or “trap shy” individuals); (4) two time models (M_t [Otis et al. 1978] and M_{t-Chao} [Chao 1989]) that assumed capture probabilities varied through time (e.g., due to weather changes); and (5) a group of models that incorporated different combinations of these sources of variation (M_{bh} [Otis et al. 1978], M_{th} [Rexstad and Burnham 1991], $M_{th-Chao}$ [Chao et al. 1992], and the variable probability removal model, M_{vpr} [Pollock and Otto 1983]). During the analyses of the grid data sets, program CAPTURE evaluated the variations in rodent capture probabilities within each data set to determine if each model’s assumptions had been met.

The web analyses relied on three assumptions: (1) rodents near the center of the web were captured with certainty ($g(0) = 1.0$) by the end of the 5-d sample period; (2) rodents did not preferentially move toward or away from the center of the web before being captured; and (3) distances from the web center to each trap location were measured accurately.

We evaluated each of these assumptions as follows: Assumption 1 (complete capture of rodents in the web center) was evaluated by examining each data set for the appearance of “new” (unmarked) rodents in the web center during the latter phases of the 5-d trapping period; if no unmarked rodents were trapped in the center after the first several nights of trapping, then the assumption of complete captures was supported. Assumption 2 (no differential movements) was evaluated by assessing mean species-specific directional movements among repeated-capture events for all individuals in each rodent species. While this approach could not reveal differential movements prior to an animal’s first capture, we could detect differential movements between first and second and subsequent captures, and assess the degree to which species might differentially move toward or away from the web center. Assumption 3 (accurate measurements) was satisfied, as each trap location’s distance had been carefully measured with meter tapes.

Evaluation of estimators

Density estimates derived from all estimators in CAPTURE and DISTANCE were compared with the

TABLE 2. Rodent survey information from web and grid trapping in each of four enclosures for 12 species that inhabit the Sevilleta National Wildlife Refuge, New Mexico, USA (1998).

Attribute†	Enclosure cell‡			
	NE	NW	SW	SE
<i>Perognathus flavus</i>				
<i>N</i>	88	81	39	58
<i>D</i>	20.6	19.1	9.4	13.8
<i>Dipodomys merriami</i>				
<i>N</i>	0	0	0	12
<i>D</i>	0	0	0	2.9
<i>D. ordii</i>				
<i>N</i>	0	0	0	6
<i>D</i>	0	0	0	1.4
<i>D. spectabilis</i>				
<i>N</i>	0	4	0	1
<i>D</i>	0	0.9	0	0.2
<i>Peromyscus boylii</i>				
<i>N</i>	2	0	11	5
<i>D</i>	0.5	0	2.7	1.2
<i>P. leucopus</i>				
<i>N</i>	5	5	21	8
<i>D</i>	1.2	1.2	5.1	1.9
<i>P. maniculatus</i>				
<i>N</i>	14	14	26	0
<i>D</i>	3.3	3.3	6.3	0
<i>Reithrodontomys megalotis</i>				
<i>N</i>	5	10	0	4
<i>D</i>	1.2	2.4	0	1.0
<i>Onychomys arenicola</i>				
<i>N</i>	6	1	6	4
<i>D</i>	1.4	0.2	1.5	1.0
<i>O. leucogaster</i>				
<i>N</i>	1	3	1	1
<i>D</i>	0.2	0.7	0.2	0.2
<i>Neotoma albigula</i>				
<i>N</i>	0	0	16	8
<i>D</i>	0	0	3.9	1.9
<i>N. micropus</i>				
<i>N</i>	16	5	0	0
<i>D</i>	3.7	1.2	0	0

† *N* = measured population size; *D* = calculated true densities (rodents/ha).

‡ Enclosure cell abbreviations refer to compass directions (see Fig. 1). The area of the NE enclosure cell = 4.2781 ha, NW = 4.2500 ha, SW = 4.1317 ha, and SE = 4.1948 ha.

known “true” densities of each rodent population using the following attributes:

1) Achieved confidence-interval coverage, based on whether or not the true density (*D*) was included within the 95% confidence interval of the estimated density (\hat{D}).

2) Mean relative mean square error ($\overline{\text{RMSE}}$, as a percentage), computed as

$$\overline{\text{RMSE}} = \frac{1}{k} \sum_{i=1}^k \frac{(\hat{D}_i - D_i)^2}{D_i} \times 100$$

where $i = 1, 2, 3, \dots, k$ density estimates. Smaller

values of $\overline{\text{RMSE}}$ indicated better estimator performance.

3) Mean relative accuracy ($\overline{\text{RA}}$, as a percentage), computed as

$$\overline{\text{RA}} = \frac{1}{k} \sum_{i=1}^k \frac{|\hat{D}_i - D_i|}{D_i} \times 100$$

where $i = 1, 2, 3, \dots, k$ density estimates. While we acknowledge that a true measure of accuracy, defined as the “exact conformity to truth” (White et al. 1982: 18), is not attainable in sampling studies, we used this equation as an estimator of the absolute deviation (+ or −) of \hat{D} from *D* across the sampled populations (Parmenter et al. 1989). Deviation values near zero indicated a high degree of accuracy.

4) Precision, as measured with the means of each model-based estimator’s coefficient of variation (CV, as a percentage); individual model CV estimates were calculated within programs CAPTURE and DISTANCE for each data set.

5) Mean relative bias ($\overline{\text{RB}}$, as a percentage), computed as

$$\overline{\text{RB}} = \frac{1}{k} \sum_{i=1}^k \frac{\hat{D}_i - D_i}{D_i} \times 100$$

where $i = 1, 2, 3, \dots, k$ density estimates (White et al. 1982:19).

Finally, for the two most accurate grid-based and web-based estimators, we evaluated the ability of each estimator to accurately estimate *D* over a range of rodent densities using linear regression analyses (\hat{D} vs. *D*); the most accurate estimator would have the highest correlation coefficient and the slope closest to 1.0. We also assessed these estimators’ sensitivity to variations in rodent cumulative capture probability (P_c , estimated as the total number of individuals captured, M_{t+1} , for each test population during grid or web sampling, divided by the total number of individuals, *N*, of that test population in each enclosure). We used linear regression analyses to test this relationship ($\overline{\text{RA}}$ vs. P_c); regressions with slope values near zero, or regressions with small correlation coefficients, would indicate that the estimators performed equally well across the observed range of cumulative capture probabilities.

The density estimates of each independent analyst were evaluated using the same statistics as described for the grid-based and web-based estimators. In addition, after pooling all the independent analyses across the 11 rodent population data sets, we calculated the mean percentage confidence-interval coverage, mean relative mean square error, mean relative accuracy, mean relative precision, and mean relative bias for both grid-based and web-based \hat{D} values. We then assessed differences between grid-based and web-based approaches.

RESULTS

General trapping results

The trapping effort involved a total of 18 424 trap nights (a “trap night” equals one trap set for one night).

TABLE 3. Population size estimates (\hat{N}), by species, from program CAPTURE (Rexstad and Burnham 1991); values for each model are $\hat{N} \pm 1$ SE.

Popula- tion no.	True N	CAPTURE model type				
		M_{t+1}	M_0	M_h	M_b	M_{bh}
<i>Perognathus flavus</i>						
1	88	46	69 ± 9.8	98 ± 14.0	56 ± 8.0	56 ± 8.0
2†	39	5
3	58	27	31 ± 3.1	53 ± 9.7	30 ± 3.2	30 ± 3.2
4	81	42	68 ± 11.1	81 ± 12	49 ± 5.7	49 ± 5.7
<i>Cricetines</i>						
5	65	39	41 ± 1.7	47 ± 4.5	50 ± 9.4	50 ± 9.4
6	22	18	18 ± 0.7	21 ± 3.3	20 ± 2.8	20 ± 2.8
7	33	20	21 ± 1.5	24 ± 3.5	20 ± 0.4	20 ± 0.4
8	33	24	24 ± 0.6	32 ± 4.8	24 ± 0.4	24 ± 0.4
<i>Peromyscus maniculatus</i>						
9	26	15	15 ± 0.9	17 ± 2.8	16 ± 2.3	16 ± 2.3
10	14	13	13 ± 0.8	14 ± 2.5	13 ± 0.3	13 ± 0.3
<i>Dipodomys</i> spp.						
11	18	15	15 ± 0.5	17 ± 2.1	15 ± 0.2	15 ± 0.2

Notes: True N is the total number of rodents present in each enclosure; M_{t+1} is the number of rodents captured during the grid sampling. Boldface values represent the most "appropriate" model selected by program CAPTURE (see Otis et al. 1978); see *Methods: Evaluation of assumptions* for model abbreviations.

† The grid sample size for population 2 was too small for CAPTURE to estimate population sizes, but is included here for consistency with the web analyses (see Table 8).

TABLE 4. Rodent density estimates, \hat{D} (as rodents per hectare; ± 1 SE), by species, together with summary statistics for each model, based on trapping area calculations using grid area and one-half trap interval.

Population no.	True density, D (rodents/ ha)	CAPTURE model type			
		M_0	M_h	M_b	M_{bh}
Density estimates					
<i>Perognathus flavus</i>					
1	20.6	48.0 ± 6.8	68.2 ± 9.8	38.9 ± 5.6	38.9 ± 5.6
2	9.4
3	13.8	21.6 ± 2.2	36.9 ± 6.8	20.9 ± 2.2	20.9 ± 2.2
4	19.1	47.3 ± 7.7	56.3 ± 8.3	34.1 ± 4.0	34.1 ± 4.0
Cricetines					
5	15.7	28.5 ± 1.2	32.7 ± 3.1	34.8 ± 6.5	34.8 ± 6.5
6	5.2	12.5 ± 0.5	14.6 ± 2.3	13.9 ± 1.9	13.9 ± 1.9
7	7.8	14.6 ± 1.0	16.7 ± 2.4	13.9 ± 0.3	13.9 ± 0.3
8	7.7	16.7 ± 0.4	22.3 ± 3.3	16.7 ± 0.3	16.7 ± 0.3
<i>Peromyscus maniculatus</i>					
9	6.3	10.4 ± 0.6	11.8 ± 1.9	11.1 ± 1.6	11.1 ± 1.6
10	3.3	9.0 ± 0.6	9.7 ± 1.7	9.0 ± 0.2	9.0 ± 0.2
<i>Dipodomys</i> spp.					
11	4.3	10.4 ± 0.3	11.8 ± 1.5	10.4 ± 0.1	10.4 ± 0.1
Summary statistics					
Achieved confidence interval coverage (%)		0	0	0	0
Relative mean square error, RMSE (%)		1412.8	3248.4	1071.5	1071.5
Relative accuracy, \overline{RA} (%)		114.6	164.3	109.6	109.6
Relative precision, \overline{CV} (%)		7.4	14.9	9.1	9.1
Relative bias, \overline{RB} (%)		114.6	164.3	109.6	109.6

Notes: Density estimates were derived from grid data sets using program CAPTURE population estimates (\hat{N} , see Table 3) divided by the effective trapping area (A), where A was arbitrarily defined as the area of the grid (1.21 ha) plus a fixed boundary strip (W) having a width equal to one-half of a trap interval ($W = 5$ m); thus, for these analyses, $A = 1.4378$ ha. Confidence intervals (95%) for \hat{D} were calculated as $\hat{D} \pm 1.96(\text{SE})$. Boldface values represent the most "appropriate" model selected by program CAPTURE (see Otis et al. 1978).

TABLE 3. Extended.

CAPTURE model type					
M_t	$M_{th-Chao}$	M_{tb}	M_{t-Chao}	M_{h-Chao}	M_{vpr}
68 ± 9.0	109 ± 31.1	65 ± 49.8	86 ± 20.0	103 ± 28.6	66 ± 10.0
...
31 ± 2.8	52 ± 14.6	$449 \pm 10,049$	46 ± 13.3	59 ± 23.3	31 ± 4.5
66 ± 10.2	73 ± 18.3	55 ± 33.5	68 ± 13.3	78 ± 18.2	58 ± 8.9
41 ± 1.4	48 ± 5.8	62 ± 107.9	44 ± 3.8	46 ± 5.1	47 ± 6.3
18 ± 0.01	22 ± 3.7	19 ± 1.9	21 ± 3.1	24 ± 6.5	30 ± 7.7
21 ± 0.9	25 ± 4.8	20 ± 0.9	23 ± 2.6	25 ± 4.2	20 ± 0.0
24 ± 0.01	29 ± 4.0	28 ± 13.4	29 ± 5.4	36 ± 13.2	28 ± 4.5
15 ± 0.1	18 ± 3.6	18 ± 14.9	17 ± 1.9	18 ± 3.0	19 ± 4.5
13 ± 0.01	15 ± 2.5	13 ± 0.9	14 ± 1.3	15 ± 2.2	13 ± 0.0
15 ± 0.01	16 ± 1.7	15 ± 0.4	16 ± 0.9	16 ± 1.5	15 ± 0.0

TABLE 4. Extended.

CAPTURE model type					
M_t	$M_{th-Chao}$	M_{tb}	M_{t-Chao}	M_{h-chao}	M_{vpr}
47.3 ± 6.3	75.8 ± 21.6	45.2 ± 34.7	59.8 ± 13.9	71.6 ± 19.9	45.9 ± 7.0
...
21.6 ± 2.0	36.2 ± 10.1	312.3 ± 6989.2	32.0 ± 9.2	41.0 ± 16.2	21.6 ± 3.1
45.9 ± 7.1	50.8 ± 12.7	38.3 ± 23.3	47.3 ± 9.3	54.2 ± 12.7	40.3 ± 6.2
28.5 ± 1.0	33.4 ± 4.0	43.1 ± 75.0	30.6 ± 2.6	32.0 ± 3.5	32.7 ± 4.4
12.5 ± 0.0	15.3 ± 2.6	13.2 ± 1.3	14.6 ± 2.2	16.7 ± 4.5	20.9 ± 5.4
14.6 ± 0.6	17.4 ± 3.3	13.9 ± 0.6	16.0 ± 1.8	17.4 ± 2.9	13.9 ± 0.0
16.7 ± 0.0	20.2 ± 2.8	19.5 ± 9.3	20.2 ± 3.8	25.0 ± 9.2	19.5 ± 3.1
10.4 ± 0.1	12.5 ± 2.5	12.5 ± 10.4	11.8 ± 1.3	12.5 ± 2.1	13.2 ± 3.1
9.0 ± 0.0	10.4 ± 1.7	9.0 ± 0.6	9.7 ± 0.9	10.4 ± 1.5	9.0 ± 0.0
10.4 ± 0.0	11.1 ± 1.2	10.4 ± 0.3	11.1 ± 0.6	11.1 ± 1.0	10.4 ± 0.0
0	0	60.0	0	20.0	0
1354.3	3409.7	65971.5	2286.3	3705.7	1734.5
113.5	166.2	335.4	145.5	177.6	135.7
4.6	19.1	270.4	15.1	22.3	12.4
113.5	166.2	335.4	145.5	177.6	135.7

TABLE 5. Rodent density estimates, \hat{D} (as rodents per hectare; ± 1 SE), by species, together with summary statistics, based on trapping area calculations using grid area and one-half MMDM.

Population no.	0.5 MMDM (m)	\hat{A} (ha)	True density (rodents/ ha)	CAPTURE model type		
				M_0	M_b	M_b
Density estimates						
<i>Perognathus flavus</i>						
1	9.9	1.6764	20.6	41.2 \pm 7.9	58.5 \pm 11.3	33.4 \pm 6.4
2	8.1	1.5870	9.4
3	9.9	1.6764	13.8	18.5 \pm 3.3	31.6 \pm 7.5	17.9 \pm 3.3
4	10.0	1.6814	19.1	40.4 \pm 8.8	48.2 \pm 10.0	29.1 \pm 5.4
Cricetines						
5	23.2	2.3970	15.7	17.1 \pm 3.1	19.6 \pm 3.9	20.9 \pm 5.4
6	27.3	2.6423	5.2	6.8 \pm 1.9	7.9 \pm 2.6	7.6 \pm 2.4
7	23.8	2.5870	7.8	8.1 \pm 2.1	9.3 \pm 2.7	7.7 \pm 2.0
8	22.2	2.3445	7.7	10.2 \pm 2.2	13.6 \pm 3.6	10.2 \pm 2.2
<i>Peromyscus maniculatus</i>						
9	20.2	2.2298	6.3	6.7 \pm 1.9	7.6 \pm 2.5	7.2 \pm 2.2
10	24.4	2.4736	3.3	5.3 \pm 1.7	5.7 \pm 2.1	5.3 \pm 1.7
<i>Dipodomys</i> spp.						
11	21.0	2.2754	4.3	6.6 \pm 1.7	7.5 \pm 2.1	6.6 \pm 1.7
Summary statistics						
Achieved confidence interval coverage (%)				80.0	70.0	90.0
Relative mean square error, RMSE (%)				500.5	1457.1	206.1
Relative accuracy, \overline{RA} (%)				44.2	80.6	38.2
Relative precision, \overline{CV} (%)				24.0	26.8	24.9
Relative bias, \overline{RB} (%)				44.2	80.6	38.2

Notes: Density estimates were derived from grid data sets using program CAPTURE population estimates (\hat{N} , see Table 3) divided by the estimated effective trapping area (\hat{A}). \hat{A} was defined as the grid area (A_{grid}) plus an estimated boundary strip of width \hat{W} , where \hat{W} was equal to one-half of the mean maximum distance moved (0.5 MMDM). Confidence intervals (95%) were calculated as $\hat{D} \pm 1.96(\text{SE})$. Boldface values represent the most "appropriate" model selected by program CAPTURE.

All 12 species of rodents were captured during the surveys (Table 2). Numbers of individuals per species varied widely within the enclosures, and we arbitrarily set 10 individuals in either the grid or web data sets as a minimum number per enclosure for density estimations. We also pooled some taxa to create larger data sets. Given these criteria, we were able to analyze a total of 11 data sets: 4 data sets of *Perognathus flavus*, 2 data sets of *Peromyscus maniculatus*, 4 data sets of combined small-bodied murid rodents (*Peromyscus* spp., *Onychomys* spp., *Reithrodontomys megalotis*), and 1 combined data set of two heteromyid kangaroo rats (*Dipodomys merriami* and *D. ordii*).

Estimator assumptions

The assumption of population closure appeared to have been met during the study. The enclosure walls retained all animals within their respective cells, except for one individual *O. arenicola* that moved through a small hole in the wall and entered the adjacent enclosure; the rodent was returned to its original cell and the hole was repaired. No rodents escaped during the handling, processing, and data recording procedures. Rodent trap mortality was extremely low; only one *O. arenicola* and one *P. flavus* died during trapping and handling, and these individuals were eliminated from

the data set. While impossible to verify entirely, we observed no evidence of rodent predator activity in the enclosures during the study. Finally, only a few juvenile rodents (all *P. flavus*) appeared in the traps after the first week of the study, and these too were eliminated from the data set.

For the web-based data sets, all three assumptions appeared to have been satisfied as well. In evaluating assumption 1 (complete capture of all rodents in the web center), examination of the rodent capture locations during nights 3, 4, and 5 of each web sample revealed no new captures in the web center, and only two instances on night 5 of unmarked animals (both *P. flavus*) being captured within 10 m of the web center. Assumption 2 (no net movements into or away from the web center) was found to be supported as well, with only small rodent net movements between captures being indicated for all species (species-specific net movements (M_n) into (–) or away (+) from the web center [mean \pm 95% CI]: *Perognathus flavus*, $n = 37$, $M_n = 1.2 \pm 4.4$ m; *Peromyscus boylii*, $n = 14$, $M_n = -6.8 \pm 11.4$ m; *P. leucopus*, $n = 22$, $M_n = 10.7 \pm 11.2$ m; *P. maniculatus*, $n = 30$, $M_n = -3.3 \pm 15.0$ m).

Grid-based density estimators

A total of 264 rodents were included in the grid-based data sets, and rodent cumulative capture prob-

TABLE 5. Extended.

CAPTURE model type						
M_{bh}	M_t	$M_{th-Chao}$	M_{tb}	M_{t-Chao}	M_{h-Chao}	M_{vpr}
33.4 ± 6.4	40.6 ± 7.5	65.0 ± 20.4	38.8 ± 30.1	51.3 ± 13.6	61.4 ± 18.8	39.4 ± 7.8
...
17.9 ± 3.3	18.5 ± 3.2	31.0 ± 9.8	267.8 ± 5994.5	27.4 ± 8.9	35.2 ± 14.9	18.5 ± 3.8
29.1 ± 5.4	39.3 ± 8.3	43.4 ± 12.6	32.7 ± 20.5	40.4 ± 9.8	46.4 ± 12.7	34.5 ± 7.3
20.9 ± 5.4	17.1 ± 3.1	20.0 ± 4.3	25.9 ± 45.2	18.4 ± 3.6	19.2 ± 4.0	19.6 ± 4.3
7.6 ± 2.4	6.8 ± 1.9	8.3 ± 2.7	7.2 ± 2.2	7.9 ± 2.5	9.1 ± 3.6	11.4 ± 4.3
7.7 ± 2.0	8.1 ± 2.1	9.7 ± 3.1	7.7 ± 2.0	8.9 ± 2.5	9.7 ± 3.0	7.7 ± 2.0
10.2 ± 2.2	10.2 ± 2.2	12.4 ± 3.1	11.9 ± 6.3	12.4 ± 3.5	15.4 ± 6.5	11.9 ± 3.2
7.2 ± 2.2	6.7 ± 1.9	8.2 ± 2.8	8.1 ± 7.1	7.6 ± 2.3	8.1 ± 2.6	8.5 ± 3.1
5.3 ± 1.7	5.3 ± 1.7	6.1 ± 2.2	5.3 ± 1.7	5.7 ± 1.9	6.1 ± 2.1	5.3 ± 1.7
6.6 ± 1.7	6.6 ± 1.7	7.0 ± 1.9	6.6 ± 1.7	7.0 ± 1.8	7.0 ± 1.9	6.6 ± 1.7
90.0	80.0	90.0	100.0	80.0	80.0	80.0
206.1	462.7	1594.1	47035.3	918.5	1696.2	448.7
38.2	43.3	81.6	229.5	66.1	89.2	55.2
24.9	23.5	30.1	280.7	28.0	32.8	26.8
38.2	43.3	81.6	229.5	66.1	89.2	55.2

abilities (calculated as M_{t+1}/N) for the data sets ranged from 0.13 to 0.93. We obtained population size estimates (\hat{N}) for 10 of the 11 grid-based data sets using program CAPTURE (Table 3); the sample size for *P. flavus* population 2 ($M_{t+1} = 5$) proved too small for analysis, although the web-based sample size was sufficiently large ($M_{t+1} = 19$). The 10 models in program CAPTURE provided a wide range of \hat{N} values; some estimators (e.g., M_h) provided consistently more accurate \hat{N} values, while others occasionally produced wildly inaccurate overestimates (e.g., model M_{tb} , with *P. flavus* population 3). However, due to the relatively small size of the trapping grid within the large enclosures (grid area ~30% of enclosure area), comparisons of \hat{N} values with the true N values in Table 3 should be treated cautiously, as not all rodents in each enclosure would necessarily have been present on the grid and at risk of capture. Because the ultimate goal was to evaluate the accuracy of various models in estimating density, we then divided the \hat{N} values presented in Table 3 with different estimated area values to produce the final \hat{D} values.

The first set of \hat{D} values that we evaluated was based on the \hat{N} values divided by an effective trapping area that used the grid area (A_{grid}) plus a fixed boundary strip (W) equal to one-half of a trap interval (or 5 m). This procedure produced large overestimates of D values (Table 4) due to the A value being unrealistically small. All models exhibited poor confidence-interval coverage and inaccurate estimates, with large relative mean

square error (\overline{RMSE}) values and positive mean relative bias values (Table 4).

The second set of \hat{D} values was generated using the grid area (A_{grid}) plus a boundary strip estimate (\hat{W}) equal to one-half of each population's mean maximum distance moved (MMDM). This procedure produced larger \hat{W} values than the one-half trap interval, which translated into larger \hat{A} values and concomitantly smaller \hat{D} values (Table 5). However, the resulting \hat{D} values still substantially overestimated the true densities, although confidence-interval coverage improved markedly (Table 5).

The third set of \hat{D} values was produced using the full MMDM values in the \hat{A} calculations, and the \hat{D} results again showed considerable improvements in confidence-interval coverage, RMSE, accuracy and bias (Table 6). All density estimators achieved $\geq 90\%$ confidence-interval coverage of D , and 2 of the 10 estimators (M_b , M_{bh}) exhibited \overline{RMSE} values of ~40% and relative bias values of <10%; these latter estimators also produced mean relative accuracy value of 16.4%, with a cv value of 35.6%. While the use of the full MMDM-adjusted effective trapping area appeared to provide the most accurate grid-based density estimates, theoretical constraints may limit the wide applicability of this method (for details see *Discussion: Analytical approaches: grids vs. webs*, below).

The last set of \hat{D} values was calculated by program CAPTURE using a nested grid analysis (Otis et al. 1978). This procedure produced generally poor results

TABLE 6. Rodent density estimates, \hat{D} (as rodents per hectare; ± 1 SE) by species, together with summary statistics, based on trapping area calculations using grid area and full MMDM.

Population no.	MMDM (m)	\hat{A} (ha)	True density (rodents/ ha)	CAPTURE model type		
				M_0	M_h	M_b
Density estimates						
<i>Perognathus flavus</i>						
1	19.8	2.2044	20.6	31.3 \pm 8.2	44.5 \pm 11.7	25.4 \pm 6.7
2	16.2	2.0052	9.4
3	19.8	2.2044	13.8	14.1 \pm 3.8	24.0 \pm 7.5	13.6 \pm 3.7
4	20.0	2.2157	19.1	30.7 \pm 9.1	36.6 \pm 10.5	22.1 \pm 6.0
Cricetines						
5	46.3	3.9207	15.7	10.5 \pm 2.8	12.0 \pm 3.4	12.8 \pm 4.2
6	54.5	4.5411	5.2	4.0 \pm 1.7	4.6 \pm 2.1	4.4 \pm 2.0
7	47.6	4.0162	7.8	5.2 \pm 1.7	6.0 \pm 2.1	5.0 \pm 1.6
8	44.5	3.7901	7.7	6.3 \pm 2.1	8.4 \pm 3.0	6.3 \pm 2.1
<i>Peromyscus maniculatus</i>						
9	40.5	3.5073	6.3	4.3 \pm 1.9	4.8 \pm 2.2	4.6 \pm 2.1
10	48.9	4.1128	3.3	3.2 \pm 1.5	3.4 \pm 1.7	3.2 \pm 1.5
<i>Dipodomys</i> spp.						
11	42.1	3.6192	4.3	4.1 \pm 1.6	4.7 \pm 1.9	4.1 \pm 1.6
Summary statistics						
Achieved confidence interval coverage (%)				100.0	90.0	100.0
Relative mean square error, \overline{RMSE} (%)				165.0	531.6	40.5
Relative accuracy, \overline{RA} (%)				26.3	38.6	16.4
Relative precision, \overline{CV} (%)				35.0	37.0	35.6
Relative bias, \overline{RB} (%)				-3.3	22.3	-8.5

Notes: Density estimates were derived from grid data sets using program CAPTURE population estimates (\hat{N} , see Table 3) divided by the estimated effective trapping area (\hat{A}). \hat{A} was defined as the grid area (A_{grid}) plus an estimated boundary strip of width \hat{W} , where \hat{W} was equal to the full mean maximum distance moved (MMDM). Confidence intervals (95%) were calculated as $\hat{D} \pm 1.96(\text{SE})$. Boldface values represent the most "appropriate" model selected by program CAPTURE.

(Table 7), undoubtedly due to the small sample sizes; while many estimators achieved high rates of confidence-interval coverage, these successes were due entirely to the large SE values (producing wide 95% confidence intervals). RMSE and relative accuracy values were consistently poor, and \hat{D} values were positively biased.

In evaluating program CAPTURE's model selection routine (see Stanley 1997), we identified and grouped the most "appropriate" model (designated in boldface in Tables 3–7) for each of the 10 rodent populations, and computed the same summary statistics as we had for each individual model. In all cases, the use of the "appropriate" models resulted in higher values of RMSE and relative accuracy, increased relative bias, and larger CV's when compared to the best individual models (M_0 , M_b , M_{bh} , and M_i). For example, in the best case situation using full MMDM values in calculating \hat{D} (Table 5), averaging the results of the "appropriate" models across the 10 data sets resulted in 100% achieved confidence-interval coverage (identical to the individual models), a mean RMSE of 607.9% (compared to 40.5% to 165.0%), a mean relative accuracy of 41.2% (compared to 16.4% to 26.3%), a mean CV of 38.0% (compared to 34.7% to 35.6%), and a mean relative bias of +17.2% (compared to -3.3% to -8.5%).

Web-based density estimators

The web trapping yielded a total of 284 rodents, and rodent cumulative capture probabilities (P_c) during the web-trapping periods ranged from 0.39 to 0.88; these P_c values averaged somewhat higher than the values observed during the grid-trapping periods, an artifact due most likely to the larger area of the webs (3.14 ha, or ~75% of the enclosure area) compared to the grids. We were able to calculate \hat{D} values for all 11 rodent data sets using program DISTANCE, although some estimators were occasionally unsuccessful with particular data sets (Table 8). One estimator (the uniform model) performed very well, exhibiting 100% confidence-interval coverage of D , low relative mean square error values (30.3% to 37.2%), good mean relative accuracy values (16% to 16.9%), low mean CV values (20.6% to 24.5%), and low mean relative bias (range from -6.3% to -12.0%). The half-normal model also functioned reasonably well, with comparable values of achieved confidence-interval coverage, relative accuracy and relative bias, though poorer values of RMSE and relative precision (Table 8). The negative exponential model performed relatively poorly, generally overestimating D and having large RMSE and CV values (Table 8). The hazard model produced inconsistent results, with half of its \hat{D} values falling relatively close

TABLE 6. Extended.

CAPTURE model type						
M_{bh}	M_t	$M_{th-Chao}$	M_{tb}	M_{t-Chao}	M_{h-Chao}	M_{vpr}
25.4 ± 6.7	30.8 ± 7.9	49.4 ± 17.8	29.5 ± 23.5	39.0 ± 12.5	46.7 ± 16.6	29.9 ± 8.0
...
13.6 ± 3.7	14.1 ± 3.8	23.6 ± 8.9	203.7 ± 4558.9	20.9 ± 8.0	26.8 ± 12.6	14.1 ± 4.1
22.1 ± 6.0	29.8 ± 8.7	32.9 ± 11.6	24.8 ± 16.3	30.7 ± 9.7	35.2 ± 12.0	26.2 ± 7.6
12.8 ± 4.2	10.5 ± 2.8	12.2 ± 3.6	15.8 ± 27.8	11.2 ± 3.2	11.7 ± 3.4	12.0 ± 3.6
4.4 ± 2.0	4.0 ± 1.7	4.8 ± 2.2	4.2 ± 1.8	4.6 ± 2.1	5.3 ± 2.6	6.6 ± 3.3
5.0 ± 1.6	5.2 ± 1.7	6.2 ± 2.3	5.0 ± 1.6	5.7 ± 2.0	6.2 ± 2.3	5.0 ± 1.6
6.3 ± 2.1	6.3 ± 2.1	7.7 ± 2.7	7.4 ± 4.3	7.7 ± 2.9	9.5 ± 4.7	7.4 ± 2.7
4.6 ± 2.1	4.3 ± 1.9	5.1 ± 2.5	5.1 ± 4.8	4.8 ± 2.2	5.1 ± 2.4	5.4 ± 2.7
3.2 ± 1.5	3.2 ± 1.5	3.6 ± 1.8	3.2 ± 1.5	3.4 ± 1.7	3.6 ± 1.8	3.2 ± 1.5
4.1 ± 1.6	4.1 ± 1.6	4.4 ± 1.8	4.1 ± 1.6	4.4 ± 1.8	4.4 ± 1.8	4.1 ± 1.6
100.0	100.0	100.0	100.0	100.0	100.0	100.0
40.5	149.8	589.6	26133.0	294.5	6102.0	932.0
16.4	25.6	36.6	153.3	29.8	40.7	19.6
35.6	34.7	39.6	287.5	38.0	41.8	37.0
-8.5	-4.0	22.9	136.1	11.8	28.0	2.6

to D , but with the other half overestimating D by large margins.

In evaluating the model selection process for program DISTANCE (based on Akaike's Information Criterion, AIC; see Akaike 1973, Sakamoto et al. 1986, Burnham and Anderson 1998), we noted that in 5 of the 11 data sets, the hazard model was selected as the most "appropriate" (see Table 8, hazard model bold-faced values for populations 4, 6, 7, 10, and 11). The inclusion of these highly inaccurate estimates in assessing the model selection process produced unusually high values for mean accuracy (1814%), mean cv (180.5%), and mean relative bias (+1806%). In addition, the negative exponential model also performed rather poorly. Therefore, we eliminated the hazard and negative exponential models from consideration, and limited the analysis to the remaining models. The subsequent analysis revealed that the use of density estimates selected by AIC produced complete 95% confidence-interval coverage of D , a mean RMSE value of 341.1%, mean relative accuracy of 27.8%, a mean cv of 28.5%, and a mean relative bias of +16.7%. As with the grid-based estimators, the use of the designated "appropriate" models did not improve the RMSE, accuracy, precision, or bias of the results compared to using the best individual models (in this case, the uniform model with cosine and polynomial adjustment functions).

Comparison of grid-based and web-based estimator performance

The grid-based estimators that exhibited the highest degree of accuracy for densities were the \hat{N} values produced by the M_b and M_{bh} models (both functioned identically) in program CAPTURE, divided by the full MMDM-adjusted \hat{A} values (compare Tables 3–7). Similarly, the most accurate web-based density estimator was the uniform model, with cosine or polynomial adjustment functions (Table 8). All of these estimators displayed mean relative accuracies of 16.0% to 16.9%, and achieved 100% confidence-interval coverage of D . Mean relative bias percentages were small in all cases. The web-based estimators were characterized by better precision than the grid-based estimators, with mean model-based coefficients of variation ranging from 20.6% to 24.5% (Table 8) vs. 35.6% (Table 6).

In evaluating the performance of these estimators across the observed range of D values (linear regression analysis), we found that while the estimators for the four best-performing models were highly correlated, the two web-based estimators exhibited the smallest deviations of slope from the predicted slope of 1.0 (Fig. 3). The regression slope of the uniform model with cosine adjustment was closest to 1.0; the grid-based models had slopes of 1.23 (M_b , M_{bh}) and 1.40 (M_{vpr}), indicating that density estimates at higher rodent densities were overestimated (Fig. 3).

TABLE 7. Rodent density estimates, \hat{D} (as rodents per hectare; ± 1 SE), by species, together with summary statistics, using nested grid analysis.

Population no.	True density	CAPTURE model type			
		M ₀	M _h	M _b	M _{bh}
Summary statistics					
<i>Perognathus flavus</i>					
1	20.6	56.7 ± 39.1	42.1 ± 26.3	33.1 ± 28.4	27.9 ± 12.6
2	9.4
3	13.8	23.1 ± 4.8	31.4 ± 13.4	20.6 ± 4.2	20.6 ± 4.2
4	19.1	49.3 ± 19.5	35.8 ± 18.2	16.8 ± 4.8	16.8 ± 4.8
Cricetines					
5	15.7	21.8 ± 8.8	30.7 ± 10.7	38.4 ± 13.4	38.4 ± 13.3
6	5.2	5.1 ± 2.2	7.0 ± 4.4	5.9 ± 2.3	5.9 ± 2.3
7	7.8	2.6 ± 4.8	16.2 ± 12.7	14.4 ± 1.0	14.4 ± 1.0
8	7.7	13.7 ± 2.8	23.5 ± 8.9	3.8 ± 5.7	15.0 ± 2.8
<i>Peromyscus maniculatus</i>					
9	6.3	1.0 ± 3.4	13.0 ± 7.5
10	3.3	9.2 ± 4.9	9.6 ± 10.8	8.6 ± 0.7	8.6 ± 0.7
<i>Dipodomys</i> spp.					
11	4.3	7.0 ± 2.6	8.6 ± 4.3	8.1 ± 2.9	8.2 ± 1.9
Summary statistics					
Achieved confidence interval coverage (%)		90.0	100.0	77.8	77.8
Relative mean square error, RMSE (%)		1449.1	1394.8	706.5	707.3
Relative accuracy, \overline{RA} (%)		91.4	116.1	73.9	76.2
Relative precision, CV (%)		86.2	59.1	45.5	25.0
Relative bias, \overline{RB} (%)		60.7	116.1	60.0	73.6

Notes: Density estimates were derived from grid data sets using program CAPTURE's nested grid analyses. Confidence intervals (95%) were calculated as $\hat{D} \pm 1.96(\text{SE})$. Program CAPTURE lacks a nested grid subroutine for Model M_{vpr} . Boldface values represent the most "appropriate" model selected by program CAPTURE.

The results of the linear regression analyses for evaluating the influence of rodent cumulative capture probabilities (P_c) on the accuracy performance of these four models indicated no significant correlations, although the models all exhibited negative slopes (Fig. 4); this would suggest that the bias of the estimators decreased as P_c values increased.

Results of the independent analysts

The approaches taken by the independent analysts varied widely with respect to model selection methods, the use of model averaging, calculation of effective trapping area (\hat{A}), pooling or truncation of the data sets, and calculation of the 95% confidence intervals (Table 9). One analyst provided two different approaches to the grid-based data analyses; hence, we report 12 total analyses from the group of 11 analysts.

For the grid-based analyses, the majority of the analysts estimated N values using program CAPTURE, with several using program MARK (White and Burnham 1999, White et al., *in press*). Data sets were analyzed in their entirety in six of the analyses; five of the analysts used data pooled across species or grids to develop species-specific capture probabilities or movement distances, while only one analyst truncated the outer grid-line capture data (due to "edge effects"). Half of the analysts employed the model selection routine in CAPTURE, while others used AIC values (for those models with maximum-likelihood estimators) to

choose the most appropriate estimator; four analysts selected models for each data set based on personal experience and judgment. Taken collectively, every model in program CAPTURE was used in the analyses at least once, with the exception of M_{vpr} , which was not included in CAPTURE's model selection routine. Five of the analysts used model-averaging techniques (Burnham and Anderson 1998) to calculate \hat{N} values. Most estimates of effective trapping area were made using the grid area plus estimated boundary strip widths (W) of either one-half MMDM values, full MMDM values, or one-half MMDM plus one-half trap interval; in contrast, three analysts used nested grids in their analyses. Confidence intervals (95%) for \hat{D} were computed using either log-normal, asymmetric calculations, or symmetrical calculations of $\hat{D} \pm 1.96(\text{SE})$.

For the web-based analyses, all analyses were performed using program DISTANCE. Seven analysts used AIC values to select appropriate models, while four relied on personal experience and judgment. Data manipulations were more common during these web-based analyses, with five analysts truncating outer rings of capture data, and seven analysts performing some degree of data pooling (either across species or trapping rings). All models in program DISTANCE were used at least once in the analyses, and model averaging was employed in four analyses. Confidence intervals (95%) of \hat{D} were based on asymmetric distributions, the bootstrap method, or the symmetrical $\hat{D} \pm 1.96(\text{SE})$.

TABLE 7. Extended.

CAPTURE model type				
M_t	$M_{th-Chao}$	M_{tb}	M_{t-Chao}	M_{h-Chao}
54.0 ± 29.4	89.2 ± 121.9	...	54.7 ± 60.8	77.2 ± 98.8
...
20.0 ± 3.9	29.2 ± 20.9	20.9 ± 3.9	20.4 ± 14.8	25.8 ± 27.5
32.0 ± 15.3	46.3 ± 30.8	...	34.2 ± 19.8	7.7 ± 3.4
21.5 ± 7.4	28.5 ± 15.1	39.8 ± 42.8	26.2 ± 9.6	25.8 ± 15.0
9.9 ± 2.3	6.8 ± 5.9	3.9 ± 1.1	5.8 ± 2.9	6.2 ± 5.6
10.0 ± 8.7	17.8 ± 120.0	...	8.5 ± 15.3	18.8 ± 318.4
14.0 ± 0.0	14.1 ± 8.5	16.7 ± 17.1	16.2 ± 6.9	24.1 ± 19.1
3.9 ± 7.9	0.3 ± 3.4	...	8.2 ± 7.7	0.3 ± 3.6
5.8 ± 1.5	0.4 ± 8.3	...	3.6 ± 8.2	...
8.6 ± 1.1	7.9 ± 3.9	7.2 ± 1.7	7.4 ± 1.9	7.7 ± 3.4
70.0	100.0	100.0	100.0	88.9
850.5	3253.9	1064.9	910.9	3482.9
72.6	117.8	82.8	60.2	131.2
50.8	440.7	56.1	89.8	383.9
65.0	81.2	72.6	60.2	110.0

The wide variety of approaches used by the independent analysts resulted in a wide array of density estimates (Table 10). Achieved confidence-interval coverage of the true density (D) was greater for web-based estimators (mean = 86.2%) than for grid-based estimators (mean = 49.9%). In addition, the web-based estimators displayed a 27% lower RMSE value (Table 10), and a slightly better relative accuracy value. However, the web-based estimators exhibited somewhat poorer relative precision. Both classes of estimators produced similar mean levels of relative bias (Table 10).

In comparing the results of the analysts (Table 10) with the single models' results from the basic analyses of programs CAPTURE (Table 6) and DISTANCE (Table 8), it appeared that the approaches used by several analysts were equally successful to that of the basic analyses of both the grid-based and web-based models. For example, Analysis 7 (Table 10) of the grid data sets achieved a 90.9% confidence-interval coverage, a mean relative accuracy of 22.2%, a mean cv of 20.2%, and a relative bias of -2.2%; these values were comparable to those of CAPTURE's M_{bh} and M_{vpr} models with MMDM-adjusted areas (Table 6). Similarly, Analysis 11 (Table 10) of the web data sets also achieved a 90.9% confidence-interval coverage, a mean relative accuracy of 18.7%, a mean cv of 24.1%, and a relative bias of -5.4%; these values were comparable to those of DISTANCE's uniform model (Table 8). However, in comparing the overall average performance of the independent analysts to the best of the basic model anal-

yses, the analysts produced lower percentage confidence-interval coverages, higher RMSE's, lower accuracy, and greater positive bias; only precision (mean cv values) appeared to be comparable (Table 10).

DISCUSSION

Analytical approaches: grids vs. webs

The results of these analyses demonstrated that estimators exist for web-based small-mammal data sets that accurately assess absolute small-mammal densities under field conditions with relatively small sample sizes. In addition, several models using grid-based data sets also provided empirically reasonable results, although the theoretical basis for these outcomes proved problematic (see below). The best of the web-based models (uniform and half-normal models) displayed a performance comparable to the best grid-based models (M_b and M_{bh} with full MMDM [mean maximum distance moved]-adjusted sampling area estimate [\hat{A}]); however, only the web-based uniform model with cosine adjustment function proved capable of computing accurate and unbiased density estimates across the entire range of observed densities (Fig. 3). The grid-based models tended to underestimate the density (D) at low densities, and overestimate D at high densities (Fig. 3). Both web- and grid-based models were able to achieve complete confidence-interval coverages of the true densities during the study, though some estimators achieved this result by having very wide 95% confidence intervals (i.e., low precision).

TABLE 8. Rodent density estimates, \hat{D} (as rodents per hectare; ± 1 SE) derived from trapping webs, by species, and summary statistics for each model.

Population no.	True density (rodents/ ha)	M_{t+1}	DISTANCE model type			
			Uniform			Negative exponential
			Cosine	Hermite	Polynomial	Cosine
Density estimates						
<i>Perognathus flavus</i>						
1	20.6	34	22.2 \pm 5.6	18.3 \pm 3.8	18.3 \pm 3.8	28.3 \pm 11.9
2	9.4	19	13.1 \pm 4.2	10.5 \pm 2.9	10.5 \pm 2.9	16.4 \pm 9.2
3	13.8	36	10.4 \pm 1.7	10.4 \pm 1.7	10.4 \pm 1.7	...
4	19.1	40	19.3 \pm 5.6	16.2 \pm 4.0	16.2 \pm 4.0	32.6 \pm 12.7
Cricetines						
5	15.7	51	14.7 \pm 2.1	14.7 \pm 2.1	14.7 \pm 2.1	...
6	5.2	15	4.3 \pm 1.1	4.3 \pm 1.1	4.3 \pm 1.1	12.4 \pm 7.9
7	7.8	17	4.9 \pm 1.2	4.9 \pm 1.2	4.9 \pm 1.2	13.1 \pm 7.9
8	7.7	28	8.1 \pm 1.5	8.1 \pm 1.5	8.1 \pm 1.5	10.5 \pm 5.7
<i>Peromyscus maniculatus</i>						
9	6.3	23	6.6 \pm 1.4	6.6 \pm 1.4	6.6 \pm 1.4	...
10	3.3	9	2.6 \pm 0.9	2.6 \pm 0.9	2.6 \pm 0.9	7.7 \pm 6.3
<i>Dipodomys</i> spp.						
11	4.3	12	3.4 \pm 1.0	3.4 \pm 1.0	3.4 \pm 1.0	9.7 \pm 6.9
Summary statistics						
Achieved confidence interval coverage (%)			100.0	100.0	100.0	100.0
Relative mean square error, \overline{RMSE} (%)			37.2	30.3	30.3	733.4
Relative accuracy, \overline{RA} (%)			16.9	16.0	16.0	62.2
Relative precision, \overline{CV} (%)			24.5	20.6	20.6	58.2
Relative bias, \overline{RB} (%)			-6.3	-12.0	-12.0	62.2

Notes: Density estimates were derived from web data sets using program DISTANCE. Asymmetric 95% confidence intervals of \hat{D} were calculated in program DISTANCE; M_{t+1} = sample size for the web-trapping periods (true N values for each population are given in Table 3). Boldface values represent the most "appropriate" model selected by AIC values (see Buckland et al. [1993] for details); if the Hazard or Negative-exponential models were selected as most "appropriate," then the next most "appropriate" model is also boldfaced.

The best web-based estimator was the uniform model with either the cosine, Hermite, or polynomial adjustment functions (Table 8). The uniform model with cosine adjustment (formerly, the Fourier series model in program TRANSECT; see Burnham et al. [1980]) had been previously evaluated for accuracy, precision, and bias during computer simulations (Wilson and Anderson 1985a) and several field studies using populations of known densities (Bollinger et al. 1988, Hone 1988, Parmenter et al. 1989, White et al. 1989, Bergstedt and Anderson 1990, Southwell 1994). These studies found that the Fourier series performed well when used in both line-transect and trapping-web applications; confidence-interval coverage of D in these studies ranged from 73% (Parmenter et al. 1989) to 100% (Hone 1988, Southwell 1994), while approximated bias ranged from -19.5% (White et al. 1989) to +17.6% (Southwell 1994). The results of our present study provide additional evidence for the preferred use of the uniform model with cosine adjustment function in estimating field densities of animal populations.

In addition to the uniform model, the other web-based model that performed reasonably well in this study was the half-normal model with Hermite or polynomial adjustment functions (Table 8). While it dis-

played 100% confidence-interval coverage of D and low bias on these rodent data sets, its performance in other studies has been more uneven. Parmenter et al. (1989), White et al. (1989), and Southwell (1994) found that the half-normal model provided confidence-interval coverages of only 18% to 67%, and was significantly negatively biased (-31.4% to -15.1%). In contrast, Hone's (1988) analyses showed much greater accuracy and low bias.

The array of grid-based estimators displayed a wide range of performances, and, in most cases, definitive causes of each model's success or failure were consistent with both theoretical considerations and previously observed results of field studies. With grid-based density analyses, independent \hat{N} (population size estimate) and \hat{A} values were combined to compute the \hat{D} value, and therefore each component must be evaluated separately. First, comparisons of the \hat{N} values shown in Table 3 to the true N values of the enclosures revealed that the most accurate population size estimates were of rodent species with low densities and large MMDM values (~45 m for the cricetines and *Dipodomys* spp., see Table 6). These species' greater movement habits would have made the entire population within the enclosures be at risk of capture in the grid traps, and

TABLE 8. Extended.

DISTANCE model type							
Negative exponential		Half-normal			Hazard		
Hermite	Polynomial	Cosine	Hermite	Polynomial	Cosine	Hermite	Polynomial
28.3 ± 11.9	28.3 ± 11.9	20.0 ± 5.8	20.0 ± 5.8	20.0 ± 5.8	15.1 ± 3.4	15.1 ± 3.4	15.1 ± 3.4
16.4 ± 9.2	14.6 ± 9.2	12.4 ± 4.7	12.4 ± 4.7	12.4 ± 4.7	16.7 ± 10.1	9.9 ± 4.2	9.9 ± 4.2
...	10.4 ± 1.7	10.4 ± 1.7	10.4 ± 1.7
32.6 ± 12.7	32.6 ± 12.7	34.2 ± 14.8	19.4 ± 5.4	19.4 ± 5.4	80.3 ± 130.2	101.1 ± 115.0	80.3 ± 130.2
...	...	14.7 ± 4.1	14.7 ± 4.1	14.7 ± 4.1	14.7 ± 2.3	14.7 ± 2.3	14.7 ± 2.3
12.4 ± 7.9	12.4 ± 7.9	16.1 ± 10.2	7.2 ± 3.3	7.2 ± 3.3	39.2 ± 59.4	48.2 ± 137.4	48.2 ± 137.4
13.1 ± 7.9	13.1 ± 7.9	5.9 ± 2.7	5.9 ± 2.7	5.9 ± 2.7	70.7 ± 242.9	70.7 ± 242.9	93.7 ± 247.4
10.5 ± 5.7	10.5 ± 5.7	9.2 ± 3.4	9.2 ± 3.4	9.2 ± 3.4	9.5 ± 5.8	9.5 ± 5.8	9.5 ± 5.8
...
7.7 ± 6.3	7.7 ± 6.3	11.4 ± 8.6	4.4 ± 2.6	4.4 ± 2.6	129.7 ± 725.4	129.7 ± 725.4	129.7 ± 725.4
9.7 ± 6.9	9.7 ± 6.9	12.4 ± 8.9	5.8 ± 2.9	5.8 ± 2.9	186.8 ± 1464.0	614.0 ± 4293.0	186.8 ± 1464.0
100.0	100.0	100.0	100.0	100.0	90.0	80.0	90.0
733.4	733.4	834.7	214.2	214.2	135 212.4	925 089.6	140 876.3
62.2	62.2	73.4	17.6	17.6	910.4	1832.6	946.3
58.2	58.2	48.1	40.4	40.4	217.7	699.0	783.9
62.2	62.2	67.3	11.5	11.5	899.9	1822.1	935.8

presumably contributed to the more accurate performance of the estimators. In contrast, the \hat{N} values for the abundant *Perognathus flavus* populations were often underestimated, particularly by the models that were ultimately successful in calculating accurate \hat{D} values (i.e., M_b , M_{bh} , M_{vpr}); however, the MMDM values for this species (shown in Table 6) were considerably smaller (~20 m), indicating that some portion of each *P. flavus* population was outside the “effective trapping area” of the grids, and not at risk of capture. If true, then the \hat{N} values for the *P. flavus* populations in each enclosure would have been predictably underestimated.

The second component, the “effective trapping area” (\hat{A}), was calculated using three different estimates of boundary strip widths (W); each of these, when combined with the \hat{N} values, had significant influences on the accuracies of the \hat{D} values. The use of the grid area plus a fixed boundary strip of one-half trap interval (5 m) produced relatively small A values, causing extremely large overestimates of density values (Table 4). These results support the historical beliefs of many small-mammal ecologists, dating back to Dice (1938) and Stickel (1954), that the use of trap-interval distances for \hat{W} would result in overestimates of densities. Wilson and Anderson (1985c:18), using computer simulations of rodent capture–recapture data for \hat{N} , and A values using only grid area, also found that these “naïve density estimates result in a severe

overestimate of the true density.” In addition to the poor performance of this approach, there also is no logical reason to believe that trap-interval distances are related to rodent movement patterns and boundary strip widths; clearly, this method should not be used in estimating rodent densities.

The use of rodent movement distances to calculate \hat{W} considerably enhanced the performance of the density estimators by increasing the size of the \hat{A} values, thereby lowering the \hat{D} values. The use of one-half of the estimated MMDM for \hat{W} improved the accuracy and bias statistics for all of the models, but the use of the full estimated MMDM values produced the best results (compare Tables 5 and 6). Wilson and Anderson (1985c) reported good success in computer simulations when using one-half MMDM values, with 71–89% confidence-interval coverage of the true D and less than +22% relative bias. These values were comparable to our results from the M_b , M_{bh} , and M_{vpr} models using one-half MMDM (Table 5), with 80% to 90% confidence-interval coverage, though substantially higher relative bias values (+38% to +55%). However, the use of the full MMDM values in calculating \hat{W} resulted in the best performance of the grid-based models, by creating the largest values of \hat{A} (Table 6).

In spite of the improved empirical performance of using MMDM for calculating \hat{W} , the use of one-half or full MMDM requires a large number of theoretical assumptions of animal movements and home-range siz-

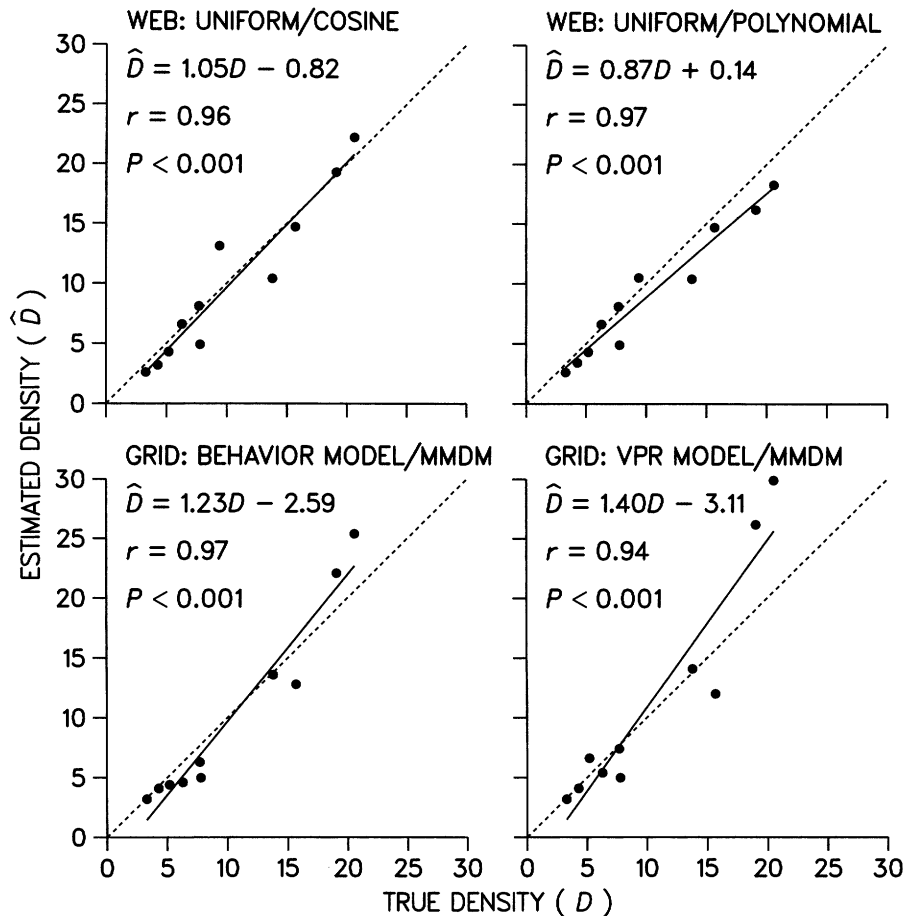


FIG. 3. Linear regression results showing the relationship between the estimated rodent density (\hat{D}) and the true density (D) for the two most accurate web-based and grid-based estimators (data from Tables 6 and 8). Diagonal dashed lines indicate predicted slope of 1.0 if $\hat{D} = D$; solid lines represent the observed regression line. While all models exhibited high correlation coefficients, only the uniform model with cosine adjustment had a regression slope very close to 1.0; the slopes of the other three estimators displayed greater deviations from the predicted slope of 1.0. The two web-based models are from the program DISTANCE (Laake et al. 1993) while the grid-based ones are from the program CAPTURE (Rexstad and Burnham 1991); MMDM = mean maximum distance moved, vpr = variable probability removal (see *Methods: Evaluation of assumptions*).

es, shapes, and degree of overlap, and many of these assumptions are of uncertain validity. The primary objective in adjusting the grid area based on animal movement is to determine the estimated maximum distance (\hat{W}) from which animals outside the grid boundaries are moving onto the grid. To do so using movement distances measured from trap capture locations requires a myriad of assumptions concerning (1) the influence of trap captures in constraining the maximum movement distances of the target animals, (2) the proportion of animals on the trapping grid that have home ranges entirely contained within the grid boundary vs. those with varying degrees of spatial overlap with the grid, (3) the influence of population demographics (age structure, sex ratios) on observed movement patterns, (4) the proportion of resident vs. dispersing (transient) animals within the effective trapping area of the grid, (5) the location of the animals' residences (burrows, nests) within their home ranges relative to the grid

boundaries, (6) the size of the grid itself, which would constrain the upper limits of MMDM values, and (7) the degree of overlap among the different animals' home ranges, through the influence of social interactions in determining home-range boundaries (territoriality vs. non-aggressive resource sharing).

The use of MMDM measures for calculating \hat{W} is further constrained by the small sample sizes of animal recaptures typically obtained during a grid-trapping effort. Small numbers of capture locations produce severe underestimates of home-range size and movement distances, leading to underestimates of the "true" effective area of a trapping grid. An accurate delineation of a rodent's average nightly movement distance, or its home-range size, would take many trap captures over weeks of trapping to assemble a sufficient sample size (e.g., Mares et al. 1980, Bergstrom 1988). Therefore, given the uncertainties in evaluating the validity of the required assumptions and constraints on using MMDM

TABLE 9. Salient aspects of analysts' methods for estimating rodent densities from the grid-based and web-based data sets.

Anal- ysis no.	Analysis program†	Model selection method‡	Model(s) selected§	Model averaging	Area calculation	Data pooling or truncation	CI calculation method¶
Grid-based data							
1	CAPTURE	Select. Rou- tine	Appropriate	no	Nested grids, 0.5MMDM	truncated	Log-normal, asymmetric
2	CAPTURE	Select. Rou- tine	Appropriate	no	Grid + 0.5MMDM	no	1.96(SE)
3	CAPTURE	Select. Rou- tine	Appropriate	simulations	Grid + 0.5MMDM	no	1.96(SE)
4	MARK, CAPTURE	Judgment	$M_0, M_t, M_b,$ $M_{bh}, M_{bh},$ $M_{tb}, M_{th-Chao}$	yes	Grid + 0.5MMDM	no	Log-normal, asymmetric
5	CAPTURE	Select. Rou- tine	Appropriate	no	Nested grids	pooled	Log-normal, asymmetric
6	CAPTURE	Select. Rou- tine	Appropriate	no	Grid + MMDM	no	1.96(SE)
7	MARK	AIC	$M_0, M_b, M_t,$ M_{tb}	yes	Grid Area \times Correct. Factor	pooled	1.96(SE)
8	CAPTURE	Judgment, AIC	M_0, M_b, M_h	yes	Nested grids	pooled	Log-normal, asymmetric
9	CAPTURE	Select. Rou- tine	M_{bh}, M_{th}	no	Grid + MMDM	no	1.96(SE)
10	CAPTURE	Judgment	M_h, M_{h-Chao}	yes	Grid + 0.5MMDM	no	Log-normal, asymmetric
11	CAPTURE	Judgment	M_h	no	Grid + 0.5(MMDM + 0.5T.I.)	pooled	Log-normal, asymmetric
12	MARK, CAPTURE	AIC	$M_0, M_t, M_b,$ M_{bh}, M_{tb}	yes	Grid + 0.5MMDM	pooled	1.96(SE)
Web-based data							
1	DISTANCE	AIC	All	yes	...	pooled	Log-normal, asymmetric
2	DISTANCE	AIC	Uniform/H- Normal	no	...	no	Poisson, asymmetric
3#	DISTANCE	AIC	Uniform/H- Normal	no	...	no	Poisson, asymmetric
4	DISTANCE	Judgment	All	yes	...	truncated/ pooled	Poisson, asymmetric
5	DISTANCE	Judgment	Uniform/H- Normal/ Hazard	yes	...	pooled	Bootstrap
6	DISTANCE	Select. Rou- tine (AIC)	Uniform/H- Normal	no	...	truncated	Poisson, asymmetric
7	DISTANCE	AIC	Uniform	no	...	pooled	1.96(SE)
8	DISTANCE	AIC	Uniform/H- Normal/ Hazard	no	...	pooled	Poisson, asymmetric
9	DISTANCE	Select. Rou- tine (AIC)	H-Normal/ Hazard	no	...	truncated/ pooled	Poisson, asymmetric
10	DISTANCE	Judgment	Uniform (Cosine)	yes for CI	...	truncated	Poisson, asymmetric
11	DISTANCE	Judgment	H-Normal	no	...	pooled	Poisson, asymmetric
12	DISTANCE	Select. Rou- tine (AIC)	Appropriate	post-stratifica- tion	...	truncated/ pooled	Poisson, asymmetric

† Program references: CAPTURE (Rexstad and Burnham 1991); DISTANCE (Laake et al. 1993); MARK (White and Burnham 1999).

‡ Select. Routine = Automatic model selection routine in Program CAPTURE or DISTANCE.

§ Appropriate = data-set-specific model chosen by selection routine.

|| MMDM = mean maximum distance moved; Judgment = Model(s) arbitrarily selected based on personal experience. AIC = Akaike information criterion. Correct. Factor = an area correction factor based on rodent home-range size estimates from radio telemetry data in other studies (see White and Shenk 2001); T.I. = trap interval.

¶ CI = 95% confidence interval; "1.96(SE)" means symmetrical calculations of the rodent density estimates $\hat{D} \pm 1.96 \times (\text{standard error})$.

Analyst no. 2 provided two grid-based analyses (numbers 2 and 3), and one web-based analysis (no. 2); hence, this information repeats data from Analysis no. 2.

TABLE 10. Rodent density estimates, \hat{D} (as rodents per hectare), by species, and summary statistics; estimates are derived from web and grid data sets by expert analysts, and data are $\hat{D} \pm 1$ SE.

Population no.	Analysts density estimates, \hat{D}						
	True density (rodents/ha)	M_{t+1}^\dagger	Trap layout	Analysis 1	Analysis 2	Analysis 3‡	Analysis 4
Density estimates							
<i>Perognathus flavus</i>							
1	20.6	46	grid	14.2 \pm 2.6	65.0 \pm 20.5	40.0 \pm 8.5	29.8 \pm 6.5
	20.6	34	web	19.7 \pm 7.5	18.3 \pm 3.8	18.3 \pm 3.8	34.6 \pm 16.6
2	9.4	5	grid	3.2 \pm 1.8	7.6 \pm 7.6	3.1 \pm 1.3	...
	9.4	19	web	11.7 \pm 5.9	10.5 \pm 2.9	10.5 \pm 2.9	19.6 \pm 16.7
3	13.8	27	grid	31.6 \pm 7.5	18.5 \pm 3.3	20.7 \pm 5.4	19.6 \pm 2.3
	13.8	36	web	12.6 \pm 6.1	10.4 \pm 1.7	10.4 \pm 1.7	24.2 \pm 15.0
4	19.1	42	grid	24.4 \pm 4.6	46.4 \pm 13.8	34.0 \pm 8.7	31.2 \pm 5.5
	19.1	40	web	28.5 \pm 14.9	33.8 \pm 14.7	33.8 \pm 14.7	32.2 \pm 15.6
Cricetines							
5	15.7	39	grid	25.9 \pm 5.8	20.9 \pm 5.4	21.2 \pm 4.5	19.1 \pm 2.8
	15.7	51	web	15.5 \pm 4.2	14.7 \pm 2.1	14.7 \pm 2.1	32.3 \pm 13.1
6	5.2	18	grid	5.9 \pm 2.3	7.6 \pm 2.4	6.9 \pm 2.5	9.0 \pm 2.1
	5.2	15	web	13.4 \pm 11.3	16.5 \pm 10.3	16.5 \pm 10.3	9.7 \pm 4.8
7	7.8	20	grid	14.4 \pm 1.0	8.2 \pm 2.4	9.8 \pm 3.9	9.4 \pm 1.1
	7.8	17	web	5.5 \pm 2.7	4.9 \pm 1.2	4.9 \pm 1.2	11.8 \pm 5.6
8	7.7	24	grid	19.2 \pm 7.2	13.2 \pm 3.5	11.5 \pm 2.9	12.2 \pm 1.9
	7.7	28	web	8.6 \pm 3.1	8.1 \pm 1.5	8.1 \pm 1.5	19.4 \pm 8.4
<i>Peromyscus maniculatus</i>							
9	6.3	15	grid	9.0 \pm 2.9	6.7 \pm 1.9	6.3 \pm 2.7	7.0 \pm 0.8
	6.3	23	web	6.4 \pm 2.6	6.6 \pm 1.4	6.6 \pm 1.4	11.8 \pm 5.6
10	3.3	13	grid	5.7 \pm 2.0	5.4 \pm 2.1	5.7 \pm 2.4	6.9 \pm 1.3
	3.3	9	web	4.7 \pm 5.4	2.6 \pm 0.9	2.6 \pm 0.9	7.5 \pm 3.9
<i>Dipodomys</i> spp.							
11	4.3	15	grid	8.9 \pm 1.8	7.0 \pm 1.0	6.3 \pm 2.3	6.6 \pm 0.8
	4.3	12	web	2.1 \pm 2.7	3.5 \pm 1.0	3.5 \pm 1.0	8.9 \pm 4.5
Summary statistics							
Achieved confidence interval coverage (%)			grid	36.4	81.8	90.9	0.0
			web	100.0	100.0	100.0	63.6
Relative mean square error, \overline{RMSE} (%)			grid	616.1	1335.5	411.5	235.9
			web	186.9	347.8	347.8	850.8
Relative accuracy, \overline{RA} (%)			grid	71.7	63.8	50.2	41.5
			web	34.6	39.3	39.3	94.3
Relative precision, \overline{CV} (%)			grid	28.2	35.2	32.6	15.9
			web	60.9	28.4	28.4	52.2
Relative bias, \overline{RB} (%)			grid	54.1	60.2	38.0	41.5
			web	17.3	17.7	17.7	94.3

$^\dagger M_{t+1}$ = sample sizes for each trapping period (true N values for each population are given in Table 3).

‡ Analyst no. 2 provided two grid-based analyses (numbers 2 and 3), and only one web-based analysis (no. 2); hence, web-based results are repeated here from Analysis 2 column. These results are not repeated in the summary analyses presented in text or in the "row means" column of this table.

for calculating \hat{W} , we would caution against the use of MMDM values for effective-trapping-area estimation in small-mammal field studies, in spite of the empirical performance observed in our study.

An alternative to using capture–recapture data to estimate animal movement distances would be to substitute known movement distances derived from radio-telemetry studies. Such data would more completely delineate home-range sizes and movement patterns, allowing for a more accurate estimate of W , and would not require the assumptions of MMDM values described

above. However, radio telemetry studies of rodent home-range size and movement patterns have not been conducted for many species of rodents, and therefore potential literature values of species-specific W estimates are unavailable. In addition, we suspect that movements and home-range sizes would vary within a given species over a number of factors, including habitat type, temporal changes in food/shelter availability, density of conspecifics, demographic structure of the population, and resident/transient status. If true, this would require on-site radio telemetry studies concomitant with any grid

TABLE 10. Extended.

Analysts density estimates, \hat{D}								
Analysis 5	Analysis 6	Analysis 7	Analysis 8	Analysis 9	Analysis 10	Analysis 11	Analysis 12	Analysis row means
67.9 ± 44.3	64.7 ± 20.4	19.7 ± 4.6	30.7 ± 20.0	49.6 ± 14.2	75.0 ± 18.0	50.7 ± 7.3	39.7 ± 7.4	45.6 ± 6.0
12.6 ± 2.7	18.3 ± 3.2	19.8 ± 3.4	28.1 ± 9.3	30.5 ± 10.7	24.2 ± 6.5	12.0 ± 2.4	30.2 ± 9.9	22.6 ± 2.4
3.3 ± 1.8	3.1 ± 1.9	1.8 ± 0.3	...	5.0 ± 3.9	...	5.2 ± 2.4	4.0 ± 1.5	4.0 ± 0.6
6.9 ± 1.8	13.4 ± 3.6	11.3 ± 2.3	15.7 ± 5.7	17.3 ± 6.7	13.7 ± 4.3	6.7 ± 1.7	17.0 ± 6.2	13.1 ± 1.3
40.2 ± 13.5	31.5 ± 7.5	10.2 ± 2.0	22.2 ± 4.7	23.7 ± 6.6	38.9 ± 12.0	27.4 ± 5.0	21.1 ± 4.4	25.5 ± 2.6
13.0 ± 2.7	15.9 ± 4.0	21.0 ± 3.6	10.4 ± 1.7	21.4 ± 7.9	17.0 ± 5.0	12.7 ± 2.4	25.5 ± 8.6	16.7 ± 1.7
51.3 ± 29.9	46.2 ± 13.7	18.1 ± 4.4	30.7 ± 17.0	35.5 ± 9.2	57.6 ± 13.0	43.5 ± 6.5	36.7 ± 7.3	38.0 ± 3.4
13.4 ± 2.8	25.6 ± 5.4	23.3 ± 3.9	32.6 ± 14.9	28.5 ± 10.1	22.6 ± 6.1	14.1 ± 2.6	33.1 ± 10.7	26.2 ± 2.3
27.3 ± 12.9	20.5 ± 5.4	15.1 ± 3.1	35.8 ± 14.0	12.8 ± 2.2	32.0 ± 5.7	17.4 ± 1.7	18.3 ± 3.5	22.2 ± 2.1
24.5 ± 8.9	19.8 ± 4.5	21.7 ± 2.3	14.7 ± 2.1	33.7 ± 11.8	24.2 ± 6.5	18.0 ± 3.1	16.4 ± 2.5	21.4 ± 2.1
8.2 ± 4.6	7.4 ± 2.4	6.5 ± 1.2	6.3 ± 2.3	4.4 ± 0.7	12.2 ± 3.4	7.8 ± 1.2	7.6 ± 1.1	7.5 ± 0.6
7.2 ± 3.1	22.1 ± 7.7	6.4 ± 1.2	24.9 ± 31.6	10.1 ± 4.5	7.3 ± 2.8	5.3 ± 1.5	4.7 ± 1.4	11.6 ± 2.2
14.4 ± 1.0	7.3 ± 2.3	8.0 ± 2.0	12.6 ± 3.4	5.0 ± 0.1	13.5 ± 3.2	8.9 ± 1.3	9.5 ± 2.2	10.1 ± 0.9
8.2 ± 3.4	4.9 ± 1.0	7.2 ± 1.3	5.3 ± 1.9	12.4 ± 5.3	8.9 ± 3.2	6.0 ± 1.6	5.9 ± 1.5	7.4 ± 0.8
19.2 ± 7.2	10.0 ± 2.2	8.7 ± 1.6	13.3 ± 1.9	6.3 ± 0.1	19.6 ± 5.8	11.5 ± 1.7	9.9 ± 1.2	12.9 ± 1.3
13.5 ± 5.2	14.4 ± 3.9	11.9 ± 1.7	8.7 ± 2.8	20.2 ± 7.7	14.5 ± 4.4	9.9 ± 2.1	9.0 ± 1.9	12.6 ± 1.4
9.1 ± 3.7	6.6 ± 2.0	5.5 ± 1.0	1.0 ± 3.5	4.6 ± 0.6	10.6 ± 2.5	6.3 ± 1.0	6.7 ± 1.7	6.6 ± 0.7
33.6 ± 31.2	7.3 ± 2.6	9.8 ± 1.5	38.1 ± 48.1	12.4 ± 5.3	8.9 ± 3.2	8.1 ± 1.9	6.3 ± 1.5	13.6 ± 3.6
3.8 ± 2.3	5.5 ± 2.1	4.7 ± 0.9	8.6 ± 2.1	3.2 ± 0.1	8.3 ± 2.1	5.2 ± 0.9	5.7 ± 1.5	5.7 ± 0.5
21.4 ± 20.5	2.6 ± 0.7	3.8 ± 1.0	14.9 ± 19.2	7.9 ± 3.8	5.6 ± 2.4	3.2 ± 1.1	2.8 ± 1.0	7.0 ± 1.9
8.6 ± 2.6	6.9 ± 2.0	5.5 ± 1.0	8.4 ± 2.2	4.4 ± 0.4	10.1 ± 4.0	6.3 ± 0.8	7.0 ± 1.9	7.2 ± 0.5
...	3.5 ± 0.8	5.1 ± 1.1	4.9 ± 2.6	...	6.5 ± 2.6	4.2 ± 1.3	3.5 ± 1.1	4.7 ± 0.7
36.4	63.6	90.9	50.0	45.5	20.0	20.0	63.6	49.9
50.0	90.9	72.7	100.0	80.0	100.0	90.9	100.0	86.2
2330.6	1511.7	79.4	609.2	606.0	3041.0	874.5	427.9	1014.3
2125.1	609.8	109.9	2673.1	732.7	175.5	69.3	288.6	744.1
107.3	72.0	22.2	72.3	42.4	133.5	58.7	48.3	65.3
114.5	57.2	27.9	136.2	82.0	42.1	18.7	34.0	61.9
44.6	32.4	20.2	65.9	20.2	26.5	17.7	22.2	30.1
43.7	25.6	17.8	59.0	39.7	33.2	24.1	28.9	37.6
95.5	58.7	-2.0	57.0	12.4	133.5	50.6	39.6	53.2
96.1	41.3	52.3	124.7	82.0	42.1	-5.4	21.7	53.1

trapping study to validate \hat{W} ; while clearly desirable, such a logistical burden would not be practical for many small mammal research programs.

The final grid-based density estimation procedure tested in this study was the nested grid approach (Otis et al. 1978). This procedure proved ineffective in estimating accurate rodent densities, displaying low precision (large mean cv% values) and large positive relative bias (Table 7). Wilson and Anderson (1985b) produced similar results for the nested grid approach on simulated rodent data sets, reporting mean cv% ranges of 45% to 169%, and relative bias values of +45% to +67%. Given the results of previous studies and the observed performance in our experiment, we recom-

mend that the nested grid approach not be used for small-mammal density estimation.

Analytical approaches: the independent analyses

With respect to the density estimation approaches taken by the independent analysts, it is interesting to note the relatively poor overall performance of the analysts' approaches (relative mean square error, $\overline{\text{RMSE}} = 1014.3\%$ for grids and 744.1% for webs, Table 10) compared to the uniform models for web data where RMSE ranged from only 30.3% to 37.2% (Table 8, bottom left). The reason for this general result is likely due to the relatively small sample sizes within the test data sets; such data provide minimal information for

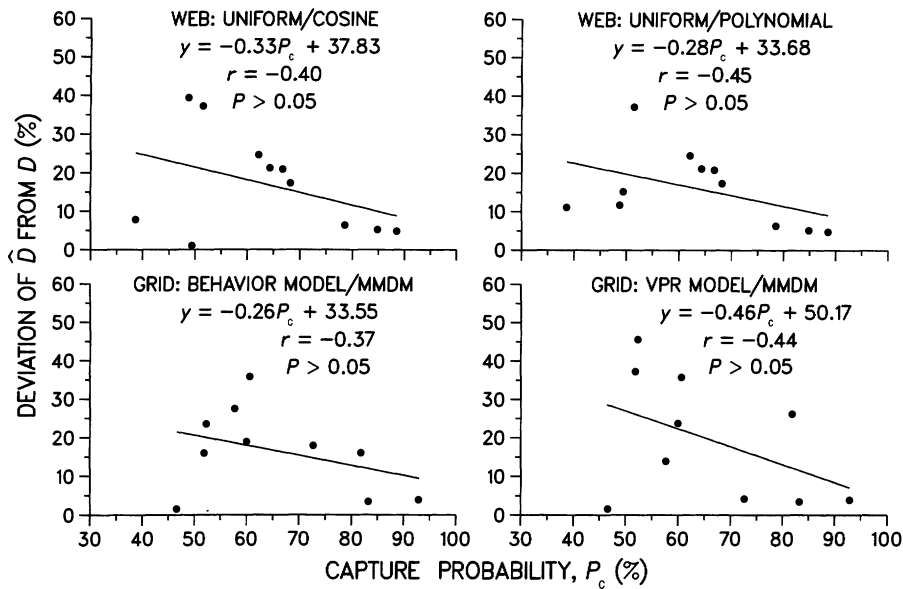


FIG. 4. Linear regression results showing the relationship between relative accuracy (as measured by the percentage deviation of the estimated density, \hat{D} , from the true density, D) and rodent cumulative capture probability (P_c) for the two most accurate web-based and grid-based estimators.

model selection routines, and therefore offer little guidance as to which analytical approaches might be most appropriate. In such circumstances, analysts must resort to past experience and personal judgments in selecting analytical models for both grid- and web-based data sets. Such was the case with our independent analysts, and the wide variety of approaches produced a comparably wide range of density estimates. This result suggests that a routine use of the web-based uniform models might be robust for small-mammal density estimation using the trapping-web design. Another useful insight relates to the results in Table 8. First, Buckland et al. (1993) strongly recommend that the negative exponential model not be used. In addition, with such small sample sizes, the use of the hazard rate model is discouraged. Finally, if one tabulates the RMSE for the best AIC model among the uniform and half-normal models, it can be seen that performance is poor (RMSE = 341.1%), due primarily to AIC selection of the half-normal model with cosine adjustment in 2 of the 11 populations. In both cases, this model produced an estimated density that was quite poor. Thus, for trapping-web data, these results suggest the use of the uniform model with a cosine adjustment function for density estimation.

Implications for future studies

In summary, the results of this study have demonstrated that several density estimators can produce accurate results on field data sets of small-mammal populations. Web-based analytical approaches are deemed superior to grid-based approaches for estimating density, due to the well-founded theoretical basis for dis-

tance-sampling techniques and the empirical success of web-based density estimators. If the basic assumptions of distance sampling can be met, it is likely that web-based density estimation can be successfully applied to small-mammal species in different ecosystems around the world. Grid-based approaches to density estimation, while also empirically successful in this study, require a large number of assumptions regarding animal movement measures, boundary widths, and effective trapping area (unless conducted with a concomitant radiotelemetry study); these assumptions reduce the value of the approaches, and restrict the potential applicability of our grid-based results to other situations.

The overall success of the estimation models in producing accurate and unbiased \hat{D} values was encouraging, given the range of sample sizes of the rodent data sets. The recommended minimum sample sizes for programs CAPTURE or DISTANCE is ~80–100 individuals (Otis et al. 1978, Burnham et al. 1980, Buckland et al. 1993, 2001), values that were not achieved in any of the 11 data sets (Tables 3 and 8). Still, while most of the test data sets comprised <40 individuals, some of the models still functioned well (though precision was low in certain instances). These results should be particularly encouraging for researchers studying small mammals, because many field sampling efforts for rodents and other small mammals typically produce sample sizes in the range observed in this study. In addition, the models worked well on estimating densities across a number of rodent species commonly encountered in North American rodent studies, including members of widespread genera in the

families Heteromyidae (*Perognathus* and *Dipodomys*) and Muridae (*Peromyscus*, *Reithrodontomys*, and *Onychomys*). Given the good performance of the density-estimation models on data sets of common rodent species with realistic field-sample sizes, and assuming a comparable performance in other ecosystems, these models should have wide applicability for small-mammal field research studies.

The application of these models in field research studies not only can produce accurate density estimates for addressing individual research questions (i.e., assessing the evidence for alternative hypotheses within a single study), but also can provide standardized results (numbers per unit area) for comparisons and syntheses among studies of different species, over different time periods, and from different ecosystems around the world (Wilson et al. 1996, Thompson et al. 1998). Syntheses of such small-mammal studies, reporting absolute densities instead of various nonstandard "indices" of abundance, would have direct applications to long-term, large-scale questions concerning biodiversity and planning of biological reserves, management of endangered species, and understanding the role of small-mammal density fluctuations and zoonotic disease outbreaks (e.g., rodent transmission of plague, Lyme disease, and hantavirus). We would certainly encourage small-mammal research ecologists to employ these models whenever possible, thereby contributing to the growing worldwide literature of small-mammal studies reporting standardized density results.

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