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BAYESIAN ESTIMATE OF THE NUMBER OF MALACHITE SUNBIRDS FEEDING AT AN ISOLATED AND TRANSIENT NECTAR RESOURCE

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Abstract.—A Bayesian method for estimating population size from recaptures when birds are captured and recorded one at a time is developed. The method is illustrated with capture-recapture data of Malachite Sunbirds (*Nectarinia famosa*) obtained over a 3-d period in the Cape of Good Hope Nature Reserve, South Africa. The estimated 540 birds that used the nectar resource probably represent about half the Malachite Sunbird population of the 7750 ha reserve. Though applicable to all population sizes, the method is particularly useful when the population is small.

ESTIMADO BAYECIANO DEL NÚMERO DE INDIVIDUOS DE *NECTARINA FAMOSA* ALIMENTÁNDOSE SOBRE UN RECURSO AISLADO Y TRANSITORIO

Resumen.—Se desarrolla un método para estimar el tamaño de poblaciones de individuos, basado en recapturas cuando las aves son capturadas y registradas una a la vez. La utilidad de este método (bayeciano) es ilustrado con la captura y recaptura de individuos de *Nectarina famosa* en un perído de tres días. El estimado de 540 aves que utilizaron néctar como recurso alimentario, probablemente representa la mitad de la población de estos pájaros en los 7750 ha de la reserva natural, Cabo de Buena Esperanza, Africa del Sur. Aunque el método puede aplicarse a poblaciones de diferentes tamaños, parece ser especialmente útil para poblaciones pequeñas.

Gazey and Staley (1986) and Zucchini and Channing (1986) independently introduced a Bayesian analogue of the Schnabel (1938) census model for estimating the size of a closed population from capture-recapture information. The special case of the Schnabel census model in which animals are trapped, marked, and released one at a time was developed by Craig (1956). Du Feu et al. (1983) showed how Craig's method could be used to estimate (du Feu estimate) the number of birds present in an area during a short period. In this paper, we develop the Bayesian analogue of the du Feu estimate and use the method to estimate the number of Malachite Sunbirds (*Nectarinia famosa*) utilizing an isolated and transient food resource at which they were mist-netted and ringed. We compare the results with those obtained by the du Feu estimate. The estimate is discussed in relation to known densities of Malachite Sunbirds in the study area.

The Malachite Sunbird occurs widely in southern Africa in a variety of vegetation types. It is predominantly a nectar-feeder, often gathering at isolated food sources. Skead (1967) recorded foraging parties of 30–40 birds (without mentioning a specific food-plant) and Niven (1968) recorded a concentration of about 100 Malachite Sunbirds attracted to a patch of *Cotyledon macrantha.* Breeding of Malachite Sunbirds on the Cape Peninsula occurs from late May to November (Skead 1967).

METHODS

We operated 180 m of mistnets from 0600 on 5 Dec. to 1300 on 7 Dec. 1987 in and around a stand of flowering Minaret Flowers (*Leonotis oxymifolia* (Burm. f.) Iwarsson) about 400 m^2 in area in dune thicket vegetation (Cowling 1984) at Olifantsbos (34°16′S, 18°3′E), Cape of Good Hope Nature Reserve, Cape Peninsula, South Africa. Although the flowering of these plants was unpredictable, taking place at any time of the year and not always at the same time each year, large numbers of Malachite Sunbirds were attracted to this stand whenever it was in flower. There were no other stands of *Leonotis* within the reserve.

Malachite Sunbirds were trapped, ringed, and released within 30 min of capture at a distance of 900 m from the netting site. The order in which the retrapped birds were caught in relation to unringed birds was recorded.

The assumptions that underlie the proposed method are identical to those of du Feu et al. (1983), Gazey and Staley (1986) and Zucchini and Channing (1986): the population is closed, so that there is no mortality, natality, emigration or immigration during the sampling period; all individuals have the same probability of being captured, regardless of whether they are marked or not; the captured individuals are all marked and released immediately.

Let N_{max} be a guess at the maximum possible number of birds in the area. Let $p_i(N)$ be our estimate that the population is of *size* N after the ith bird has been handled. Initially, we set $p_0(n) = \frac{1}{N_{max}}$, $n = 1 \ldots N_{max}$. Suppose that, when the ith bird is captured, the number of birds already ringed is m. Given that the population size is N, the probabilities that this bird is ringed or unringed are then m/N and $(N - m)/N$, respectively. If the ith bird is unringed, it follows from Bayes' Theorem that

$$p_i(N) = k \frac{N - m}{N} p_{i-1}(N)$$

where

$$k = \left(\sum_{N=m}^{N_{max}} \frac{N - m}{N} p_{i-1}(N) \right)^{-1}.$$

Similarly, if the ith bird is ringed,

$$p_i(N) = k \frac{m}{N} p_{i-1}(N)$$

where

$$k = \left(\sum_{N=m}^{N_{max}} \frac{m}{\mathbf{N}} p_{i-1}(N) \right)^{-1}.$$

In this way, the probability distribution of the population size is iteratively refined. Useful estimates of the population size are given by the mean, median, and mode of this probability distribution. A 95% confidence interval can be obtained from the 2.5% and 97.5% percentiles of the probability distribution. Each unringed bird captured shifts the distribution to the right, increasing the estimated population size; each retrapped bird shifts the distribution to the left, leading to a decrease in the estimated population size. As the number of birds handled, i, increases, and provided the assumptions are met, the probability distribution becomes more concentrated, and the successive estimates of population size more stable.

If the initial estimate of N_{max} is set too small, the estimated population size converges towards this limit. For reasonably large numbers of birds handled, the initial choice of N_{max} has very little influence on the final estimates; thus no harm is done if N_{max} is overestimated (Zucchini and Channing 1986).

The calculations for a simplified example are shown in Table 1. The method lends itself to implementation on a personal computer: a FORTRAN program may be obtained from the first author.

RESULTS

We made 255 captures of 202 different Malachite Sunbirds during 2.5 d. Eight birds were retrapped more than once. From the handling sequence, the number of unringed birds caught between each retrapped bird was derived (Table 2). From these data, the Bayesian estimates of the mean, median, and mode from the final (255th) probability distribution were 540, 534, and 523 respectively. The 95% confidence interval of the population size was 429 to 684 birds. We obtained the same results when the initial estimates of N_{max} were 800 and 1500. The du Feu estimate of the population size was 525 and the 95% confidence interval was 405 to 645.

DISCUSSION

As du Feu et al. (1983) pointed out, all the assumptions of statistical models are rarely completely satisfied. The trapping period was short relative to the flowering period of the *Leonotis* stand, which lasts several weeks, and was near the middle of this period. Immigration, emigration, and death during the trapping period were probably sufficiently small that the assumption of a closed population is, at least, plausible.

Because 80% of all the birds caught were first-year birds (having fledged between one and five months earlier), most birds were equally inexperienced and equally catchable. One way to examine the assumption of

TABLE 1. Illustrative example of the Bayesian method, showing how the probability distribution $p_i(n)$ after each capture (given in the columns) becomes more concentrated: e.g., after the eighth capture, the probability that the population has size four is 0.292. The last three rows of the table provide summary statistics of the successive probability distributions. The initial estimate of the maximum population size, N_{max}, was ten.

Iteration or capture number i	0	1	2	3	4	5	6	7	8
Unringed (U) or ringed (R)		U	U	R	U	U	R	R	R
$p_i(1)$	0.100	0.100	0.000	0.000	0.000	0.000	0.000	0.000	0.000
$p_i(2)$	0.100	0.100	0.071	0.181	0.000	0.000	0.000	0.000	0.000
$p_i(3)$	0.100	0.100	0.094	0.161	0.110	0.000	0.000	0.000	0.000
$p_i(4)$	0.100	0.100	0.106	0.136	0.139	0.075	0.129	0.202	0.292
$p_i(5)$	0.100	0.100	0.113	0.116	0.142	0.123	0.169	0.212	0.245
$p_i(6)$	0.100	0.100	0.118	0.101	0.137	0.149	0.169	0.178	0.171
$p_i(7)$	0.100	0.100	0.121	0.089	0.130	0.161	0.157	0.141	0.116
$p_i(8)$	0.100	0.100	0.124	0.079	0.122	0.165	0.141	0.111	0.080
$p_i(9)$	0.100	0.100	0.126	0.072	0.114	0.165	0.125	0.087	0.056
$p_i(10)$	0.100	0.100	0.127	0.065	0.107	0.162	0.111	0.070	0.040
Mean	5.500	5.500	6.364	5.127	6.392	7.358	6.830	6.286	5.776
Median	5	5	6	5	6	7	7	6	5
Mode	—	—	10	2	5	8	6	5	4

trap-shyness or trap-proneness is to consider the retraps as new birds and apply the same method to the retraps of the retraps. If the estimate obtained from this subset of the data is larger than the estimate from the full data set, it would indicate trap-shyness; a smaller estimate would indicate trap-proneness. Unfortunately, the number of birds retrapped more than once (eight) was too small to produce a reliable estimate of the population size, and we are therefore unable to check this assumption. In this, as in other capture-recapture methods, the overall effect of trap-shyness is to inflate the estimates of population size; trap-proneness has the opposite effect.

The period between capture and release was sufficiently short in relation to the whole trapping period for it not to be a source of serious bias. The fact that the birds were released 900 m from the netting site overcame the potential problem of birds flying directly back into the nets on release. Retraps of some birds were made within 30 minutes of their first capture, indicating that the distance moved was not excessive.

The Bayesian method has advantages over the du Feu estimate. It is computationally and conceptually simpler. More importantly, the confidence intervals are based on an exact probability distribution and not on a Normal approximation to this distribution, the standard deviation of which has also been estimated. For a large sample size, such as that obtained here, the final result does not depend on the initial guess at the

TABLE 2. The number of unringed birds trapped between each retrap of a ringed bird at Olifantsbos, Cape of Good Hope Nature Reserve, 5–7 Dec. 1987.

41,* 5, 20, 12, 4, 1, 5, 6, 5, 0, 12, 1, 1, 9, 2, 1, 5, 11, 6, 5, 6, 3, 0, 2, 3, 0, 4, 4, 2, 2, 1, 0, 0, 0, 4, 4, 1, 1, 6, 1, 0, 1, 0, 0, 4, 0, 0, 0, 0, 0, 0, 1†

* The number of birds caught before the first retrap.
† The last bird caught was a retrap.

maximum population size, provided that this exceeds the actual population size (Zucchini and Channing 1986). The exact distribution of population size is skewed to the right (Gazey and Staley 1986) indicating that there is more uncertainty about the upper limit of the population size than the lower limit (Raftery et al. 1987); consequently the confidence interval should be asymmetric about the mean. Gazey and Staley (1986) also showed that population estimates derived from the traditional Schnabel model are biased and are consistently smaller than the Bayesian estimates. This property is demonstrated by this example.

A further advantage of the Bayesian methods of Gazey and Staley (1986), Zucchini and Channing (1986), and this paper over the Schnabel census and the du Feu estimate occurs when the total population size is small (less than about 100 individuals). The asymptotic approximations to the normal distribution used to find confidence intervals are then increasingly unreliable. One fault is that the lower limit of confidence intervals can be less than the known minimum number of animals in the closed population: Seber (1973:134–136) gives an example relating to Cricket Frogs (*Acris gryllus*) in which the total number of frogs trapped and marked was 92, but the 95% confidence interval, based on the assumption of asymptotic normality was (90, 100). The illustrative example (Table 1) demonstrates an extreme situation. The captures (four unringed and four ringed) were simulated from a population of size five: after only eight captures the Bayesian estimate of the probability distribution is suggesting that four or five is the most likely population size (Table 1), the 95% confidence interval being (4, 10). In contrast, the 95% confidence interval for the du Feu estimate is an absurd (2, 8). For these very small population sizes, for which the Bayesian procedure provides meaningful results, the asymptotic properties upon which the confidence intervals for the du Feu (and Schnabel) estimates are based break down completely.

We do not suggest that all the estimated 540 birds fed exclusively at Olifantsbos. This number represents the size of the "pool" of birds for which this food resource was within their home range and the number of birds that would be caught if trapping were continued indefinitely (and the assumptions remained correct). For further discussion of the concept of a pool of birds utilizing a resource, see Summers et al. (1985).

The average annual density of Malachite Sunbirds in dune thicket vegetation at Olifantsbos is 0.59 birds ha^{-1} (MWF unpubl. data). By far the dominant vegetation types in the Cape of Good Hope Nature Reserve

(7750 ha) are, however, Upland Fynbos (50%), Restionaceous Plateau Fynbos (30%) and Restionaceous Tussock Marsh (20%) (Taylor 1984) in which Malachite Sunbirds occur at mean annual densities of 0.22, 0.00039 and 0 birds ha^{-1} respectively (MWF unpubl. data). The number of Malachite Sunbirds in the reserve could thus be of the order of 1000, about double the estimated number using the *Leonotis* stand at Olifantsbos which, though on the coast, is fairly centrally located within the reserve.

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