A METHOD FOR ESTIMATING TURNOVER IN SPRING BLACKBIRD ROOSTS

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Abstract: Aerial applications of a fluorescent, pigmented material can be used to mark large numbers of roosting blackbirds. Subsequent collection of marked birds provides data on the population dynamics of these species. A roost can be repeatedly marked with a unique color with the objective of estimating the turnover rate and number of birds that use the roost within a given time frame. This paper presents an estimation method for these parameters and illustrates the method using data collected from red-winged blackbird (*Agelaius phoeniceus*) spring migration roosts in South Dakota and Minnesota.

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Blackbirds and crop damage are seemingly synonymous in many parts of the United States. Of particular concern is the annual loss of several million dollars of ripening sunflower in North and South Dakota and Minnesota. Although several blackbird species cause these losses, including the yellow-headed blackbird (*Xanthocephalus xanthocephalus*) and common grackle (*Quiscalus quiscula*), the primary species is the red-winged blackbird. Dolbeer and Stehn (1983) compiled data from North American Breeding Bird Surveys 1966–81, and reported that the redwing was the most numerous bird recorded on census routes; the Dakotas and Minnesota were among the 10 states with the highest blackbird densities.

Data on the dynamics of redwing populations in the central United States are essential for population management strategies that have potential for reducing agricultural losses. Band recovery analyses (Neff and Meanley 1957; DeGrazio et al. 1969; Meanley 1971; Dolbeer 1978, 1982; Besser et al. 1983), use of colored leg streamers and subsequent sighting reports (Guarino 1963, Bray et al. 1977), radio-instrumented birds (Bray 1973, Besser et al. 1981), and potential differentiation of regional populations by morphological and plumage characteristics (Dyer 1964, Power 1970, James et al. 1984) have all provided data on dynamics of redwing populations. Although Heisterberg et al. (1984) studied the movements and turnover rates of blackbirds and starlings among several winter roosting sites in the southeastern United States in a single winter, no previous study has addressed questions related to timing and magnitude of large population migrations and subsequent dispersal in breeding areas within a single season.

In response to this informational need a unique method was developed for mass marking roosting blackbirds with aerial applications of a fluorescent, pigmented material visible only under long-wave ultraviolet light (B. E. Johns, unpubl. data). Briefly, this material is a liquid formulation of an acrylic adhesive, a wetting agent, a defoamer, an antifreeze (propylene glycol), water, and a fluorescent-colored organic resin particle with a consistency much like talcum powder. This formulation is sprayed from an aircraft flying 15–20 m above large roosting concentrations during the 20 minutes immediately following sunset. The liquid dries and adheres to the feather surface with some lodging in the barbules, and usually remains on feathers until molt. The technique has been used successfully to mark approximately 8.2 million male redwings in a northwestern Missouri roost in March 1982, and 2.4 million males in southeastern South Dakota in March 1983. Subsequent collections of these birds during the breeding season from several northern states and southern Canadian provinces provided information on dispersal from these communal roosting sites (C. E. Knittle, unpubl. data). In these 2 studies investigators spray-marked each roost once during migration. However, different particle colors provide the opportunity to mark a single roost several times during a spring migration. Such multiple marking efforts could yield information on the total numbers and turnover (ingress-egress) rates of birds using a congregating roost during a given period. The objective of this paper is to present a method

for estimating these parameters and to illustrate their application by using data collected from 2 marking experiments.

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METHODS

Estimation of Turnover Rate

The parameter of primary interest is turnover rate of the roost population between any 2 consecutive sampling periods. Turnover rates are defined as $1 - S_i$, where S_i represents the probability that a bird is a member of the roosting population from immediately after the ith sampling occasion to time of the (i + 1st) sampling occasion. Another estimable parameter of interest is U, which represents the total number of different individuals using the roost from immediately after the 1st sampling occasion to the last occasion.

Before statistics necessary to the estimation method are defined, a clarification of sampling assumptions is necessary. In practice the sampling (collection) of birds on each occasion may be performed during 1 or 2 days. However, all data are pooled and treated as an instantaneous sample. This step assumes that the population is static during this period, at least relative to change in the population between consecutive occasions. Furthermore, some sampling occasions are immediately preceded by a marking operation. For notational purposes the marking and the associated subsequent sampling operation are treated as the same occasion. The following assumptions are made concerning the underlying sampling process and associated field procedures: (1) there is no loss of marks during the experiment, (2) all marks are correctly identified, (3) the sample of birds collected on each occasion is representative of the roost population at that time, (4) birds suffer independent fates, (5) mortality during the experiment is negligible, (6) the probability that a bird emigrates from the roosting population is independent of the length of time it has been using the roost, and (7) a bird cannot return to the roost after emigrating.

The following statistics and constants are now defined:

t = number of sampling occasions,

n_i = number of birds collected and examined for marks on the ith occasion, $i = 1, \ldots, t$,

N_i = roost population size on the ith occasion, $i = 1, \ldots, t$,

m_{ij} = number of birds in the ith sample 1st marked on the jth occasion, $j = 1, \ldots, i$, $i = 1, \ldots, t$,

$\hat{R}_i$ = estimated number of newly marked birds added to the population on the ith occasion $= N_i m_{ii}/n_i = N_i \hat{z}_i$, $i = 1, \ldots, t$, and

$\hat{M}_i$ = estimated number of marked birds in the population on the ith occasion marked before the ith occasion $=$

$$N_i \sum_{j=1}^{i-1} m_{ij}/n_i = N_i \hat{p}_i,\ i = 1, \ldots, t.$$

The estimation problem involves multiple releases of batch-marked birds and subsequent removal samples. The maximum likelihood estimators of the parameters could be derived using a multinomial likelihood function as is often done with capture-recapture and bird banding models (Seber 1982). However, a simpler and more intuitive derivation can be achieved by following the logic of Cormack (1973). He suggested that a probability such as S_i be estimated by the corresponding proportion, incorporating the common sense idea that the largest relevant group of individuals should form the base for the proportion. This principle leads to the estimator:

$$\hat{S}_{i+1} = \hat{M}_{i+1}/(\hat{M}_i + \hat{R}_i - m_{ii}),\quad i = 1, \ldots, t - 1. \tag{1}$$

Note that $\hat{S}_i$ is simply the ratio of the largest known (marked) group of birds alive and present in the population just before the (i + 1st) occasion to the largest known group alive and present just after the ith occasion. The form of equation (1) is the same as the survival estimator given by Jolly (1965) in his intuitive derivation of estimators for the Jolly-Seber capture-recapture model. Given the set of estimates $\hat{S}_i$, the logical unbiased estimator of U becomes:

$$\begin{aligned}\hat{U} &= N_1 + (N_2 - N_1\hat{S}_1) + \ldots \\ &\quad + (N_t - N_{t-1}\hat{S}_{t-1}) \\ &= \sum_{i=1}^{t-1} N_i(1 - \hat{S}_i) + N_t.\end{aligned} \tag{2}$$

Approximate variance and covariance expressions for the estimators can be derived by using the delta method. For simplicity, we note that $m_{ij} \ll (M_i + R_i)$, so that the contribution of the random variable m_{ij} to $\mathrm{Var}(\hat{S}_i)$ is assumed to be negligible.

These expressions are:

$$\mathrm{Var}(\hat{S}_i) = S_i^2\left(\frac{1 - p_i - z_i}{n_i[p_i + z_i]} + \frac{1 - p_{i+1}}{n_{i+1}p_{i+1}}\right), \quad (3)$$

$$\mathrm{Cov}(\hat{S}_i, \hat{S}_{i+j}) \begin{pmatrix} 0 \\ -S_iS_j\dfrac{1 - p_{i+1} - z_{i+1}}{n_{i+1}[p_{i+1} + z_{i+1}]} \end{pmatrix} \begin{matrix} \text{, if } j > 1, \\ \text{, if } j = 1, \end{matrix}$$

$$\mathrm{Var}(\hat{U}) = \sum_{i=1}^{t-1} N_i\mathrm{Var}(\hat{S}_i) + 2\sum_{i=1}^{t-2} N_iN_{i+1}\mathrm{Cov}(\hat{S}_i, \hat{S}_{i+1}).$$

Estimates of these expressions can be obtained by substituting estimated values for S_i, p_i, and z_i.

EXAMPLES

Two roosting congregations of redwings were spray marked in March 1985. The larger was located at Lake Thompson, near DeSmet, South Dakota. It initially held about 0.75 million male redwings in about 2,800 ha of mixed cattail (*Typha* spp.) and common reeds (*Phragmites communis*) although birds occupied only the interspersed islands of common reeds. The 2nd area contained 2 marshes, the smallest approximately 40 ha in size and the other, about 2 km away, approximately 900 ha. These marshes were located in west-central Minnesota along the East Fork of the Chippewa River near Benson and initially harbored approximately 0.5 million male redwings. Both marking sites were situated on known migratory routes (J. F. Besser, pers. commun.) about 200 km apart, and were surrounded by idle crop fields, pastures, and a myriad of small creeks, lakes, and potholes.

Evening flightline counts were conducted upon 1st arrival in each study area (Meanley 1965, Arbib 1972). The marking operations began within 2 days after the initial population arrived at each site. Counts also were conducted during the evening of each marking operation and upon departure from the study site (in South Dakota only). Two marking operations were conducted at each site at about 7-day intervals, with a different pigment used on each of the 4 occasions. Formulations were applied by 2 fixed-wing aircraft beginning at sunset and continuing until dark or until the formulation was exhausted. The day after each spray operation, male redwings were shot and collected at feeding sites within a 25-km radius of each marsh. A follow-up collection was done at Lake Thompson 4 days after the last spray. All redwings were examined for marks the same day they were collected.

Table 1 presents the data necessary for estimating the parameters S_i and U at each of the 2 roost sites. Although Benson was sprayed twice, only 1 turnover rate was estimated because no follow-up collections were made. Use of equations (1), (2), and (3) resulted in the estimates $1 - \hat{S}_1 = 0.1107$ ($\widehat{\mathrm{SE}} = 0.0117$), and $\hat{U} = 702{,}267$ ($\widehat{\mathrm{SE}} = 6{,}507$). Lake Thompson also was sprayed on 2 consecutive occasions, but the follow-up collection allowed 2 turnover rates to be estimated. The estimates are $1 - \hat{S}_1 = 0.3517$ ($\widehat{\mathrm{SE}} = 0.0657$), $1 - \hat{S}_2 = 0.0757$ ($\widehat{\mathrm{SE}} = 0.0597$), $\hat{U} = 1{,}375{,}274$ ($\widehat{\mathrm{SE}} = 67{,}742$). Thus, turnover rates during the 22–28 March period at Benson and the 25–29 March period at Lake Thompson were both relatively low, whereas the Lake Thompson roost experienced a higher rate of turnover during the week of 18–25 March. An estimated 2 million different male birds used these 2 roost sites during the study period.

DISCUSSION

The estimation method presented for the purpose of utilizing mass-marking data to study the dynamics of spring migration roosts involves aspects of both band-recovery and capture-recapture estimation theory. A fundamental difference is that the number of marked birds added to the population has to be estimated, which requires that the roost size be known. The accuracy of flightline counts to estimate roost population size is unknown, and represents a source of bias of unknown magnitude. It is obvious from equation (1), however, that if the counts, N_i, are subject to a consistent proportional bias, then the estimator of S_i remains unbiased. Conversely, the estimate of U will be subject to a bias equal to the bias in the counts, as evidenced by equation (2). In practice use of the same, experienced observers on each occasion should make unknown population size a negligible source of bias in the estimates. A 2nd

Table 1. Data used to calculate turnover rates in spring roosts of male red-winged blackbirds at Benson, Minnesota and Lake Thompson, South Dakota, 1985. The number of birds collected in the ith sample that were 1st marked on the jth occasion, m_{ij}, is listed in the table under date of 1st marking.

Collection date	i	N_i[a]	N birds collected n_i	Date of 1st marking: 22 Mar $j = 1$	28 Mar $j = 2$	
Benson, MN						
22 Mar	1	556,160	286	139		
28 Mar	2	640,700	224	84	115	
				18 Mar $j = 1$	25 Mar $j = 2$	29 Mar $j = 3$
Lake Thompson, SD						
18 Mar	1	731,000	300	157		
25 Mar	2	834,000	325	97	202	
29 Mar	3	1,055,048	125	20	64	0

[a] Population estimate from evening flightline counts (Meanley 1965, Arbib 1972).

major assumption is that mortality rate during the experiment is negligible. The veracity of this assumption will vary with environmental conditions and other unknown factors. However, if an annual mortality rate of 60% (R. A. Stehn, unpubl. data) is assumed, then mortality during a 3-week period should be no more than 3%, assuming a constant, instantaneous rate. It is possible, therefore, that estimated turnover rates are positively biased by a few percentage points, but we believe that a bias of this magnitude is not biologically meaningful.

Both the mass-marking technology and the associated statistical methods have the flexibility to be adapted to other estimation problems involving roost population dynamics. Obviously, age- and sex-specific estimates of turnover through a single roost could be made by recording the data separately for these classes. One also could consider marking and sampling birds at several different congregating roosts along the migration pathway (if such roosts could be identified) to piece together the location and timing of spring migration routes of identifiable populations. The estimation method used here would require generalization, but the development of such methods is logically possible.

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BROWN-HEADED COWBIRD PARASITISM AND HABITAT DISTURBANCE IN THE SIERRA NEVADA

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Abstract: I studied nest parasitism by the brown-headed cowbird (*Molothrus ater*) in the northern Sierra Nevada to determine parasitism rates of host species, effects of differing availabilities of human- and livestock-based foods (habitat disturbance) on parasitism rates, and impacts on host populations. Twenty-six of 206 nests and family groups with dependent young (including 8 species) were parasitized. Parasitism was strongly associated with habitat disturbance; 27.1% of groups of susceptible host species in highly disturbed areas contained cowbird young vs. 8.7% in less disturbed areas. Parasitized family groups contained 76% fewer host young than unparasitized groups. Productivity of susceptible species was reduced by 20.6 and 6.6% in highly and moderately disturbed areas, respectively, and by 6.1% in the total study area. Hosts that prefer riparian habitats are most likely to decline due to cowbird parasitism.

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Recent invasion of the Sierra Nevada by the brown-headed cowbird has raised concerns over its effects on native birds. Because Sierran birds have not previously been in contact with cowbirds, and thus may not have evolved effective defenses, cowbird brood parasitism could cause reductions in vulnerable species (Gaines 1977, Rothstein et al. 1980). Such impacts have been documented for the Kirtland's warbler (*Dendroica kirtlandii*) (Mayfield 1977) and have been suggested for other species in California (Gaines 1974, Goldwasser et al. 1980) and elsewhere (Brittingham and Temple 1983).

An indirect method for evaluating potential population impacts is to determine rates of parasitism of host nests and family groups with dependent young. Differences in parasitism rates have been found in various parts of the Sierra Nevada. Gaines (*in* Rothstein et al. [1980]) reported high rates of parasitism associated with declines in certain hosts in Yosemite Valley. Rothstein et al. (1980) also found high rates of parasitism at Mammoth Lakes in the eastern Sierra Nevada. In contrast, Verner and Ritter (1983) found low parasitism rates in the southern Sierra Nevada.

Availability of human-based foods has been suggested as important in determining numbers and dispersion of cowbirds and the intensity of host parasitism in the Sierra Nevada (Rothstein et al. 1980, 1984; Verner and Ritter 1983). Cowbirds frequently feed in disturbed areas where high energy foods are concentrated, including residential areas with bird feeders, campgrounds, livestock concentration areas, and garbage dumps. Rothstein et al. (1984) reported that cowbirds travelled up to 6.7 km from feeding sites to parasitize host populations. Verner and Ritter (1983) showed a decrease in abundance of the warbling vireo (*Vireo gilvus*), a frequently parasitized host, near cowbird feeding sites. To date, however, no study has specifically related amounts of human habitat disturbance and associated foods with rates of cowbird parasitism at a variety of sites within a single study area.

Study objectives were to: (1) identify host species and rates of parasitism, (2) determine if parasitism rates differed between areas with different availabilities of human-based foods, (3) evaluate the potential impacts of parasitism on host populations, and (4) compare rates and patterns of parasitism in the northern Sierra Nevada to those found previously in the central and southern Sierra.

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