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Separating Components of Detection Probability in Abundance Estimation: An Overview with Diverse Examples

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Estimation of population abundance of rare and elusive species critically depends on the estimation of detection probability under a particular sampling method. If we ignore the issue of animals not being available, then we obtain an estimate of the size of the available component of the population rather than the total population size. The available component may be only a small portion of the total population. In addition, this component may vary with time and with important auxiliary variables in ways that are so complex that it is unsatisfactory for monitoring the population (see Chapter 4).

Animals have to be “available” to a sampling method to be detected. In many animal populations not all animals are available to be captured using a particular sampling method. There may be many reasons for this. For example, in an aerial survey of dugongs (sea cows) off the coast of Australia, some dugongs may be underwater and invisible to the observers searching for them in the aircraft. Even if animals are available, they still have to be detected. This perception process is also uncertain, so, for example, if a dugong is on the surface of the water, observers in the aircraft may still miss it.

In this chapter we consider in detail a model for detection probability that accounts for the processes of availability and perception. Methodology

for estimating these two components of detection probability is illustrated with three diverse examples involving aerial surveys of marine mammals (dugongs), point counts of terrestrial birds, and capture-recapture studies of terrestrial salamanders. The statistical methodology used in the three examples is very different.

We will use the dugong survey as a first example of a solution to a general problem of lack of availability (Marsh and Sinclair 1989; Pollock et al. in press). We then will show that very similar conceptual problems arise in many other settings and biometricians are now seeking solutions to them. Two other problems we consider are (1) estimation of density of birds based on point counts in which birds are detected by their calls but birds do not always call (i.e., they are unavailable for auditory detection; Farnsworth et al. 2002); and (2) population estimation of terrestrial salamanders, which presents a similar conceptual and practical problem because salamanders may be underground where they cannot be counted or captured (i.e., they are physically unavailable to capture because they are not present on the surface; Bailey et al. 2004a,b). Many formulations ignore the unavailable part of the population, but doing so may be unsatisfactory unless this component is a very small and constant part of the population.

Absolute Abundance Estimator

In studying wild animal populations to estimate population size and other parameters, typically not all animals are detected and/or not all of the area is sampled, so that a census or complete count of the population is impossible. Therefore, the population size has to be estimated using sampling methods. Skalski (1994) presented a framework for combining finite sampling theory and density estimation of individually sampled units. Here, we consider the sampled units collectively in estimating abundance. Two key elements are the proportion of the area actually sampled and the detection probability of animals in the study area that is actually sampled. The counts can be adjusted to obtain the population size estimate using the canonical equation (Lancia et al. 1994; Williams et al. 2002),

$$\hat{N} = \frac{C}{p_{area} \hat{p}_d}, \quad (3.1)$$

where \hat{N} is the estimator of population size, C is count of animals seen, p_{area} is proportion of area sampled, and \hat{p}_d is the estimator of the fraction of animals detected (i.e., seen or caught).

Here we assume that the proportion of the area sampled is known and that the sampling design for the area uses probabilistic sampling such as simple random sampling (Thompson 2002a). Note, however, that the population size estimator in equation (3.1) will vary depending on the sampling approach. For example, if stratified random sampling were used, then equation (3.1) would be used separately in each stratum and then summed across strata. Although this is an important component of the problem with its own complexities, we focus in the remainder of this chapter on the detection component.

There are many ways to estimate the detection probability, \hat{p}_d , such as using capture-recapture sampling, distance sampling, or many others. We have presented the standard formulation for abundance estimation, but we sometimes need a more general detection model that takes account of animals being unavailable. Availability can be defined by the presence or absence of animals on the surveyed areas or may be defined by the survey technique, which may or may not have the ability to detect the animal of interest.

General Absolute Abundance Estimator

A more general equation involves first taking account of availability of animals for detection and then the detection of animals that are available,

$$\hat{N} = \frac{C}{p_{area} \hat{p}_a \hat{p}_{da}}, \quad (3.2)$$

where \hat{N} is the population size, C is the count of animals, p_{area} is the proportion of the area sampled, \hat{p}_a is the estimator for the probability of being available, and \hat{p}_{da} is the estimator for the conditional probability of detection given availability. This equation is not really new, but it is often not emphasized. If we use equation (3.1) when equation (3.2) is appropriate, we just obtain an estimate of the population size of the available component. We will see in our later examples that this may be a small component of the total population and furthermore that this component may vary with time and with important auxiliary variables in such complex ways that it is unsatisfactory for monitoring the population. We now proceed to the dugong aerial survey example to illustrate one methodology for estimating the components of detection probability and then how to use them in sound abundance estimation.

Aerial Survey Methodology That Accounts for Nonavailability of Dugongs

The dugong (*Dugong dugon*) is a member of the order Sirenia. Dugongs are herbivorous marine mammals that occur in some 37 countries in the Indo-West Pacific. In Australia, dugongs occur in seagrass habitats along some 15,000 km of the northern coast. The water turbidity in these areas is variable, ranging from clear to very turbid over a very short distance. Dugongs have a patchy distribution and often occur at very low densities. Marsh and her colleagues at James Cook University in Townsville, Australia, have studied dugongs extensively (e.g., see Marsh and Sinclair 1989). Here we will focus on the aerial survey methodology used to estimate the density and population size of dugongs.

Marsh and her colleagues used a stratified random sampling design with a strip sampling method. They chose strip sampling instead of line transect methodology because dugongs are at the surface for only 1–2 seconds, which makes it impossible to reliably estimate their distance from the transect line. Flights are conducted at a standard height (137 m) and speed (185 km/h). Each flight crew consists of a pilot and survey leader plus tandem teams of two independent observers on each side of the aircraft (six total). The two observers on each side of the aircraft survey a strip of width 200 m (Marsh and Sinclair 1989).

Modeling the availability process involves estimation of the probability of an animal being available (\hat{p}_a). This is a very difficult parameter to estimate for the dugong surveys and must be done external to the aerial survey with additional data collected in a dedicated study. Artificial dugong models were fitted with timed depth recorders and taken by boat to the test area off the coast. They were lowered into the water next to the boat. Observers in a helicopter at the standard aerial survey height determined the depth at which the models become visible as they were raised in the water column. This enabled Marsh and colleagues to divide the water column into available and nonavailable zones of detection under a range of different conditions of water clarity, depth, and sea state. The dive profiles of 15 dugongs fitted with timed depth recorders were recorded in a separate study. The combination of these data sets enabled the research team to estimate the probability of dugongs being available for detection under various combinations of depth, sea state, and turbidity. The fraction of time that animals spent above the depth where they were visible (available) was an estimate of the probability of being available. Table 3.1 gives estimated

availability probabilities with standard errors. Notice the variability in these probabilities depending on depth and other water conditions. The assumptions for this availability process estimation are:

- The depth at which dugong models become visible is measured without error.
- The depth at which dugong models become visible is the same as for real dugongs.
- Depth profiles of individually monitored dugongs are representative of the whole population of dugongs being studied in the aerial survey.

Table 3.1

Estimated availability probabilities (p_a) and their standard errors for various strata of survey depths and turbidities calculated based on data from the dugong models and the individual dive profiles of telemetered wild dugongs.

Survey condition	Water quality	Depth range	Visibility of sea floor	Depth of zone of visibility of models ^a	Depth of zone of visibility (m) used to calculate p_a	p_a (SE)
Optimal	Clear	Shallow	Clearly visible	Visible at bottom	All	1
	Variable	Variable	Visible but unclear	2.44	2.5	0.652 (0.0452)
	Clear	> 5 m	Not visible	4.32	4.0	0.462 ^b (0.057)
	Turbid	Variable	Not visible	1.23	1.5 ^c	0.474 (0.0525)
Marginal	Clear	Shallow	Clearly visible	Visible at bottom	Visible at bottom	1
	Variable	Variable	Visible but unclear	1.21	1.5 ^c	0.474 (0.0525)
	Clear	> 5 m	Not visible	0.69	1.5 ^c	0.296 ^b (0.0724)
	Turbid	Variable	Not visible	1.43	1.5 ^c	0.474 (0.0525)

^aAveraged for models 2.0 m and 2.5 m long.

^bBased on records from four dugongs with mean, median, and modal maximum dives of > 6 m and a corresponding subset of the data from one dugong that spent considerable time in water > 5 m deep (see text for explanation).

^cBased on minimum dive depth detectable on 15 telemetered wild dugongs (see text for explanation).

- The flight speed is fast enough for the dugong to be available only for an "instant."
- There is independent availability of group members in a detected group of dugongs.

Modeling the probability of an animal being detected given that the animal is available involves using two independent observers on each side of the aircraft. The probability of a dugong being detected by at least one observer is p_{da} and is estimated in the following way. If n_1 is the number detected by the mid observer, n_2 is the number detected by the rear observer, and m_2 is the number detected by both observers, then $\hat{p}_1 = m_2/n_2$, $\hat{p}_2 = m_2/n_1$, and $\hat{p}_{da} = 1 - (1 - \hat{p}_1)(1 - \hat{p}_2)$. This is an extension and adaptation of the Lincoln-Petersen method (Seber 1982; Pollock et al. 1990) used in two-sample, capture-recapture studies. The assumptions are that counts within the 200-m strip are measured accurately, that there are no matching errors between the two observers, and that detection probabilities for all groups for each observer are equal.

We used Program MARK (White and Burnham 1999) to generalize these models to allow for detection probability conditional on availability to vary by seat (mid or rear), side (port or starboard), and location of the survey. We then used AIC (Akaike's information criteria; Akaike 1973) to pick the simplest model that explained the data adequately. Alternatively, model-averaged estimates can be used. MARK also can be used to determine if the detection probability conditional on availability is dependent on individual group covariates, such as size of group, sea state, glare, distance class, etc.

We used the generalized Horvitz-Thompson estimator for population size based on the detection probability p_i of each individual group of size $\delta_{i\tau}$ such that $\hat{p}_i = p_{area} \hat{p}_{ai} \hat{p}_{dai}$ and $\hat{N} = \sum_{i=1}^v (\delta_i / \hat{p}_i)$, where v is the number of distinct groups detected. We used a simulation or parametric bootstrap method that included all sources of variation in the estimates to develop an estimator of the standard error of population size and density.

Although results of these surveys were quite precise (Table 3.2), they were expensive, as were the extra data needed for estimation of probability of being available for detection. The estimation of probability of being available was based on the dive profiles of only 15 dugongs. Also, the artificial models may have been detectable at different depths from real dugongs. Ideally, the study using the artificial models should have been repeated to broaden the range of conditions. Marsh and colleagues also

Table 3.2.

Population size estimates and standard errors for a recent aerial survey of dugong for the Northern Great Barrier Reef in 2000.

Block	Population estimate	Standard error
1	73	36
2	1613	661
3	1726	615
4	1041	380
5	2843	958
6	473	255
8	631	248
11	347	318
13	471	102
14	586	536
Total	9804	1550

plan to expand the sample of animals used in the depth profiles. The detection given available estimation also can have small biases using the two-observer method, even though a proper protocol was used (Marsh and Sinclair 1989; Pollock et al. in press). With these provisos, we emphasize that this study is an enormous improvement over not including the unavailable portion of the population in the analysis, as is the case in many other aerial surveys, including surveys over areas where the availability bias varies enormously.

Point Count Methodology That Accounts for Nonavailability of Birds

Bird point count studies have been widely used to assist in the management of terrestrial birds. For example, the Breeding Bird Survey run by the U.S. Fish and Wildlife Service (U.S. FWS) has 3,000 roadside routes in the United States and Canada. Each route is 25 miles, with 50 points per route. Each count is a 3-minute, unlimited-radius point count. The survey was begun by Chandler Robbins of the U.S. FWS in 1966 and has become a

very important source of information on population trend for many species (Robbins et al. 1986; Peterjohn and Sauer 1993).

Traditionally, the basic point-count survey counted all birds seen or heard during a fixed time interval. The survey contained no estimate of detection probability; analyses generally assumed detection probability was invariant. This approach is now considered inadequate and antiquated. Two recent overview papers by Thompson (2002b) and Rosenstock et al. (2002) stressed the importance of properly estimating detection probability for sound inference based on point counts.

There are now four methods of estimating detection probabilities for point count surveys: distance methods, multiple observer methods, time-of-detection methods, and combinations of the three methods. Two of these methods, distance sampling (Buckland et al. 2001) and multiple observer methods (Nichols et al. 2000; Pollock et al. 2003), assume that birds are available to auditory detection (e.g., sing) during the point count. A new method, the time-of-detection method (Farnsworth et al. 2002), allows for birds not singing, which is a type of nonavailability of birds because in many forest bird point counts a bird is effectively undetectable if it does not sing during the sampling interval.

Distance sampling (Buckland et al. 2001) is founded on the premise that detection is based on a sighting function, $g(r)$, that is a monotonic declining function with distance r and assumes $g(0)$ is 1. Distance methodology assumptions are: birds that are very close to the station will always be detected; there is no movement of birds (i.e., attraction or repulsion) during the survey; all distances are measured without error; and sightings of different birds are independent events. In our context, an additional assumption is that all the birds sing and are thus available for detection during the point count.

Multiple observer methods of estimating detection probability involve primary and secondary observers (Nichols et al. 2000) or two independent observers (Pollock et al. 2003). For simplicity, we will only discuss using the Lincoln-Petersen Method with two independent observers who each map their bird locations independently and match the birds heard—only by observer 1, only by observer 2, or by both observers—to estimate the birds missed. Note that this is basically the same approach as that used by Marsh in her aerial surveys of dugongs described above. The model assumptions are (1) there is no change in the population of birds within the detection radius during the point count (i.e., the population is closed and birds are not moving in or out); (2) there is no double-counting of

individuals, and birds are matched between observers accurately; (3) all birds of a given species are equally detectable for a given observer (no heterogeneity); and (4) if counts with limited radius are used, observers accurately assign birds to within or beyond the radius used. In our context, an additional assumption is that all the birds sing at least once during the time of the point count.

Time-of-detection sampling methodology is new and was presented in an important paper by Farnsworth et al. (2002). They noticed that most detections are by sound in forested habitats and for cryptic species. Birds can be detected only if they sing, but now we can estimate how many are unavailable (i.e., do not sing). Effective detection probability is now the product of the probability that a bird sings during the count interval and the probability that the song is heard by an observer. Note that this is just a breakdown in detection probability developed in the introduction but now adapted for the situation where detection is only by sound. (We emphasize that the bird is present in the survey area but is unavailable because it does not sing.)

Now we consider the simple case in which the point-count is divided into two equal time intervals. We define n_1 as number of birds first counted in a fixed-radius plot in period 1 and n_2 as the number of birds first counted in period 2 only. Further, we assume detection probability is the same for both periods such that $E(n_1) = Np$ and $E(n_2) = N(1 - p)p$, where N is the population size in all the fixed-radius (r) plots and p is the detection probability, and E is the expected value (mean). This is of the same form as the removal method used for animal trapping studies in which the trapped animals are not returned to the population (Zippin 1958; Seber 1982).

If we use n_1 and n_2 as estimates for the expected means in the previous equations, we can solve these intuitive moment equations for N and p and obtain estimators $\hat{p} = (n_1 - n_2) / n_1$ and $\hat{N} = n_1 / \hat{p}$. The assumptions of the time-of-detection method are (1) there is no change in the population of birds within the detection radius during the point count (that is there is no movement in or out), (2) the observer can accurately follow each individual bird so no bird is counted twice, (3) all birds have a constant probability of being detected during each interval, and (4) observers accurately assign birds to within or beyond the radius used.

The two key assumptions are (1) and (2). If birds are moving around a lot, it will be difficult for observers to follow them and the probability of double-counting birds is significant. Further, birds may move into the cir-

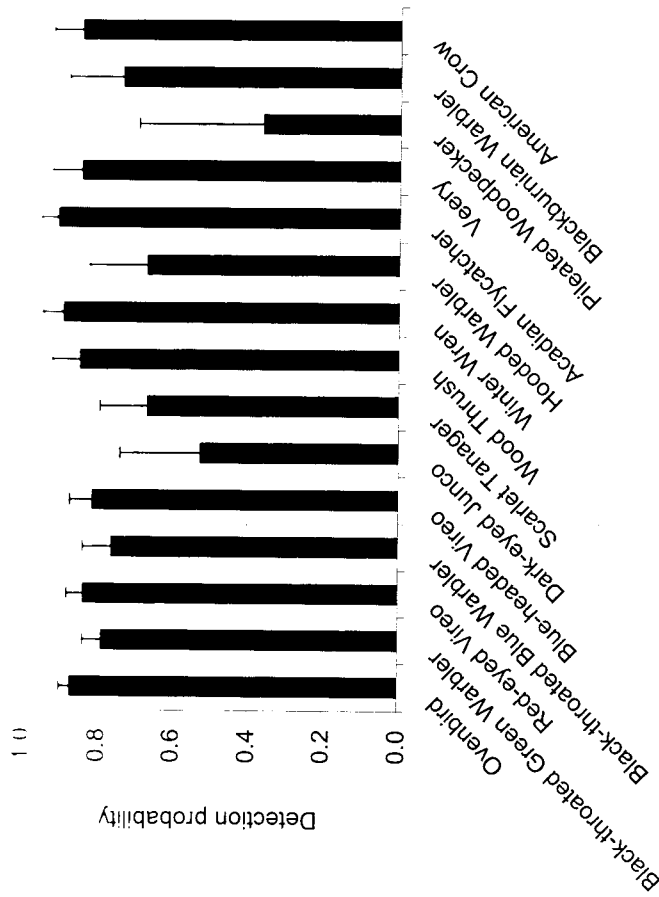


Figure 3.1. Estimated detection probability based on time-of-detection method during unlimited-radius counts for the 15 most frequently encountered species, ordered from most common (left) to least common (right) (from Farnsworth et al. 2002). Error bars represent one estimated standard error.

cle undetected and then sing and be detected. However, we believe there will be surveys where these assumptions are reasonable.

Many surveys have recorded birds counted into three time intervals (Ralph et al. 1995). The use of three intervals allows for heterogeneity of detection probability between birds. Farnsworth et al. (2002) discuss this and also extend the theory by allowing the multiple intervals to be of varying length. We illustrate with some results from Farnsworth and colleagues' point count surveys in the Great Smoky Mountains National Park (Figure 3.1).

We strongly recommend that combined methods be used in practice as much as possible. In particular we note that combined methods involving the time-of-detection method enable separation of probability of being available from probability of detection, given available. In our example, we were able to estimate only the overall probability of detection. There is also the need for careful evaluation of the effects of movement into the plot after the count has commenced.

Capture-Recapture Methodology That Accounts for Nonavailability of Salamanders

Bailey et al. (2004a,b) were concerned about population estimation for terrestrial salamander populations in the Great Smoky Mountains National Park in North Carolina and Tennessee. Salamanders are suspected to be reasonable indicator species of old growth forest health, and there is a need for more extensive monitoring programs of many amphibian species.

One objective of the study (Bailey et al. 2004a,b) was to evaluate the effectiveness and biases of salamander count indices that are very widely used because they are much less expensive than capture-recapture methods. Studies using count indices assume that detection probability is constant over time and space and further that all salamanders are available to be counted. Clearly, the first assumption is often violated. Further, there are special problems with sampling salamanders because they are very sensitive to desiccation and generally require cool, moist habitats. Thus, they often occur below the surface of the ground to avoid unfavorable moisture regimes on the surface and to escape predators. Salamanders below the surface are hence unavailable to be captured under standard sampling protocols that only sample the surface population.

Bailey et al. (2004a,b) used capture-recapture methods to study salamander abundance at different sites over 3 years. They established 15 sites during 1999 and 20 sites each year during 2000 and 2001 in the Mt. LeConte Quadrangle of Great Smoky Mountains National Park. An elastomer marking technique (Northwestern Marine Technology Inc., Shaw Island, Washington, USA) was used to mark more than 5,300 salamanders in 3 years. Every year, sites were sampled on 3–4 consecutive days (secondary samples) during each of four primary periods about 10–14 days apart. Individual capture histories were compiled for each site and each year (52 site-years in total were used for their analysis).

Bailey et al. (2004a,b) used primary and secondary sampling periods each year so that they could use the robust design (Pollock 1982; Pollock et al. 1990). This design allows combination of open and closed population models in one analysis. Pollock (1982) originally assumed it would be beneficial for allowing heterogeneity of capture probabilities between animals. Kendall and Nichols (1995) and Kendall et al. (1997) noted that this design could be very useful to estimate the temporary emigration probability (i.e., 1-the probability of an animal being available for capture). Their work

has now given rise to extensive literature on temporary emigration models (see Williams et al. 2002).

For each site year, Bailey et al. (2004a) fitted 12 competing models with the robust design option in Program MARK (White and Burnham 1999). These models allowed temporary emigration or not; trap response present or not; and time variation in capture probabilities and population sizes between primary periods. They assumed that survival probability between the primary periods was 1 because it was so short (~10–14 days). They used the QAIC_c criteria for model selection. This is an extension of the Akaike information criteria (Akaike 1973) to account for small samples and overdispersion. Bailey et al. found that temporary emigration models were selected 80.7% of the time and models that allowed a trap-shy response were selected 63.5% of the time. Temporary emigration matters a great deal; the average temporary emigration parameter estimate was 0.87 ($\hat{SE} = 0.01$). The temporary emigration parameter estimates varied widely over years and sites, with a low of 0.62 and a high of 0.99. Dry, disturbed sites had higher values than wet, more pristine sites. On average only 13% of the animals were on the surface available for capture during each primary sampling period. Further, although the conditional probability of capture given available was 0.30 ± 0.01 , the overall estimated probability of detection, which Bailey et al. (2004a) referred to as the effective capture probability, was only 0.04 ($\hat{SE} = 0.002$; $0.13 \times 0.30 = 0.04$). Thus, using the robust, capture-recapture design, we can estimate overall detection probability and its different components for these salamanders.

Table 3.3 illustrates how including temporary emigration in the model affects estimates of both capture probability and surface (available) population size. In the absence of temporary emigration, estimates of population size are still unbiased if emigration is random, but refer to the total population, not just the available or surface population. Further, using unadjusted count indices to compare salamander populations over time and space would be very unwise because only a small and variable portion of the population is available to be counted at any time.

Discussion

We have shown with a few examples that nonavailability problems for population size estimation are extremely widespread. They come into play in studies such as aerial surveys of dugongs and other marine mammals (manatees, whales, dolphins), which spend a high proportion of their time

Table 3.3.

Time-specific estimates of conditional capture probability, $p_{i,c}$, recapture probability, c_i , and population size, $N_{i,c}$, for salamanders on an undisturbed site (R0004, 2001). One hundred twenty-four individuals were caught; 22 individuals were captured on more than one sampling occasion. Note that $n =$ number of animals captured in each primary period and $m =$ number of n animals recaptured within each primary period. The "best" model (using QAIC_c selection) included temporary emigration, time variation, and behavioral (trap-shy) effects. We also present models with and without temporary emigration and those that contain time variation in surface (available) population size. Standard error estimates are inflated by $\sqrt{\hat{c}} \bullet SE(\hat{\theta})$ with $\hat{c} = 1.54$.

Study	n	Models with temporary emigration					
		\hat{p}_i (SE)	\hat{c} (SE)	\hat{N} (SE)	$\hat{p}_{i,c}$ (SE)	\hat{c} (SE)	\hat{N} (SE)
	56	0.33 (0.10)	0.06(0.02)	79.98 (15.81)	0.34 (0.14)	0.06(0.02)	76.95 (20.09)
	23	0.16 (0.07)		79.98 (15.81)	0.17 (0.12)		43.14 (24.31)
	41	0.22 (0.09)		79.98 (15.81)	0.15 (0.19)		82.62 (75.83)
	21	0.12 (0.07)		79.98 (15.81)	0.04 (0.04)		147.42 (163.46)

Study	m	Models without temporary emigration					
		\hat{p}_i (SE)	\hat{c} (SE)	\hat{N} (SE)	$\hat{p}_{i,c}$ (SE)	\hat{c} (SE)	\hat{N} (SE)
	3	0.05 (0.02)	0.06(0.02)	368.14 (108.75)	0.34 (0.14)	0.06(0.02)	76.95 (20.09)
	2	0.02 (0.01)		368.14 (108.75)	0.04 (0.02)		162.36 (76.73)
	3	0.03 (0.01)		368.14 (108.75)	0.02 (0.01)		460.23 (238.05)
	2	0.01 (0.01)		368.14 (108.75)	0.01 (0.01)		730.46 (551.66)

AIC_c = 0.0; AIC_c weight = 0.57.
 AIC_c = 4.59; AIC_c weight = 0.06.
 AIC_c = 3.08; AIC_c weight = 0.12.
 AIC_c = 3.07; AIC_c weight = 0.12.

underwater; bird point counts, in which birds may not sing and hence may be undetectable; and surveys for terrestrial salamanders that spend time underground and hence are undetectable. Some other situations in which nonavailability could be a problem include aerial surveys of terrestrial mammals (elk, deer, moose) in habitats with areas of very dense vegetation

where some animals are so well hidden that they are not available for detection from the air; and surface counts of ant and other insect colonies, in which only the foraging component of the population is available for detection. Solutions to this problem are difficult and will usually be species- and sampling-method specific, as illustrated in this chapter. In some situations it may not be possible to estimate the probability of being available; however, we have shown that failing to include this component can cause severe problems of interpretation, especially when this probability is low and/or variable in space and time.

Common methods of estimating detection probability in animal counts are distance sampling (e.g., the point count method illustrated above) and multiple observer methods (e.g., dugong and bird surveys). These methods do not take into account animals being unavailable. Additional methods such as those illustrated here have to be used to correct for the unavailable portion of the population. This is particularly important if the portion unavailable fluctuates in space or time. Further, we have shown that for captured animals, standard capture-recapture methods cannot account for nonavailability unless the robust design is used. An exception is when special telemetry tags are used. In that case, for example, mark-resight aerial surveys using a marked subpopulation with radio tags could account for nonavailable animals that have moved outside the study area.

The time-of-detection method used to take account of non-singing birds can be employed routinely to estimate total detection probability, including the probability of being available. The biologist needs to record first-detection-time categories for all the birds; this is often quite feasible in practice. By contrast, in the dugong aerial survey, the information needed to correct for availability cannot be collected routinely due to expense and logistics. Similarly, in terrestrial salamander studies, it is not logistically feasible due to expense to conduct elaborate mark-recapture studies at all count locations. We believe, however, that in many examples, it is possible to design special studies into a larger count survey in a double-sampling framework (Thompson 2002a; Pollock et al. 2002). For example, a large sample of plots could have salamanders counted under a well-defined protocol with the detailed capture-recapture study restricted to a small random subsample of the plots in order to estimate the two detection probability components. These component estimates then could be used to adjust the counts appropriately.

When studies are planned to map the distribution of cryptic animals in space or to monitor the size of populations through time, we strongly rec-

ommend that methods be developed for separating and estimating the components of detection probability. Without this approach, it is unlikely that the results of the survey program will be reliable or useful.

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REFERENCES

- Alkaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pp. 267–281 in B. N. Petrov and F. Csaki, eds., *Second International Symposium on Information Theory*. Akademiai Kiado, Budapest, Hungary.
- Bailey, L. L., T. R. Simons, and K. H. Pollock. 2004a. Estimating detectability parameters for plethodon salamanders using the robust capture-recapture design. *Journal of Wildlife Management*. 68:1–13.
- _____. 2004b. Spatial and temporal variation in detection probability of plethodon salamanders using the robust capture-recapture design. *Journal of Wildlife Management*. 68:14–28.
- Buckland, S.T., D. R. Anderson., K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. *Introduction to Distance Sampling*. Oxford University Press, London.
- Farnsworth, G., K. H. Pollock, J. D. Nichols, T. R. Simons, J. E. Hines, and J. R. Sauer. 2002. A removal model for estimating the detection probability during point counts divided into time intervals. *Auk* 119:414–425.
- Kendall, W.L., and J. D. Nichols. 1995. On the use of secondary capture-recapture samples to estimate temporary emigration and breeding proportions. *Journal of Applied Statistics* 22:751–762.
- Kendall, W.L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78:563–578.
- Lancia, R. A., J. D. Nichols, and K. H. Pollock. 1994. Estimating the number of animals in wildlife populations. pp. 215–253 in T. Bookhout, ed., *Research and Management Techniques for Wildlife and Habitats*. The Wildlife Society, Bethesda, Maryland.
- Marsh, H., and D. F. Sinclair. 1989. Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. *Journal of Wildlife Management* 53:1017–1024.
- Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon, and P. J. Heglund. 2000. A double-observer approach for point counts. *Auk* 117:393–408.
- Peterjohn, B. G., and J. R. Sauer. 1993. North American breeding bird survey annual summary 1990–1991. *Bird Populations* 1:1–15.
- Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:752–757.
- Pollock, K. H., M. Alldredge, J. D. Nichols, T. R. Simons, G. L. Farnsworth, and J. R. Sauer. 2003. Modeling availability and perception processes for detection in point counts of bird populations. Unpublished manuscript.
- Pollock, K. H., H. Marsh, I. Lawler, and M. Alldredge. In press. Modeling availability and perception processes for strip and line transects: An application to dugong aerial surveys. *Journal of Wildlife Management*.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. *Wildlife Society Monographs* 107:1–97.

- Pollock, K. H., J. D. Nichols, T. R. Simons, G. L., Farnsworth, L. L. Bailey, and J. R. Sauer. 2002. The design of large-scale wildlife monitoring studies. *Environmetrics* 13:105–119.
- Ralph, C. J., S. Droege, and J. R. Sauer. 1995. Managing and monitoring birds using point counts: Standards and applications. pp. 161–168 in C. J. Ralph, J. R. Sauer, and S. Droege, eds., *Monitoring Bird Populations by Point Counts*, USDA Forest Service General Technical Report PSW-GTR-149, USDA Forest Service, Albany, California.
- Robbins, C. S., D. Bystrak, and P. H. Geissler. 1986. *The Breeding Bird Survey: Its First Fifteen Years, 1965–1979*. U.S. Fish & Wildlife Service Resource Publication 157, U.S. Fish & Wildlife Service, Washington, D.C.
- Rosenstock, S. S., D. R. Anderson, K. M. Giesen, T. Leukering, and M. F. Carter. 2002. Landbird counting techniques: current practices and an alternative. *Auk* 119: 46–53.
- Seber, G. A. F. 1982. *Estimation of Animal Abundance and Related Parameters*. 2nd ed. Macmillan, New York.
- Skalski, J. R. 1994. Estimating wildlife populations based on incomplete area surveys. *Wildlife Society Bulletin* 22:192–203.
- Thompson, S. K. 2002a. *Sampling*. 2nd ed. Wiley, New York.
- Thompson, W. L. 2002b. Towards reliable bird surveys: Accounting for individuals present but not detected. *Auk* 119:18–25.
- White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. *Analysis and Management of Animal Populations*. Academic Press, San Diego.
- Zippin, C. 1958. The removal method of population estimation. *Journal of Wildlife Management* 22:82–90.