Small mammals: their productivity and population dynamics

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2. Density estimations of small mammal populations

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Accurate estimation of population density is perhaps the most important objective of IBP-related research. Not only is it worth studying on its own merit, but it is used in all calculations of standing crops and transfer coefficients between functional units of ecosystems. Inaccurate estimates of density decrease the precision of predictions about ecosystems. Many other variables in field ecology can be totally or partially studied in the laboratory and the results extrapolated to field conditions. Density must be measured *in situ* with many uncontrolled variables introducing biases into the estimates. Most problems associated with density measures in small mammal populations stem from the failure to recognize their spatial and temporal dynamic nature and the complexity of behavioral responses to census techniques.

Our objective in this paper is to discuss the available methods for obtaining density estimates in small mammal populations and to make recommendations concerning future work in this area. Literature citations have been selected to illustrate key points and not to supply an exhaustive list of all appropriate papers. The general outline of the paper follows the approximate sequence of decisions and actions taken during the conduct of the census procedure. As in actual field studies, some issues presented later directly modify earlier decisions discussed in the article. We realize that there is not just one way to take a census of small mammal populations, but there are certain key decisions that modify the subsequent usefulness of the data. Frequently the imposition of secondary objectives, such as elucidating community structure, confound the results beyond practical limits of interpretation.

Statement of objectives

The formulation of the objectives should precede the beginning of the work and not be an afterthought that results from an attempt to write a cohesive paper from a set of data collected in an almost random manner. For our purposes we will assume that we are discussing the

design of a study whose primary objective is as follows: to obtain a reliable estimate of the density of various species represented in some typical small mammal community. This estimate must be calculated with appropriate confidence intervals and some method of checking the model of calculation must be available to give credibility to the estimate. We realize there are several vague terms in our statement of the objective, but given the general nature of this paper these are unavoidable. As will become obvious, the design of specific studies depends not only upon the situation in question and the specific objective but also upon the secondary objectives. Rather than set specific secondary objectives at this time, we will present a series of conditional cases as we discuss typical decisions that determine the experimental design.

Precensus decisions concerning classification variables

Many variables affect the probability of capture. Some of these are discrete or classification variables (e.g., trap type) and decisions regarding them are usually made prior to the beginning of the census period. Others are uncontrolled and in many cases continuous variables (e.g., weather) and are normally recorded during the census period. Of course other variables fall into both of these categories (e.g., season) and the order of discussion in no way implies anything about their relative importance.

Census methods and trap types

Population density of small mammals has been estimated using a variety of traps and techniques. The three main categories of methods used for detection of small mammals are non-trapping, removal trapping, and non-removal trapping. The method used in a census should be based upon the species to be studied, the duration of time of the study (either a point in time estimate or sequential estimations through time) and the secondary objectives.

Several types of non-trapping techniques are available for small mammal detection. Density estimation using direct observation is possible for some small mammals using a removal plot technique (Hanson, 1968). Indirect observation using tracking boards (Lord *et al.*, 1970), dropping boards (Emlen *et al.*, 1957), sand transects (Bider, 1968) and runway counts (Lidicker, 1973) can be used to detect the relative but not the actual numbers of small mammals. Recently,

Marten (1972) described a method for small populations of rodent using live trapping and marking with subsequent estimation using tracking boards. It is doubtful that this technique can be used for a wide variety of species.

In certain situations, excavation of burrows is an effective technique for density estimation. This has been done in an open field (Smith 1968*a*) and inside a temporary enclosure (Dieterlen, 1967*c*) or coupled with poison (Gromadzki & Trojan, 1971) to prevent escape while digging. Digging out burrows of *Peromyscus polionotus* gave more accurate estimates than trapping (Smith, 1968*a*); however, this technique is not practical for most small mammals. Mice have been captured by hand from flooded burrows (Andrzejewski & Gliwicz, 1969; Ryszkowski *et al.*, 1971), from under shocks of grain (Linduska, 1942), or from nest boxes (Brant, 1962) but these methods are probably not practical for most small mammals.

Removal census methods find their greatest use in density estimation for a point in time (Hayne, 1949; Grodziński, Pucek & Ryszkowski, 1966; M. H. Smith *et al.*, 1971). Three basic types of traps used in removal studies are the kill traps, live traps, and pitfall traps. The most efficient trap for most rodents is the kill trap (for a review see Wiener & Smith, 1972). Small snap traps are probably more efficient than live traps for some insectivores (Kale, 1972). For insectivores and certain rodents pitfall traps have a high capture efficiency (Edwards, 1952; Aulak, 1967; Brown, 1967; Pucek, 1969; Hamer *et al.*, 1971). Density estimates using removal procedures can be made using live traps when animals are needed for other reasons.

Non-removal census methods are more time consuming but provide sequential density estimates for the intact population and allow the analysis of other population parameters (Brant, 1962; Tanton, 1969; Tanaka, 1972). Live traps and pitfalls are commonly used with this technique. Pitfalls are more efficient in studies of certain small mammals (Andrzejewski & Wroclawek, 1963; Chelkowska, 1967; Pucek, 1969; Dub, 1971*a*). Differences in the efficiency of live traps of different sizes are debatable (Quast & Howard, 1953; Kisiel, 1972); obviously large traps can be insensitive to tripping by smaller species (Grant, 1970). In addition, other aspects of trap construction alter species-specific probabilities of capture (Brant, 1962; Hansson, 1967).

A problem common to both removal and non-removal census techniques is the determination of numbers of traps per station. Multiple traps per station avoid saturation of trapping stations and

result in a higher capture rate for the population, but too many traps at a station lowers the probability of capture per trap (Andrzejewski *et al.*, 1966). Combinations of trap types at each station may also offset inclement weather bias due to trap sensitivity (G. C. Smith *et al.*, 1971; Wiener & Smith, 1972) or species-specific preference for different traps (Aulak, 1967). Hansson (1967) found that two or more single-capture live traps per station were more successful than a single multiple-capture live trap in reducing biases caused by behavioral interactions. These considerations are particularly important in high density situations (Tanaka, 1963*a*).

Bait

The presence or absence of bait as well as the type of bait explains part of the variability in trap response. Certain baits elicit a higher trap response than others, although the response may change among different age and sex classes or among the different habitats (Fowle & Edwards, 1954; Carley & Knowlton, 1968; Patric, 1970). Bait accept-ability also varies seasonally (Fitch, 1954) and is a function of the availability of food in the habitat (Smith & Blessing, 1969). In the worst situation failure of traps to capture certain animals may actually be explained by ineffectiveness of the bait. Specific baits can be used to capture a variety of mammals including shrews and rodents (Beer, 1964), and these should be used when studying small mammal communities. Animals also respond to traps without bait, but in most instances their response is enhanced by its presence (Andrzejewski & Wroclawek, 1963; Carley & Knowlton, 1968; Balph, 1968; Buchalczyk & Pucek, 1968).

Bait is sometimes placed at each station for one to seven days before the census period begins (Grodziński, Pucek & Ryszkowski, 1966; Tanton, 1969; Zejda & Holisova, 1971). There is usually good acceptance of the prebait but this varies according to species and possibly repro-ductive class (Holisova, 1968; Myllymäki, 1969–70; Myllymäki, Paasikallio & Häkkinen, 1971). One reason for prebaiting is to increase the initial probability of capture by conditioning the animals to the trapping situation. Prebaiting accelerates the rate of capture, decreases its variance (Gentry, Golley & Smith, 1971) and increases the probability that the data will fit a regression model for population estimation (Hayne, 1949; Zippin, 1956; Tanaka & Kanamori, 1969). The technique has also been used to mark animals prior to the census to measure the edge effect (Ryszkowski, 1971*a*).

Under certain circumstances prebaiting can allow populatio: estimates to be made in less time (Tanton, 1969). In addition, it i absolutely essential for some methods of population estimation (Smitl *et al.*, 1969–70), but there are instances where it does not work (Grod ziński, Pucek & Ryskowski, 1966; Gentry *et al.*, 1968). Other disadvan tages include the probable concentration of animals on the edge of th: sampling area resulting in an inflated density estimate (Zejda & Holi sova, 1970; Gentry, Smith & Beyers, 1971*a*) and a disruption of th: spatial organization of the populations. This would prevent the use o the data for studying social organization (Calhoun, 1964; Gentry Smith & Beyers, 1971*b*). If it is possible to study social organizatioi from trapping results, then it would seem best to avoid prebaiting unles: it is needed to mark animals for calculation of the edge effect. In non removal studies prebaiting adds additional food and may thus affec: subsequent population dynamics (Gentry, 1968; Smith, 1971). Pre baiting is another complicating variable whose simple effects anc interactions with the myriad of other variables that we must deal witl are mostly unknown.

Trapping configurations

The spatial arrangement of the traps is usually determined by the shape and amount of habitat available and the intensity of effort required foi an adequate sample. The basic configurations are transects, grids, oi some modification thereof. Transect or line trapping is most often used in studies of short duration when the primary objective is the collection of specimens and secondarily the estimation of relative density (Calhoun & Arata, 1950–7). A census line alone cannot be used to determine absolute density unless habitat and species-specific calibration factors are known (Stickel, 1948; Hansson, 1967).

The simplest use of line trapping for density estimation can be accomplished by trapping on a census line followed by trapping on an assessment line (cross line method; Fig. 2.1*a*). Animals captured on the census and assessment lines can be marked and released or removed. The assessment line should be placed at an acute angle to the census line and trapping conducted for a short period (M. H. Smith *et al.*, 1971). The angle would depend upon the expected area of effect around the census line and the spacing of the trap stations on the assessment line, thus optimizing the number of stations in each area. In the ideal situation there would be a minimum of ten stations in the area of effect

and a like number in the area unaffected by the trapping at either end of the assessment line. The primary advantage of the cross line is the relatively small amount of effort and habitat required for its operation. Unfortunately, the use of this simple design will be complicated by the variance in the spatial locations of animals responding to differences in
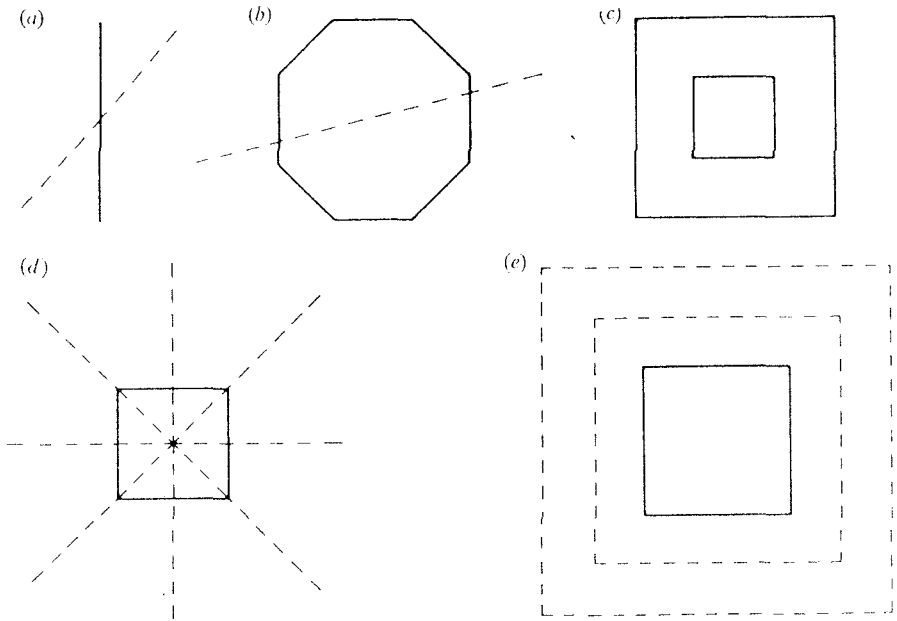

Fig. 2.1 Sample configurations of trapping methods used to estimate density. Configurations are not drawn to scales. Solid and dashed lines represent census and assessment lines respectively. (*a*) Cross lines; (*b*) octagon with one assessment line; (*c*) grid with inner square indicated; (*d*) grid with eight assessment lines; and (*e*) grid with outer concentric squares or assessment lines. Trapping is usually conducted on grid or census line first, followed by trapping on assessment lines.

habitat (Olszewski, 1968). Little is known about the dispersion of small mammals in a relatively homogeneous habitat (Opuszynski & Trojan, 1963; Wallin, 1971).

The problems associated with the cross line method can be overcome by using several sites and the pooled results to calculate density. The lines may be scattered or connected to form a continuous line, either straight or circular. Assessment lines must be arranged so they do not modify the capture rates on other lines near or in the area of effect (Kaufman *et al.*, 1971). In practice the circular census line is easier to locate in the habitat if it is in the shape of an octagon (Wheeler &

Calhoun, 1968; Fig. 2.1*b*). It also does not require a long linear stretch of homogeneous habitat.

Two basic octagon designs have been used, although the success of this method is not completely demonstrated (Gentry, Smith & Chelton, 1971; Kaufman *et al.*, 1971). In theory there should be a lower rate of capture along the assessment line as it goes through the area of effect around the census line. This phenomenon refers solely to unmarked animals if those captured on the census line were marked and released. In one study, assessment line trapping revealed an unexpected increase in the number of captures around the census line (Gentry, Smith & Chelton, 1971). Variation in the probability of capture along the assessment lines due to prior trapping on census lines violates one of the basic assumptions of the method (Hansson, 1974). More work is needed to check this and other assumptions, but it is possible that the assessment lines were not long enough to extend into the unaffected area.

The length of the assessment lines depends upon the distance animals are likely to move during the census period. Adamczyk & Ryszkowski (1968) found that *Clethrionomys glareolus* and *Apodemus flavicollis* move an average of 157 and 180 m, respectively and long range movements have also been reported by Faust *et al.* (1971) and Tanton (1969). It is now apparent that our initial view of the distribution of small mammals in a relatively static spatial pattern was erroneous.

A grid is a series of parallel lines with some common distance between them. It is frequently used in studies of relatively long duration where sequential trapping is used to give information concerning temporal (usually seasonal) fluctuations in population characteristics. Grids are usually rectangular and located in the middle of relatively homogeneous habitat. They should be large enough to easily include the average distance moved by the small mammals being studied. One of the primary biases may be a sampling area that is too small to adequately study density-related population processes.

Trapping can be used to estimate population number which can then be divided by the area of the grid to give an estimate of density. This approach usually results in an overestimate of density because it fails to recognize that the sampling area is larger than the grid (M. H. Smith *et al.*, 1971). Data gathered from grids can be used in two ways to calculate the area sampled. The first compares the number of captures at outer stations to those at inner stations (Hansson, 1969*a*; Pelikan, 1970; Smith *et al.*, 1969–70). The other approach involves use of prebait to mark animals as residents on the grid (Ryszkowski, 1971

Fig. 2.1*c*). These inner grid techniques have certain disadvantages (Gentry, Smith & Beyers, 1971*b*; M. H. Smith *et al.*, 1971), and this has resulted in modifications of the grid configuration.

Two basic modifications exist: one uses assessment lines extending from the grid (M. H. Smith *et al.*, 1971; Fig. 2.1*d*), and the other uses outer concentric squares of traps removed from the edge of the grid (H. D. Smith *et al.*, 1972; Fig. 2.1*e*). Both techniques attempt to measure movement relative to the censusing activity on the grid by examining the spatial location of animals in the border zone. Published results utilizing these configurations are few and need replication in a variety of environments. We know of a series of such tests for the grid and assessment lines, but the results are as yet unpublished. Preliminary analyses indicate the usefulness of this technique in habitats ranging from deserts to lowland hardwood forest.

There is a need to combine a series of configurations and techniques into one study to compare the resulting density estimates. Ryszkowski, Gentry & Smith (1971) proposed a comparison of the method of using prebaiting to determine density from the trapping records on the grid (Ryszkowski, 1971*a*) with that utilizing assessment lines (M. H. Smith *et al.*, 1971). Four such tests have been conducted, and the preliminary analysis indicates good agreement in most cases (i.e., density estimates ± two standard errors overlap for the two methods).

Grid size and trap spacing are also important variables. As a grid is increased in size the relative bias of the edge effect should be reduced until it is negligible (Faust *et al.*, 1971), although this requires a grid that is larger than those commonly used. Small grids may give approximately the same results as larger ones (Myllymäki, Paasikallio & Häkkinen, 1971; Pelikan, 1971; Zejda & Holisova, 1971), but these studies have not calculated density with confidence intervals so it is difficult to evaluate the results. Grid size is also a function of trap spacing which is critical to the measurement of other population characteristics, such as apparent home range (Hayne, 1950).

Trap spacing is important in modifying density estimates (Tanaka, 1966) and should be based on the animals' ability to detect traps at some distance defined here as the 'recognition distance'. In a preliminary analysis of species in a lowland hardwood forest of South Carolina, the recognition distance was 2.9 m which is approximately 1/5 of the common trap spacing (15 m) used in this area (Gentry, Golley & Smith, 1971) or 1/30 of the home range diameter. Calhoun has suggested spacing traps at 1/6 the average diameter of the home range of the dominant

species (Smith *et al.*, 1969–70). Wheeler & Calhoun (1967) introduced the concept of 'perception swath' in discussing trap spacing, which is approximately twice the recognition distance. Theoretically trap spacing should be based on the recognition distance but more work is needed to empirically define this value. A trap spacing of 15 m may be a good compromise for most of the common species studied throughout the world; this certainly appears to be the case in the southeastern United States (Smith *et al.*, 1969–70).

Habitat

Small mammal species have become adapted to certain habitat types where their needs for food, shelter, moisture, etc., are satisfied. The habitat may be vertically stratified allowing more species to co-exist (Getz & Ginsberg, 1968; Rosenzweig, 1973). Certain habitat features (e.g., uprooted trees) influence movement patterns and the intensity of contacts between individuals (Olszewski, 1968). Arboreal species represent a special problem and may not be adequately sampled unless traps are placed in trees (Gentry *et al.*, 1968). Fossorial and semi-fossorial species present a similar problem. These considerations suggest that density may be more appropriately calculated as a function of volume rather than area. Density should also be calculated on a habitat-specific basis where study areas include more than one habitat type (Blair, 1941). Therefore, the type of habitat, its degree of heterogeneity, and special features must be considered when undertaking a population census.

Season

Small mammals exhibit annual cycles in numerous population and individual variables (Smith, 1974). These cycles have a bearing on the approach to census studies both directly and with respect to the achievement of secondary objectives. The choice of season(s) and techniques of censusing, therefore, should be partly based upon whether the information needs to be collected once, periodically during the year, or over the entire annual cycle.

Two major variables, density (Briese & Smith, 1974) and trap response (Hansson, 1967; Pucek, 1969), undergo annual fluctuations. Animals that hibernate or estivate have a probability of capture of zero at certain times. Therefore, population densities in the same or different habitats should be estimated during the same time of the year. The

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reproductive season and period of peak density are two important times for such studies (Ryszkowski, 1969*b*). In southern latitudes where breeding seasons sometimes extend throughout the year (Davenport, 1964), sampling must be more frequent. Changes in trap response throughout the year require census techniques that account for changes in the probability of capture, in order that annual changes of density are not primarily a reflection of fluctuations in trap response.

Models

Selection of the appropriate statistical model should be one of the early considerations in planning a population census. Concern must be given to assumptions in the selected model, inclusion of checks on the validity of these assumptions, sample sizes required by the model, and secondary objectives. Generally, the more assumptions that can be met the more efficient the population estimate will be (Cormack, 1968).

Although estimates of population size may not be seriously affected by an inadequate model (Junge, 1963) the variance estimate will be biased (Cormack, 1972) and may be imprecise even when the assumptions appear to be met (Roff, 1973*a*). Therefore, empirical estimates of the variance should be used (Paulik & Robson, 1969; Roff, 1973*a*).

Duration of the census

The duration of the study will be partly determined by the sample size necessary to provide a density estimate with a specified level of precision. In determining the duration of a study the factors to be considered are: the model for analysis, likelihood of violations of the assumptions in the model, desired level of precision for estimates, sample size (n), and intensity of sampling, as well as the secondary objectives.

Precision is the probability that $\hat{N}$ (estimated population size) does not differ from the true population size (N) by more than pN, where p is the level of accuracy (see (2.1); Robson & Regier, 1964),

$$1 - \alpha \leqslant P\left(-p < \frac{\hat{N} - N}{N} < p\right) \tag{2.1}$$

where α is the selected probability level and $1 - \alpha$ is the precision. The level of accuracy suggested for population estimates was given as 0.10.

Roff (1973*a*) studied sampling intensities (n/N) necessary to achieve a coefficient of variation of 0.05 (accuracy = 0.10) for Petersen and

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Jolly–Seber estimators and found that as the population increases sampling intensity may be allowed to decrease, although sample size increases. Formulae given by Roff were used to estimate sampling intensity and sample size at the 10 per cent level of accuracy (Table 2.1).

Table 2.1. *Sample sizes* (n)† *necessary to obtain* 10 % *level of accuracy of the population size* (N)

Petersen method			Jolly (3 sample)		
N	n/N	n	N	n/N	n
5	0.987	5	5	0.923	5
25	0.944	24	25	0.832	21
50	0.899	45	50	0.767	38
75	0.861	65	75	0.719	54
100	0.828	83	100	0.682	68
125	0.799	100	125	0.649	81
150	0.775	116	150	0.621	93
175	0.752	132	175	0.596	104
200	0.732	146	200	0.573	115
225	0.714	161	225	0.553	124
250	0.697	174	250	0.533	133
275	0.681	187	275	0.516	142
300	0.667	200	300	0.499	150
325	0.653	212	325	0.485	158
350	0.641	224	350	0.471	165
375	0.629	236	375	0.458	172
400	0.618	247	400	0.445	178
425	0.608	258	425	0.433	184
450	0.597	269	450	0.422	190
475	0.589	280	475	0.412	196
500	0.579	290	500	0.402	201

† The tabulated values were obtained by selecting N, setting the coefficients of variation at 0.05 (Roff, 1973a) and solving for n/N and n. Petersen CV $\sqrt{[(1 - P)/(NP^2)]}$. Jolly–Seber CV $= \{[(1 - P)^2/N](1 + 1/P)\}^{\frac{1}{2}}$. $P = n/N$ or sampling intensity.

A practical suggestion for mark-recapture techniques is that the product of the number marked and the number examined for marks should equal four times the population size ($nM = 4N$; Robson & Regier, 1964). When populations are small ($N < 15$), Boguslavsky (1956) provides a means for terminating sampling by examination of sequential captures.

If regression formulae are used to calculate $\hat{N}$ for removal studies then accuracy increases with the duration of sampling (i.e., the number

of nights traps are set; M. H. Smith *et al.*, 1971). Accuracy is not greatly affected by the duration of study when multinomial formulae are used, but is primarily determined by the sampling intensity. Tables for sampling intensities necessary to obtain desired levels of accuracy are available for this method (Zippin, 1958).

The final solution to the determination of duration must result from optimization of all factors so that assumptions of the selected model are met, desired levels of precision obtained, and requirements of special sampling schemes satisfied.

Additional variables affecting probability of capture

Weather

Activity patterns of most vertebrates are affected by changes in weather (Briese & Smith, 1974; Gibbons & Bennett, 1974). For example, terrestrial animals show increased activity on warm, cloudy nights with even greater activity when these conditions are accompanied by rain (Bider, 1968), but responses of these animals to weather changes may be delayed for up to four days (Sidorowicz, 1960). In addition, weather affects abundance (Smith, Gentry & Pinder, 1974) and 'trappability' of small mammals (Sidorowicz, 1960; Mystkowska & Sidorowicz, 1961).

Usually the effects of weather on small mammal activity are discussed in general terms or in respect to the most obvious weather variable. For example, Gentry & Odum (1957) considered weather and winter activity of old-field rodents, while Blair (1951) and Caldwell & Connell (1968) studied the relation between activity of the old-field mouse (*Peromyscus polionotus*) and clear moonlit nights. However, attempts to statistically evaluate individual weather variables on small mammal activity are few (Gentry *et al.*, 1966; Marten, 1973). These studies show that weather effects are difficult to isolate due to the correlation and interactions between rainfall, humidity, temperature, moonlight, barometric pressure, season, habitat, species, etc., although a possible approach to this problem might involve principal component analysis (Hinds & Rickard, 1973).

Increases in probability of capture with changes in weather seem to result from greater distances moved rather than changes in trap response, Several lines of evidence indicate this is true. Pitfall methods, not involving trap response in the classic sense, reveal that movement is influenced by weather changes (Briese & Smith, 1974), and rainy

weather produces an increase in captures on the edges of grids durin
removal trapping (Gentry, Golley & Smith, 1971). Further, reinvasion c
an area is correlated with mean monthly air temperature (Smith
1968b). It should follow that the area of removal or range of movemen
is also a function of weather. The effect of weather on density estimation
can be minimized by selecting a model which does not require a constan
probability of capture over the duration of the study (Kaufman *et al.*
1971).

Behavioral response to traps

Differential trappability will result from variability in explorator
behavior and response to novel objects (Balph, 1968). Species that ar
neophilic are caught at a faster rate than those that are more neophobi
(Faust *et al.*, 1971) and individuals within a species also show a wid
range of response to traps (Young *et al.*, 1952; Petrusewicz & Andrze
jewski, 1962; Sheppe, 1966a; Balph, 1968). When considering thi
behavioral response, several interrelated factors (age, sex, reproductiv
condition) must also be considered.

Age affects trappability because of the animal's prior experience anc
social rank. Older animals frequently rank higher in social stature anc
may be caught first and more often than young individuals. This ha
been shown for both removal (Carley & Knowlton, 1968; Gentry *et al.*
1968) and non-removal trapping (Andrzejewski & Rajska, 1972
Summerlin & Wolfe, 1973). Variability in trap response within pop
ulations is suggestive of social effects (Petrusewicz & Andrzejewski
1962; Gliwicz, 1970), while intracohort variability is also associatec
with sex and breeding conditions (Gliwicz, 1970). In removal studies
reproductive males are taken at a higher rate (Myllymäki, 1969–70
Myllymäki, Paasikallio, Pankakoski & Kanervo, 1971) and capture
rates are higher during the breeding season (Chelkowska, 1967; Gliwicz,
1970).

Olfactory or auditory stimulation may alter the probability of
capture (Calhoun, 1964). In multiple-capture traps, the presence of
Apodemus flavicollis inhibited the trappability of other *Apodemus* and
Clethrionomys glareolus (Kalinowska, 1971). Additionally the presence
of *Clethrionomys* had no effect on *Apodemus* and enhanced the capture
of other *Clethrionomys*. Subordinate *Sigmodon hispidus* tended to avoid
traps when treated with conspecific scent, but dominant individuals did
not (Summerlin & Wolfe, 1973).

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Non-removal trapping presents a problem since there is usually a change in probability of capture between initial and subsequent captures. Animals are placed in two groups, trap-prone and trap-shy, on the basis of frequency of recapture (Tanton, 1965; Andrzejewski et al., 1971). This may be equivalent to the neophobic–neophilic division discussed earlier. Tanaka (1956) denotes three types of populations: Type I, initial capture rate < recapture rate; Type II, initial capture rate > recapture rate; Type III, initial capture rate = recapture rate. Most populations and species of rodents tend to be Type I while few are Type III (Tanaka, 1963b). Prebaiting fails to change the trap response of the population from Types I or II to Type III (Tanaka, 1970). In reality, trap response is probably a continuously distributed variable but the shape of the function for the inter- and intra-specific cases needs documentation.

Movement patterns

Trapping alters the behavior of small mammals, their responses being further complicated by age, sex and breeding condition. For example, males traverse larger areas than females, thereby increasing the probability of encountering a trap (Howard, 1960; Brown, 1969). Among invading animals, males constitute the highest proportion of captures, females and subadults being intermediate and juveniles the lowest (Myllymäki, 1969–70; Dub, 1971b; Myllymäki, Paasikallio & Häkkinen, 1971). Evaluation of differential movement requires a comparison of the numbers of animals in each sex–age category in the surrounding populations and under these conditions differential movement may be shown to be apparent rather than real (Briese & Smith, 1974).

If the area of the border zone is not taken into account, movements of animals on to the edge of sampling areas bias density estimates upwards. This edge effect can be the result of normal movements of animals living partially on the grid (Ryszkowski, 1969b) or animals may also move into vacant areas upon the removal of residents (Chelkowska & Ryszkowski, 1967). The difference between removal rates of individuals marked by prebaiting and those that are unmarked (Pucek & Olszewski, 1971; Gentry, Smith & Beyers, 1971a) is due to delayed movement onto the grid (M. H. Smith et al., 1971). Recognition of the spatial dynamic nature of the small mammal community is, therefore, essential to the proper design of census studies.

Interspecific removal rates

Up to this point we have been mainly concerned with interactions of intraspecific behavior with census techniques. Calhoun (1964) observed interspecific differences in small mammal capture rates and suggested that differences were related to social organization of the small mammal community. Differences in the removal rates (summarized in Table 2.2)

Table 2.2. *Relative removal rates of some small mammal species*

Species	Fast†	Intermediate†	Slow†
Rodents:			
Apodemus agrarius		12	12
Apodemus flavicollis	7, 9	12	12
Clethrionomys gapperi	8, 13		
Clethrionomys glareolus	9, 12	7	
Micromys minutus	12		
Microtus pennsylvanicus		11	
Microtus pinetorum			2, 8
Mus musculus			10
Napaeozapus insignis		13	
Ochrotomys nuttalli	13	5, 6	1, 2, 3, 4, 13
Peromyscus gossypinus	1, 2, 3, 4, 5, 6		
Peromyscus leucopus	8, 13	13	
Peromyscus maniculatus	13	13	
Rattus exulans		10	
Rattus rattus	10		
Reithrodontomys humulis			14
Sigmodon hispidus	14		
Insectivores:			
Blarina brevicauda	1	8, 11	2, 3, 4, 5, 6, 13
Sorex araneus			7, 9
Sorex cinereus			8
Sorex longirostris		1	1
Sorex minutus			9
Suncus murinus	10		

† 1. Gentry, Golley & Smith (1968); 2. M. H. Smith *et al.* (1971); 3. Kaufman *et al.* (1971) 4. Gentry, Smith & Chelton (1971); 5. Faust, Smith & Wray (1971); 6. Gentry, Golley & Smith (1971); 7. Pucek & Olszewski (1971); 8. Calhoun (1964); 9. Aulak (1967) 10. Barbehenn (1969); 11. Barbehenn (1974); 12. Grodziński, Pucek & Ryszkowski (1966); 13. Nabholz (1973); 14. Briese & Smith (1974).

can create serious problems in assessing densities. *Peromyscus gossypinus* is removed from grids at a faster rate than *Ochrotomys nuttalli* or *Blarina brevicauda* (Gentry, Golley & Smith, 1971). In one case *O. nuttalli* did not appear until day 6, and in another, *B. brevicauda* did not appear until day 12; these species and perhaps others would not have been

detected by the Polish standard minimum grid (Table 2.2; Grodziński, Pucek & Ryszkowski, 1966). Polish investigators observe small inter-specific differences in rodent capture rates (Pucek & Olszewski, 1971). Trapping periods are short (3–5 days) and prebaiting is routinely used (Grodziński, Pucek & Ryszkowski, 1966); insectivores are removed by pitfall traps (Aulak, 1967).

Calhoun's (1964) hypothesis on species-specific removal rates is based on the spatial arrangement and movement patterns within the small mammal community. From this hypothesis the dominant species should be captured at a more rapid rate and have larger home ranges than the subordinate species. In contrast, Faust *et al.* (1971) found that *B. brevicauda*, a species removed at a slower rate, had the largest home range. One of Calhoun's assumptions is that the distribution of species in the small mammal community is not clumped, but this assumption is rarely met and different species have different removal rates even when spatially separated (Gentry, Golley & Smith, 1971; Kaufman *et al.*, 1971).

An alternative to Calhoun's hypothesis is that species differ in their reaction to traps (neophobia versus neophilia; Faust *et al.*, 1971). Also, initial trap response may be different from subsequent responses (Tanaka, 1963*b*; Balph, 1968; Faust *et al.*, 1971). Regardless of the reasons for different removal rates, they do create problems in estimating densities, but any model which does not require a constant probability of capture over the duration of the study will lessen the effect of differential removal rates. Continued application and development of these models should be encouraged.

Statistical methods for density estimation

Population estimation by non-removal techniques

Since 1889 when Petersen suggested a method of population estimation using the ratio of marked to unmarked captures (LeCren, 1965), the investigation of theoretical models of population estimation has been a dynamic field. We will consider some general models for mark–recapture and removal studies (see Cormack, 1968; Hanson, 1967 for reviews) followed by some special methods to solve some of the problems encountered in population estimation.

Assumptions commonly made by mark–recapture models are:
(1) The animals do not lose their marks.
(2) The captures are correctly recorded as marked or not marked.

(3) Marking does not affect the probability of survival.

(4) The population is either open or closed, therefore
- (*i*) no gain or loss of members during sampling, or
- (*ii*) there is recruitment and immigration but death and emigration affect marked and unmarked animals equally (in this case survival rates are assumed to be constant, i.e., not correlated with age), or
- (*iii*) knowledge is available from other sources which permits an allowance to be made for migration, birth and death prior to the analysis of the data.

(5) The population is randomly sampled so that either
- (*i*) every animal has the same probability of capture, or,
- (*ii*) if there exist strata within the population which have different probabilities of capture then the marked animals are proportionally distributed through these strata.

With the Petersen method (Lincoln index) one period of marking is followed by one period of recapture. This method requires that assumptions (1), (2), (3), (4.*i*) and (5.*i*) hold. The population estimation is made by

$$\hat{N} = \frac{Mn}{m} \qquad (2.2)$$

where:

M = number of marked animals released from the first sample;

n = number of animals in the second sample;

m = number of marked animals in the second sample.

Because $\hat{N}$ overestimates N by $1/m$ the equation $\hat{N} = m(n + 1)/(m + 1)$ with bias of e^{-m} has been suggested by Bailey (1952) for small populations.

If M_i (the total number of marked animals in the population before the *i*th sample) is known, then the Schnabel (1938) estimate

$$\hat{N} = \Sigma n_i \cdot M_i / \Sigma m_i \qquad (2.3)$$

where:

n_i = number in the *i*th sample;

m_i = number in the *i*th sample that are marked;

may be used with sequential sampling and is identical to a series of Petersen estimates (Cormack, 1968).

Bailey's (1951) triple-catch method gives a deterministic estimate of birth and death rates (Cormack, 1968) but has been shown to be less efficient than the Jolly–Seber estimates (Roff, 1973a).

The Jolly–Seber stochastic model sequentially estimates population size and requires assumptions (1), (2), (3), (4.*ii*) and (5.*i*) above. This more general method uses more information from the population, and allows for the removal of animals during the study and the estimation of survival, immigration and probability of captures. The population size at time *i* is found by

$$N_i = \frac{n_i}{m_i} \qquad \hat{M}_i = n_i + \frac{n_i Z_i S_i}{m_i\, r_i} \qquad (i = 2, \ldots, k - 1) \qquad (2.4)$$

where samples are taken on *k* occasions and the population size is estimated at time *i* and where:

$\hat{M}_i$ = estimated number of marked animals in the population at time *i*;

Z_i = number marked before the *i*th sample which are not caught in the *i*th samples but are caught subsequently;

S_i = number released from the *i*th sample;

r_i = number of the S_i that are caught subsequently.

Other formulae are given by Jolly (1965). Biases resulting from unequal catchability, birth and survival rates have been discussed by Cormack (1972).

A recent model suggested by Manly & Parr (1968) is a special case of the Jolly–Seber model (2.3). Its usefulness comes from a modification of assumption (4.*ii*) so that mortality rates may be age related (Manly, 1970). Population size at time *i* is found by

$$\hat{N}_i = \frac{n_i \cdot m'_i}{r'_i} \qquad (2.5)$$

where:

m'_i = total number of animals marked and known to be alive at time *i* (in class Z_i);

r'_i = the number of m_i caught at time t_i.

The mathematical models which these methods are based on must be shown to hold before an estimator may be justifiably used. Assumptions (1), (2), and (3) are required by all mark–recapture models and can be met by careful marking and recording procedures. Assumption (4) can

be checked by experimental techniques and/or an alternate model chosen or formulated. However, the most frequently violated assumption is that of equal catchability (assumption (5). This is a major weakness of mark–recapture methods because changes in trappability cannot readily be detected by statistical methods (Roff, 1973*b*) or compensated for by statistical refinements (Hanson, 1967). A possible solution for heterogeneity of trapping may be provided by using different trapping techniques for marking and recapturing (Junge, 1963). Eberhardt (1969) and Barbehenn (1974) recommend that traps should be shifted at least once during the sampling period. Every technique, both biological and statistical, must be used to check and countercheck the validity of the assumptions (Cormack, 1968).

The estimation of the variance by empirical techniques has been recommended because biases in both the estimated population size and the variance result when the requirements of the model are not met (Cormack, 1972). Another reason is that the variance is so highly correlated with the number of recaptures that the confidence limits sometimes exclude the true value of N. Empirical confidence limits may be calculated by selecting before the study begins the sampling intensity for which the coefficient of variation equals 0.05 and then obtaining the required sample size (Table 2.1). The confidence limits around $\hat{N}$ are then equal to $\pm 0.10 \ \hat{N}$ (Roff, 1973*a*).

New models and modifications of old ones for special applications continue to be suggested. Hanson (1967) and Rupp (1966) have shown that mark–recapture and removal methods are special cases of change-in-ratio estimators. Chapman & Junge (1956) have suggested a Petersen model which substitutes assumption (5.*ii*) for (5.*i*). Seber (1962) discussed modifications to the Jolly–Seber model when the number of recaptures are small. Tanton (1965*b*) proposed a population estimator for cases of unequal catchability when the frequency of recaptures follows the negative binomial distribution, but the method will work with other distributional functions. He extrapolates the function for the zero class and adds the animals in all classes to estimate N. If Tanton's method is valid, it represents a new approach, but we must devise ways to check both the accuracy and assumptions of his technique.

Population estimation by removal techniques

Population size may be estimated using two basic approaches (1) total enumeration or (2) sampling (Hanson, 1967). Enumeration of all

individuals (N) in a population from a known area (A) yields a true density value (D). Using this approach on a small island or in an enclosed area, trapping is directed toward total removal without the complication of migration. If the population is distributed over a greater area, it becomes necessary to subsample to estimate density. Total enumeration within sample plots randomly placed in the habitat can be used to estimate mean number of animals per plot as well as the standard error (Hanson, 1967). This method requires numerous temporary enclosures and is not practical for small mammals. When enclosed sample plots and removal trapping are used for the estimation of density ($\hat{D}$), there are two values that need to be estimated, population size ($\hat{N}$) and the area from which that population was removed ($\hat{A}$).

The simplest estimation of N is the total number of animals removed from an unenclosed plot. This technique assumes that nearly all animals in the population are caught. An index calculated from the mean difference between other estimates of numbers and the total number of individuals caught can be used to test this assumption (Grodziński, Pucek & Ryszkowski, 1966). This technique may be useful for studies in which a relative density is sufficient.

The most commonly used technique for estimation of populations for removal studies is the linear regression technique relating daily captures (Y) to previous number captured (X) (Hayne, 1949; Zippin, 1956). This technique assumes that (1) births, deaths, immigration and emigration do not occur or, if they do, their effects cancel each other out, (2) probability of capture is constant for all individuals, (3) probability of capture remains constant throughout the census period and (4) trapping effort during successive removals remains the same (Hanson, 1967). In this situation

$$Y = a_1 + a_2 X \qquad (2.6)$$

where a_2 is the probability of capture, (P_c), $a_1 = P_c N$ and $\hat{N} = X$ when $Y = 0$. A curvilinear regression technique that could be used for removal trapping is described by Tanaka & Kanamori (1967).

Using these assumptions, the number of animals captured on any day is the product of the probability of capture and the number of animals on the plot, but this approach is not applicable in most studies since the probability of capture does not remain constant (Gentry, Golley & Smith, 1971; Janion *et al.*, 1968). Variation in P_c can be reduced by shortening the period of removal (Buchalczyk & Pucek, 1968) – in certain situations some species on the area are not censused during

short periods of removal (Gentry *et al.*, 1968) – and prebaiting has also been used to increase probability of capture as well as its constancy (Grodziński, Pucek & Ryszkowski, 1966; Babinska & Bock, 1969; Gentry, Golley & Smith, 1971). Large daily variations in P_c decrease the correlation coefficient (r) and make resulting population estimates questionable (M. H. Smith *et al.*, 1971). Because of the non-independence of consecutive daily captures and the cumulative nature of X, r is biased upward (Acton, 1966). As a minimum, if the fit of the line is non-significant at $P \leqslant 0.05$, then this method of estimation can not be used. For short trapping periods the significance value of r is large (e.g., $r_{(0.05)} = 0.997$ for 3 days and $r_{(0.05)} = 0.950$ for 4 days) (Steel & Torrie, 1960) and confidence intervals are very large (M. H. Smith *et al.*, 1971). Many trapping studies conducted over a few days have probably yielded statistically nonsignificant population estimates.

Estimation of population size when probability of capture does not remain constant is possible using a maximum likelihood method and assuming a geometrical distribution (form specified) of captures across a time scale (Janion *et al.*, 1968). The mean of the conditional distribution of time of capture for the animals is used in conjunction with published tables to yield $\bar{P}_c$ and $\hat{N}$. Their formulae cannot be used without their tables, and thus are not included here. Procedures for estimation of confidence intervals were not provided by the authors. In addition no way is provided to check the assumption of the specified geometrical distribution; we feel that calculation of confidence intervals and application of the technique should depend at least partly on the fit of the data to the model. The technique can be used for data gathered by both removal and non-removal trapping.

Estimation of population size can also be made using the assessment line technique (Kaufman *et al.*, 1971; M. H. Smith *et al.*, 1971). This procedure does not require a constant P_c for all individuals through time. Movement in the border zone can occur without violating the assumptions of the method, since area is estimated from captures along assessment lines. The technique does assume that (1) for the habitat being studied there is relatively constant average rate of capture over distance and (2) P_c in and out of the area of effect is equal. It is necessary that density be high enough for the slope of the regression line in the unaffected area to be statistically different from zero. Since estimation of number by this technique is intimately associated with the estimation of density and area sampled, we will give the detailed method in a later section.

Area and density estimation

The simplest method of estimating density ($\hat{D}$) is by the formula

$$\hat{D} = \hat{N}/A_g \tag{2.7}$$

where A_g is the area of the grid and associated confidence intervals for $\hat{D}$ are calculated with $\hat{N}$. In this section, we will assume $\hat{N}$ is estimated by some method previously described and will not specify or reference the method here. The arbitrary border zone method simply adds a border of a certain distance from all sides of the grid. This distance is usually some multiple of the trap spacing or is based on information about average distances moved by species (Stickel, 1954; Pelikan, 1967). In this case

$$\hat{D} = \hat{N}/(A_g + A_b) \tag{2.8}$$

where A_b is the area of the border zone. Both of these approaches make unreasonable or unsubstantiated assumptions about the area of sampling.

Two techniques exist for calculating the border zone without pre-baiting (Hansson, 1969; Smith *et al.*, 1969–70). Both of these rely on the distribution of captures from outer to inner trap stations. The edge effect is demonstrated by the increased number of captures at outer traps compared to those at traps near the center of the grid. Smith and co-workers plotted probability of capture per station (P_{cs}) against the distance from the edge of the grid moving inward and P_{cs} was then calculated from the cumulative number of captures/cumulative number of traps for each concentric belt of stations from the outside inwards. *Simultaneous solution of two linear functions provided an estimate of the width of the border zone (W_b).* Thus

$$\hat{A} = (W_g)^2 + 4W_g \cdot W_b + \pi W_b^2 \tag{2.9}$$

where $\hat{A} = A_g + A_b$ and W_g is the width of the grid. Density is calculated as in (2.7). W_b in this method is probably equal to r in Hansson's technique (1969). For consistency we will use W_b instead or r and W_g in place of a in the discussion of his approach. Hansson gives

$$\hat{N}_b/b^2 = \hat{N}_a/(W_g^2 + 4W_g \cdot W_b + \pi W_b^2) \tag{2.10}$$

where $\hat{N}_b$ is the estimated number from an inner homogeneous square, b is the width of this inner square and $\hat{N}_a$ is the estimated population in the area sampled. W_b and b are calculated by inspection of the data and testing the distribution of captures with a chi-squared heterogeneity

test. Basically the inner square includes as much area as possible without the chi-squared test showing spatial heterogeneity. A series of tests should be conducted and the resulting statistics compared. One bias in the technique is that these tests are not independent and therefore the level of probability increases as a function of the number of tests ($P >$ 0.05 with more than one test). In both methods W_b is supposed to approximate to the radius of an average home range for the species captured. Density in Hansson's technique is calculated as in (2.7) with $\hat{N}_a = \hat{N}$. Neither Hansson nor Smith *et al.* give a method for calculating the confidence intervals for the sampling area, but it should be possible to use the variance in captures per station in the outer and inner areas to make these calculations.

M. H. Smith *et al.* (1971) discuss another method, the 'inner square' method, which has been extensively used (Aulak, 1967; Buchalczyk & Pucek, 1968; Adamczyk & Ryszkowski, 1968; Pelikan, 1970). In this method

$$\hat{D} = \hat{N}_b / A_b \tag{2.11}$$

where A_b is the area of an inner square of sampling stations and is equal to b^2 in (2.9). No attempt is made to estimate the width of the border zone; associated confidence intervals for $\hat{D}$ are calculated with $\hat{N}_b$. This method assumes that immigrants do not penetrate the inner square, but this assumption may not be justified (M. H. Smith *et al.*, 1971).

Bias due to the penetration of immigrants to the inner square may be reduced by shortening the census period or in using a prebait to mark the residents on the grid. In the latter method (Ryszkowski, 1971*a*), it is assumed

$$\hat{D}_b = \hat{D}_s \tag{2.12}$$

where $\hat{D}_b = \hat{D}$ in (2.17) and $\hat{D}_s$ is the density in the total sampling area. In addition

$$\hat{D}_b = \hat{N}_b / \hat{A}_b \tag{2.13}$$

with

$$\hat{A}_b = 75^2 + 4(75W_b) + \pi W_b^2 \tag{2.14}$$

and $\hat{N}_b$ is calculated from those animals marked or captured in the inner square.

For the total area

$$\hat{D}_s = \hat{N}_a / \hat{A} \tag{2.15}$$

and

$$\hat{A} = 225^2 + 4(225W_b) + \pi W_b^2 \tag{2.16}$$

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for a 16×16 grid with a 15 m interstation interval. From (2.11), (2.12) and (2.16)

$$\hat{N}_b/\hat{A}_b = \hat{N}_a/\hat{A} \qquad (2.17)$$

and from (2.13), (2.15) and (2.14)

$$\hat{N}_b/(75^2 + 4(75W_b) + \pi W_b^2) = \hat{N}_a/(225^2 + 4(225W_b) + \pi W_b^2) \qquad (2.18)$$

Since $\hat{N}_b$ and $\hat{N}_a$ can be solved by other techniques, (2.17) can be solved for the width of the border zone (W_b). Then, substituting W_b into (2.13) and solving for $\hat{A}_b$ or into (2.15) and solving for $\hat{A}$, (2.10) and (2.14) can be solved for density. A bias could be introduced in this method if the width of the border zone for the inner area is not equal to that for the total area or if the densities in the two areas are not equal. Because of the interaction between prebaited stations in the middle of the grid and the lower intensity of such interaction on the edge of the grid, this assumption may not be justified and needs to be checked (Gentry, Smith & Beyers, 1971*b*). In addition, no method for the calculation of confidence intervals is given for $\hat{A}$.

Another technique that uses outer belts of traps (dense line) around the grid to assess the border zone was described by H. D. Smith *et al.* (1972). In a sense the total grid is the inner square in this method. Application of the technique has been confined to a single mark–release study but by prebaiting on the dense line and later removal on the grid, the technique can be modified with appropriate mathematical formulae to work for either approach. Placement of the dense line is extremely important and currently has to be determined by trial and error. A method of calculation for the confidence intervals is given. This technique needs to be tested in a variety of habitats and some general rules for the placement of the dense line derived from the data.

The last method to be discussed is the assessment line technique first elaborated by Wheeler & Calhoun (1967). The lines pass through areas influenced by the removal trapping and areas not affected. Absence of animals captured during the census is detected by a decrease in the rate of capture over distance. The technique can be applied using many unique combinations of census lines, census grids and assessment lines (Gentry, Smith & Chelton, 1971; Kaufman *et al.*, 1971; M. H. Smith *et al.*, 1971). Modifications of this technique can be used in mark–release studies (Nabholz, 1973). Calculations for both $\hat{N}$ and $\hat{A}$ are incorporated into this method.

We will illustrate the method of calculation for a census grid and eight assessment lines (M. H. Smith *et al.*, 1971). Accumulating captures along a trap line results in a straight line (Gentry, Smith & Chelton, 1971; Kaufman *et al.*, 1971; M. H. Smith *et al.*, 1971) which can be calculated by the least squares method (Steel & Torrie, 1960). The slope (B) of this line represents the ambient rate of capture per unit
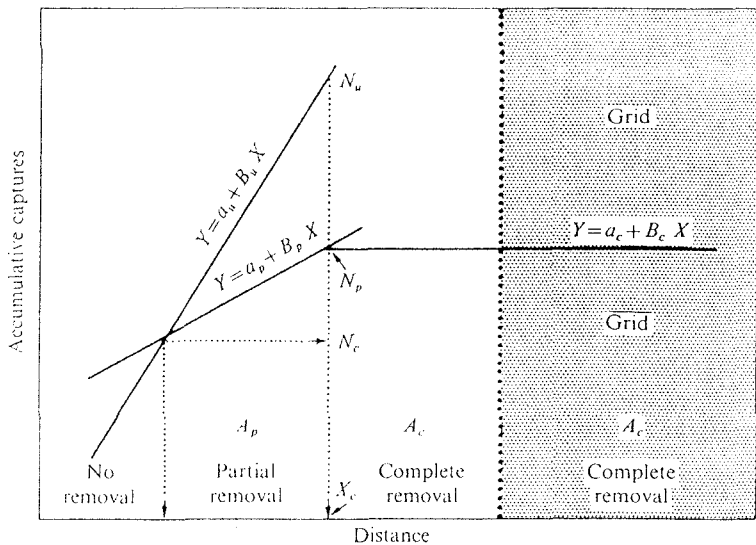

Fig. 2.2 Linear relationships between accumulative captures on the assessment lines as a function of distance from the outer ends of the assessment lines to the ends inside the grid. X_c denotes the edge of the area (A_c) from which all mammals had been removed. A_p is the area of partial removal. N_u equals the number of animals that would have been caught along the assessment lines up to X_c if A_p were equal to 0, N_p the accumulative number of animals actually caught at X_c, and N_c the number of animals that would have been caught if A_c had included the entire area of A_p (modified from figure in M. H. Smith *et al.*, 1971).

distance for a given number of trapping nights; B is dependent upon the density of small mammals and environmental factors responsible for varying P_c during the trapping period. If all of the mammals have been removed from the sampling area, B will abruptly change at the edge of the sampling area and will equal 0 inside this area (Fig. 2.2). The exact point of change in B can be calculated by the simultaneous solution of the two equations for the straight lines,

$$Y = a_c + B_c X \tag{2.19}$$

and

$$Y = a_u + B_u X. \tag{2.20}$$

Y is equal to the accumulative number of captures, X is distance in meters and a is the intercept of the line. The subscripts refer to the area of complete removal (c) and the unaffected area (u). Normally B_u would be statistically greater than B_c and can be tested by a one-tailed t test between the number of captures at each station in the two areas. Differences in the rate of capture should not be tested by a direct comparison of the slopes since the associated errors are biased because of the cumulative nature of Y and the non-random character of X. Another problem is associated with the decision concerning which points to include in the calculations of (2.19) and (2.20). Normally the change in the rate of capture in the two areas is obvious, but the inclusion of the ambiguous points into the calculations of either (2.19) or (2.20) results in little difference in the point of intersection of the lines. Similar considerations apply if there is an area of partial removal.

The point (X_c) along the assessment lines representing the edge of the area of complete removal ($\hat{A}_c$) can be calculated by

$$X_c = \frac{a_c - a_u}{B_u - B_c}. \tag{2.21}$$

The width in meters (W_c) of $\hat{A}_c$ outside the grid is

$$W_c = L_a - X_c. \tag{2.22}$$

L_a is the length of the assessment lines outside the grid or 120 m for the 16×16 grid used by M. H. Smith *et al.* (1971). If the captures were accumulated with the end of the assessment lines farthest from the grid as the starting point, then the size of the sampling area

$$\hat{A}_c = (2W_c + W_g)^2 \tag{2.23}$$

with W_g equal to the length of the side of the grid. Dividing the actual number of mammals caught on the grid (N_g) by $\hat{A}_c$ yields density ($\hat{D}$).

In addition to $\hat{A}_c$, there is usually an area of partial removal ($\hat{A}_p$; Fig. 2.2). The width (W_p) of $\hat{A}_p$ can be calculated in a manner similar to that in which W_c was calculated. An equivalent area of complete removal ($\hat{A}_{cp}$) must be calculated for $\hat{A}_p$. The number of animals (N_u) that would have been captured on the assessment lines if there had not been an area of partial removal is equal to Y_u, and

$$Y_u = a_u + B_u X_c \tag{2.24}$$

The number actually caught up to the edge of the area of complete removal (N_p) can be calculated by

$$Y_p = a_p + B_p X_c; \tag{2.25}$$

$N_p = Y_p$ at this point. $\hat{N}_c$ is equal to the number of animals that would have been caught on the assessment lines if the area of complete removal had extended up to the edge of the area of partial removal.

$$\hat{A}_{cp} = \frac{\hat{N}_u - N_p}{\hat{N}_u N_c} \cdot \hat{A}_p \qquad (2.26)$$

In other words, $\hat{A}_{cp}$ equals the ratio of animals that should have been caught on the assessment lines if there had been no area of partial effect to those actually caught in this area times the size of the area of partial effect. This assumes $\bar{P}_c$ is equal for animals of the same species in the unaffected area and in $\hat{A}_p$. Interspecific individual or daily variation in $\bar{P}_c$ does not invalidate the method of calculation. Since trapping in these areas is accomplished along the assessment lines on the same nights, environmental effects on $\bar{P}_c$ in the two areas should be approximately the same.

From the above it follows that

$$\hat{D} = \frac{N_g}{A_c + A_{cp}} = \frac{N_g}{A_s} \qquad (2.27)$$

Confidence intervals must be calculated for the density ($\hat{D}$). N_g is assumed to be approximately equal to N, the real number of animals in $\hat{A}_c + \hat{A}_{cp}$. Thus N_g does not have a confidence interval. $\hat{D}$ will be in error by an amount equal to

$$D - \hat{D} = \frac{N - N_g}{\hat{A}_c + \hat{A}_{cp}}. \qquad (2.28)$$

This error is probably negligible, and there is no known way to estimate size of the error since P_c is not constant over time.

Both $\hat{A}_c$ and $\hat{A}_{cp}$ have confidence intervals. Normally the errors associated with the straight line could be used to place confidence intervals about a given point (Steel & Torrie, 1960). However, the trap stations are not picked or spaced at random and accumulative captures cannot decrease with distance, so the sampling errors associated with X and Y are biased.

If the data for each assessment line were treated separately, then there would be eight independent area estimates for $\hat{A}_c$ and eight for $\hat{A}_{cp}$. Standard errors could be calculated in the usual way (e.g., with

$$S_{\bar{A}} = \sqrt{\left(\frac{\Sigma\{\hat{A}_c^2 - [(\Sigma\hat{A}_c)^2/n]\}/n}{n - 1} \right)} \qquad (2.29)$$

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$n = 8$ for the 8 assessment lines). However, there are usually insufficient captures on single assessment lines to use this method of calculation.

Three of the techniques discussed appear to be promising for density estimation. These are the assessment line technique (Kaufman *et al.*, 1971; M. H. Smith *et al.*, 1971) dense line technique (H. D. Smith *et al.*, 1972) and prebaiting technique (Ryszkowski, 1971*a*). Each needs to be tested in a variety of habitats and experimental validation via comparative studies is needed (e.g., Ryszkowski *et al.*, 1966).

The discussion thus far has been limited to estimating density (D) at one location. A more important question is that of obtaining an average density ($\hat{D}$) for a habitat, region or some other geographical or ecological unit. For example, Spitz (1972) has shown that samples from small areas of a few hectares may poorly represent the dynamics of the population living in an area of several hundred hectares. Whatever the sampling scheme, it must be designed to account for the vast habitat heterogeneity encountered and be simple enough (e.g., cross line method) to enable sufficient replication. The number of samples required for a given level of confidence in the density estimate may be calculated from the range in density and the mean density across sampling plots (Table 2.3). Replication needed to attain a given level of confidence decreases

Table 2.3. *Number of samples (N_s)† needed to estimate the mean density ($\bar{D}$) with a standard error equal to 10% of the mean given different ranges (R_a) in $\hat{D}$ across samples.* $N_s = \{(R_a/6)/(0.10\hat{D})\}$

Density range (R_a)	Mean density $\bar{D}$									
	1	2	3	4	5	10	25	50	100	500
1	3	1	1	1	1	1	1	1	1	1
5	69	17	8	4	3	1	1	1	1	1
10	278	69	31	17	11	3	1	1	1	1
15	625	156	69	39	25	6	1	1	1	1
20	1 111	277	123	69	44	11	2	1	1	1
25	1 736	434	193	109	70	17	3	1	1	1
50	6 939	1 736	771	434	278	69	11	3	1	1
100	27 778	6 944	3 088	1 736	1 112	278	44	11	3	1
500	694 444	173 611	77 154	43 399	27 778	6 944	1 111	278	69	3
1 000	2 777 778	694 444	308 654	173 618	111 116	27 778	4 445	1 111	278	11

† Samples of one cannot be used to calculate a standard error and should be used only as an indication of the low number of replicates required.

with an increase in the mean density and a decrease in the range. The amount of effort required to estimate the mean density with appropriate confidence intervals is generally quite large because most situations are characterized by a relatively small mean and large range in density.

Recommendations

The large number of variables which affect density estimates require that appropriate experimental designs be used to validate existing techniques and develop new ones. Critical variables must be controlled, manipulated or held constant in both open and closed populations to provide a wide data base from which conclusions can be drawn. Such data for known populations are particularly needed.

Long-term trapping studies are needed for a variety of habitats and species. Extended trapping periods allow a more critical view of the factors which influence probability of capture. Data of this type are necessary to understand the role of social interactions, movement patterns, reproductive cycles and environmental factors influencing the probability of capture.

A single method for estimating densities may not be applicable to the variety of situations encountered in small mammal studies. Future studies should not be devoted to just a consideration of one or two standard census methods but should be designed to ensure accurate density estimations. When large amounts of data have been gathered in this manner, broad comparisons between species, habitats and geographical areas will be possible.