Multistate estimates of survival and movement in relation to colony size in the sociable weaver

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We estimated survival and movement probabilities in relation to breeding-colony size in the sociable weaver (*Philetairus socius*) by using multistate statistical methods, in which survival and movement to time $t + 1$ is conditional on an individual's colony size at time t. The sociable weaver is a colonial, cooperatively breeding species that builds a massive communal nest, with colony size ranging from fewer than 20 to more than 500 individuals in some areas. We conducted an 8-year capture/mark/recapture study of sociable weavers near Kimberley, South Africa. By comparing the fit of different multistate models to our data, we found evidence that annual survival probability of adults was lower in small colonies (less than 30 individuals) and medium-sized colonies (30–60 individuals) than in large colonies (more than 60 individuals). First-year survival of birds banded as juveniles also increased with natal colony size. Statistically, however, these effects were weak, and models without an effect of colony size were equally well supported by our data. Movement probabilities illustrated that individuals seldom moved between colonies of different size classes, and showed a preference to use colonies of size classes similar to what they had occupied the preceding year, even when changing colony sites between years. The potential survival differences among birds in different colonies, if real, translated into differences of 39–45% in average lifespan. First-year survival is probably enhanced through antipredator advantages of being in larger groups during the fledgling period. Adult survival in larger groups may be increased by thermal advantages of a large nest during cold winter weather. The fidelity of weavers to a particular colony-size class between years may reflect phenotypic specialization for certain group sizes. *Key words:* coloniality, dispersal, life history, *Philetairus socius*, sociable weaver, social behavior, survival. *[Behav Ecol 14:463–471 (2003)]*

The evolution of coloniality in birds and other vertebrates is poorly understood despite numerous field studies over the past several decades. The predominant approach has been to measure various social and ecological costs and benefits in relation to the size of a breeding group and, from that, to infer the selective pressures that led to the evolution and/or maintenance of coloniality (Brown and Brown, 1996, 2001a; Brown et al., 1990; Hoogland, 1995; Hoogland and Sherman, 1976; Møller, 1987; Tyler, 1995; Wiklund and Andersson, 1994). However, these costs and benefits are often measured in different currencies, and it can be difficult to specify the relative importance of each. An alternative approach is to use reproductive success as an integrative measure of the suite of effects on fitness related to group size (Brown and Brown, 1996; Danchin and Wagner, 1997).

To date, the work that has directly addressed the fitness effects of colony size has focused on measuring one component of fitness, annual fledging success. No studies have rigorously estimated annual survival probability of breeders in relation to colony size. Similar to fledging success (Danchin and Wagner, 1997; Danchin et al., 1998), annual survival probability integrates many of the disparate costs and benefits of coloniality into a single, readily interpretable component of fitness. However, estimating survival in relation to colony size is not straightforward because animals may often occupy colonies of different sizes in different years, and their survival in each successive time period will be conditional on the colony they occupied during each interval. This problem thus requires statistical methods that incorporate an individual's changing state, the probability that it changes states, and the effect of each state on its subsequent activity.

The development of multistate methods for estimating state-dependent annual survival probabilities in natural populations of animals is one of the most important statistical advances in evolutionary ecology in recent years (Lebreton and Pradel, 2002; Nichols and Kendall, 1995). These techniques allow one to model the survival to time $t + 1$ of animals that are stratified by location or other state variables (e.g., breeding condition, reproductive success) as conditional on their state at time t. Whenever these states can change for a given individual between capture occasions, classical Cormack-Jolly-Seber models and their refinements (that assume fixed states; Lebreton et al., 1992) are not appropriate.

In addition to estimating how survival is conditional on state, one can also use multistate methods to estimate the probability that an animal undergoes a transition from one state to another, e.g., from being a breeder to being a nonbreeder. Whenever the states are physical locations, the transitions represent probabilities of movement. Although the theory behind multistate methods is well developed (see Brownie et al., 1993; Hestbeck, 1995a; Nichols et al., 1992, 1994; Schwarz et al., 1993), few attempts have been made to apply these techniques to natural populations or to use them to address evolutionary questions. Those studies having employed multistate methods to date (see Hestbeck 1995b; Hestbeck et al., 1991; Lindberg et al., 1995; Spendelow et al., 1995) have been primarily concerned with estimating physical movement between different breeding areas with the goal of population management. Multistate estimates of survival and movement

are especially appropriate for studying colonial species, in which individuals are often stratified in space by their occupancy of different colony sites and in which individuals may move between different colonies over time (Spendelow et al., 1995). Both survival and movement rates may vary among individuals in relation to their individual attributes such as colony size.

In this article, we use mark-recapture and multistate statistical methods to estimate annual survival probabilities of sociable weavers (*Philetairus socius*) in relation to the size of the breeding colony an adult bird occupied the previous season. By using single-state methods, we also investigate how postfledging survival of juveniles is influenced by the size of their natal colony. We use our results to determine whether breeding in colonies of different sizes confers net costs or benefits to these birds. In addition, we examine intercolony movement, in which we estimate the probability of a bird making a transition from one colony to another from time t to time $t + 1$, and we interpret how the movement probabilities vary in relation to both colony size and the site a bird used at time t. Movement probabilities potentially reveal patterns or rules used by the birds to choose among groups of different sizes, and have been used in some species to estimate dispersal within a metapopulation (Spendelow et al., 1995). The sociable weaver is a highly communal passerine, in which all members of a colony cooperate to build a single massive grass nest with separate nesting chambers for each pair. Colonies vary in size from less than 20 to more than 500 individuals (Maclean, 1973), making these weavers especially suitable for studying the effect of colony size on survival and movement probabilities. To our knowledge, this study is the first for any species to use multistate methods to estimate survival and movement specifically in relation to colony size.

METHODS

Study site

The study was conducted at Benfontein Game Farm, situated 6 km southeast of Kimberley, on the border of the Free State and Northern Cape provinces, South Africa (approximately 28°53′ S, 24°49′ E). The study site, in the southern part of Benfontein, consists of open savanna and is dominated by Stipagrostis grasses and the camelthorn tree, *Acacia erioloba*. The area is semiarid, experiencing low and unpredictable rainfall (mean ± SD = 431 ± 127 mm/year; Weather Bureau, Pretoria), with most of the precipitation falling during the summer months. The daily temperature ranges are typically broad, with cool/warm nights and hot days in summer (approximately 8°C–40°C) and cold nights and mild days in winter (approximately −8°C–25°C).

Study animal

The sociable weaver is endemic to southern Africa, with its core distribution being in the Northern Cape and Namibia (Maclean, 1973; Mendelsohn and Anderson, 1997). Sociable weavers weigh 26–30 g, with the sexes being indistinguishable by plumage in the field. The males have a slightly longer tarsus (but the range overlaps with the females'); the sexes show no significant differences in mass (Doutrelant C and Covas R, unpublished data). Sociable weavers feed predominantly on insects (80% of their diet) but also on seeds and other plant products (Maclean, 1973). They are colonial, cooperative breeders and experience great variation in colony size (two to 500 individuals per colony; Maclean, 1973) and in the number of helpers attending one brood (up to nine helpers per brood; Maclean, 1973). In our study area, colony size ranged from 10–

200 individuals; colonies at Benfontein are on average smaller than those in the Kalahari to the west of our study area (Anderson MD, personal observation). The weavers build a huge nest with separate chambers in which a pair (with their offspring and possibly other birds) roost and breed. The nest is built on a variety of sturdy structures, from *Acacia* trees to telephone poles (Maclean, 1973). At Benfontein, the nests are almost exclusively constructed on *A. erioloba* trees, and the nest mass is maintained by the whole colony throughout the year. The colony can remain active for several decades, being occupied by successive generations of weavers that continuously add to the nest structure (Maclean, 1973), although nests and colony sites are also abandoned at times (Marsden, 1999). At night, the birds roost in the chambers within the nest mass. They also return to the nest during the day to escape predators (Covas R, personal observation) or to seek protection from the daytime temperatures during summer (Maclean, 1973).

Sociable weavers breed aseasonally in response to rainfall. Maclean (1973) found that a breeding response would follow approximately 20 mm of rain, regardless of the season. Rainfall is also a major determinant of the duration of the breeding period, the number of broods raised (one to eight), and clutch size (two to six eggs; Covas R, unpublished data; Maclean, 1973). In our study area, the weavers usually start breeding in September or October (see below), with the duration of the breeding season varying from 3–9 months. When conditions are favorable, the weavers can breed throughout the year, but with insufficient rainfall (and resultant food), they sometimes delay reproduction for more than a year (Maclean, 1973; this study). Reproductive success can vary dramatically among years and within a single season, with nest predation being the main cause of failure (up to 100% nesting failure in some colonies; Covas R, unpublished data).

Field methods

From August 1993–November 2000, we conducted a capture/ mark/recapture study at Benfontein. The study area contained approximately 25 sociable weaver colony sites. At 16–18 of these, we captured the residents twice a year. During the first 5 years, our capture effort was distributed throughout the year (one or two colonies caught each month). Beginning in mid-1998 we concentrated our capture efforts during one to two consecutive months at the beginning and end of the breeding period. The birds were captured with mist nets, which were placed before dawn around the nesting tree. Before sunrise, we approached the colony and flushed the birds into the nets. A small number of birds usually managed to escape (by flying over the nets), but the capture success was typically above 80%. Those birds that escaped were counted and added to the number of birds caught; this total was considered to be the colony size in that period. The birds were removed from the nets, placed individually in linen bags, and processed. The duration of the procedure depended on the size of the colony but usually lasted 1–3 h. The birds were ringed with a unique numbered ring from the South African Bird Ringing Unit (SAFRING) and in later years with an individual color combination. Juvenile weavers molt into adult plumage when they are approximately 4 months old, and before that, their age can be estimated by assessing the development of the black patch on the face and throat (Maclean, 1973; Covas R, unpublished data). We considered two age classes: juvenile (younger than 4 months) and adults (fully developed patch, older than 4 months). The juveniles remain with the families for an extended period, and no subadults were ever observed to leave the natal colony (Maclean, 1973; Covas R, unpublished data). Thus, we confidently assumed that the colony where a juvenile was caught was its natal colony.

During the first 5 years of the study, the breeding activity of the birds was not directly monitored. To determine when the breeding season took place in these years, we used the development of the black patch of juveniles caught to back-estimate the month of hatching. Information on the presence/absence of brood patches also provided an indication of the breeding season. In the other years, we directly determined when nesting occurred by regularly checking the contents of nest chambers. In total, we considered eight breeding periods (there was no capture effort during June 1997–May 1998): August 1993 (beginning of the study), October 1993–April 1994, October 1995–April 1996, October 1996–March 1997, October 1998–December 1998, September 1999–May 2000, and September 2000–January 2001.

Statistical methods

We estimated annual survival probabilities and tested for significant differences between different groups of birds by using the general methods of Lebreton et al. (1992) and of Burnham and Anderson (1998). We used program MARK (Cooch and White, 1998; White and Burnham, 1999) to generate maximum-likelihood estimates of survival, recapture, and movement probabilities. MARK is a software package that computes survival, recapture, and movement parameters by using an information matrix derived from recapture histories. MARK compares and tests the fit of different statistical models, facilitating the ranking, evaluation, and plausibility of competing biological hypotheses (Lebreton et al. 1992).

We use the general notation of Lebreton et al. (1992), in which annual survival probability is denoted ϕ; recapture probability, p; and movement probability, ψ. Subscripts indicate whether parameters in a model are time-dependent (e.g., ϕ_t, p_t), vary with age (and if so, with how many age classes, e.g., ϕ_{a2}, p_{a2t} for two age classes), are constant over time and groups (e.g., ϕ, p), are group specific (e.g., ϕ_g, p_g), or are group and time specific (e.g., $\phi_{g \cdot t}$, p_t). By using program RELEASE (Burnham et al., 1987), we assessed the overall fit of our data set to the assumptions inherent in the single-state Cormack-Jolly-Seber (CJS) model for survival and recapture (Lebreton et al., 1992). We used RELEASE's single-state goodness-of-fit test, as no tractable multistate tests are currently available (Lebreton and Pradel, 2002); however, data sets that meet the single-state assumptions (e.g., no overdispersion, no predominance of transients, no trap-dependence) are probably generally robust for multistate analysis (Lebreton JD, personal communication). After that, we challenged our data with a variety of more biologically relevant models incorporating various combinations of age, group, and time dependence in survival, recapture, and movement parameters.

We compared the statistical fit of competing models with the Akaike Information Criterion (AIC$_c$; Akaike, 1973; Burnham and Anderson, 1998) corrected for sample size as provided by MARK. In theory, the model with the lowest value of AIC$_c$ is the so-called best model. The AIC$_c$ is a formal statistical criterion to select among competing models; the currently accepted convention (Burnham and Anderson, 1998) is that models with AIC$_c$ that differ by two or less are indistinguishable statistically. In general, for model selection and hypothesis testing, we relied on "AIC$_c$ weights," a measure of a model's relative probability of being the best model for the data, compared to alternative models (Burnham and Anderson, 1998). We assessed potential differences in survival or movement among different groups of birds by comparing different models, some of which separately modelled the effect of each group, whereas others considered the groups as a common pool. We do not present results of fits of all models tried within MARK; rather, in the tables we generally show only those eight to 10 competitive models with the lowest AIC$_c$ that tested legitimate a priori survival and movement hypotheses. The number of estimable parameters in our models was also provided by MARK based on the chosen model structure and the statistical information provided by our data.

Because sociable weavers are unpredictable, aseasonal breeders, the time intervals in between our capture occasions were not constant (see above). Fortunately, MARK allows an analyst to choose the time intervals between successive capture occasions. For the eight capture occasions, corresponding to the eight breeding periods that occurred July 1993–January 2001, we used seven time intervals of 0.67, 2, 0.92, 1.2, 0.58, 1.4, and 0.67 years, respectively. Each interval was defined as the time from the start of the nonbreeding period until the end of the successive breeding period. Therefore, as in most mark-recapture studies, the breeding season was considered to take place in an instant in time with zero mortality and movement during that breeding season. However, all survival, recapture, and movement probabilities reported here are annualized ones, that is, for a 12-month period, allowing comparison with other studies. Although some birds were also caught during nonbreeding periods, a bird had to be caught during a breeding period to be designated as surviving to that period. Birds were designated as adults if older than 120 days on capture and as juveniles if younger than 120 days.

Multistate parameter designations

Natal-colony and breeding-colony sizes were defined as the number of birds present at a colony site during that breeding period. Because natal-colony size was a fixed, single-state parameter that was unchanging for each individual, we used actual colony size as a covariate for each bird (initially banded as a juvenile) in single-state analyses. However, we used three classes for breeding-colony size: small (less than 30 individuals), medium (30–60 individuals), and large (more than 60 individuals). This was necessary because of the many colonies we studied and the resulting large number of parameters inherent in multistate models. We had to reduce the number of these parameters to avoid data sparseness across individual colonies. The colony-size classes were based a priori on results from preliminary analyses that showed significant differences in clutch size, hatching success, and fledging mass among colonies of these sizes (Covas R and Doutrelant C, unpublished data). The number, spatial distribution, and mean colony-size classification (averaged over all years) of the colony sites in the study area are shown in Figure 1.

For each adult bird for which we knew its breeding colony in at least 1 year, we also classified it according to whether it occupied a colony site for the first time in a given year or whether it had been known to use that site in the previous nesting season, regardless of colony size. We use the designations S_f, M_f, and L_f for birds using small, medium, and large colonies, respectively, for the first time at a particular site, and the designations S_r, M_r, and L_r for birds using small, medium, and large colonies, respectively, at a site where they had been the previous year. This allowed us to examine movement probabilities for birds among colony sizes independent of the effect of site per se. Models that contained both an effect of colony size and site-usage history thus had six states; those that ignored site usage had three states, treating S_f and S_r the same, M_f and M_r the same, and L_f and L_r the same. For studying the effect of colony size on movement in first-year birds, we again used the same colony-size classes. However, the sample size of birds initially banded as juveniles
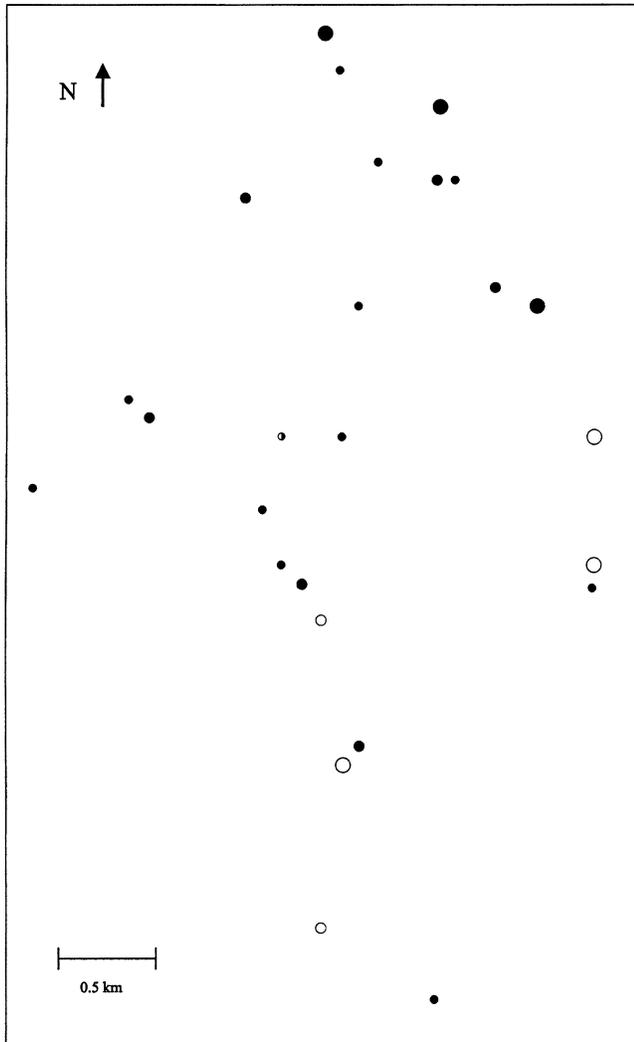
Figure 1
Schematic diagram showing the number, spatial distribution, and average size of sociable weaver colony sites in the study area. Locations were based on GPS readings. The different-sized dots represent sites with small, medium, or large colonies, based on mean colony size over all breeding periods of the study. Open circles are colony sites at which birds were never captured, and the half-filled circle indicates a colony site that was abandoned in the later years of the study. The open savannah woodland characteristic of the study area continued to the south and east of the area shown, and to the north and west the vegetation abruptly changed into treeless grassland (unsuitable for sociable weavers).

was too small to allow us to study the effect of site usage per se, because models with both colony size and site usage had too many states (six) for the limited amount of data available. With the six states for adults, we had 36 defined transition (movement) probabilities, corresponding to various scenarios in which a bird changed sites and colony sizes, changed sites but its colony size remained the same, stayed at the same site but the colony size there changed, or remained at the same site with the same colony size between years (see below).

RESULTS

Goodness-of-fit testing

By using our entire data set ($N = 1486$ total birds marked and released), we found that the sociable weaver data met the general CJS single-state assumptions under model ϕ_t, p_t. Neither test 3.SR ($\chi_5^2 = 7.72$, $p = .17$) nor test 3.SM ($\chi_3^2 = 1.60$, $p = .66$) in RELEASE, both being tests for transients, showed a significant departure from the frequencies expected under the CJS model. Similarly, there was no indication of any trap-dependence in weaver captures, as judged from test 2.CT in RELEASE ($\chi_3^2 = 3.91$, $p = .27$). For these reasons, it was not necessary to correct our values of AIC_c for overdispersion in subsequent tests.

Effects of natal-colony size on survival

By using each juvenile's actual natal-colony size (range, 11–99) as a continuous covariate, we used MARK to model survival estimates (ϕ) as a function of natal-colony size and compared models with and without natal-colony size as a covariate for our sample of birds first banded as juveniles ($N = 369$ total birds marked and released) (Table 1). The AIC_c values for the top two candidate models—one without and one with an effect of natal colony size on survival—differed by less than two (Table 1). Thus, each model and the hypothesis on which it was based had some support in our data. However, because the model without an effect (model 1; Table 1) was 1.6 times as likely (based on AIC_c weights) as the one with an effect of natal colony size (model 2), it would appear that any influence of natal colony size on first-year survival was small. The slight effect of natal colony size was positive: The trend from model 2 was for first-year survival to increase with colony size, with the estimated logit regression coefficient being 0.10674. From that regression, first-year survival probabilities varied from 0.617–0.707 over the observed range of colony sizes in the Benfontein population. All of the better-fitting candidate models incorporated an effect of natal-colony size at time t on recapture probability (p) at time $t + 1$. This reflects the fact that our capture effort was not apportioned evenly among colony sizes; in particular, we had more small colonies in the study area and more effort in the smaller colonies in the later years of the study. There was no evidence of an age-related effect on survival probability for birds banded as juveniles (models 3 and 4) or an effect of time (models 7–9; Table 1).

Effects of breeding-colony size on adult survival

Unlike natal-colony size, breeding-colony size was a multistate variable, with individuals potentially able to switch from one colony-size class (or from one colony site) to another between breeding periods. The survival probabilities we estimated from MARK assume that an individual's probability of survival from period t to period $t + 1$ depend only on its colony-size class at period t and is unaffected by its colony size in period $t + 1$, a seemingly reasonable assumption for sociable weavers. This analysis used all birds for which a breeding-colony-size class was known ($N = 950$ total birds marked and released), and included birds first banded as adults and any bird first caught as a juvenile and later as a breeder (for birds banded as juveniles, their capture histories in this analysis began when they were first encountered as a breeder).

The multistate model with the lowest AIC_c value (model 10; Table 2) treated the large colony-size class (more than 60 individuals) as distinct from the small and medium classes combined. Although this model was 1.7 times as likely (based on AIC_c weights) as the next best-fitting model (11; Table 2) without a colony-size effect, the top two models differed by only 1.1 in AIC_c, and thus, each had some support in our data. Again the effect of colony size on survival appeared weak. From model 10, we estimated average ($\pm SE$) annual survival probability of birds breeding in small and medium colonies as 0.660 (± 0.023) and for those in the large colonies as 0.751

Table 1

Single-state models to assess the effect of natal-colony size on survival and recapture probabilities in sociable weavers

Model	AIC_c	AIC_c weight	Number of estimable parameters	Deviance
(1) ϕ, $p_{cs \cdot t}$	735.7	0.508	13	708.8
(2) ϕ_{cs}, $p_{cs \cdot t}$	736.7	0.310	14	707.7
(3) $\phi_{cs \cdot a2}$, $p_{cs \cdot t}$	739.3	0.081	16	706.1
(4) $\phi_{cs \cdot a2}$, $p_{cs \cdot t}$	739.3	0.081	16	706.1
(5) ϕ, p_t	744.1	0.010	8	727.7
(6) ϕ_{cs}, p_t	745.2	0.008	9	727.2
(7) $\phi_{cs \cdot t}$, p_t	749.0	0.001	17	713.6
(8) ϕ_t, p_t	751.6	0.000	13	724.7
(9) $\phi_{cs \cdot t}$, $p_{cs \cdot t}$	753.1	0.000	24	702.2

Models with an effect of natal-colony size (subscript cs) used colony size as a continuously distributed covariate. Model 3 constrained survival of both age classes as a function of natal-colony size; model 4 constrained only first-year survival as a function of natal-colony size.

(± 0.040). Comparison of model 10 with model 12 (Table 2) suggests that the small- and medium-sized classes are not functionally distinct in terms of their possible effect on breeders' survival. The other models with effects of colony size (some using all three size classes and others considering small as distinct from medium and large combined) had AIC_c values that were larger by two or more and thus were less plausible (Table 2). All multistate models used for survival estimation considered colony sizes without regard to what colony site a bird had used; when we modelled survival as a function of both size and site-usage history (six states for survival), our data were too sparse to get convergences for those models in MARK. As with the single-state analysis of natal colony size, all of the better-fitting multistate models incorporated an effect of colony size at time t on recapture probability at time $t + 1$ (Table 2).

Effects of colony size on movement by breeders and first-year birds

Movement (i.e., between-state transition) probabilities (ψ) are essentially a measure of individual dispersal to and from both a given colony-size class and a physical colony site. Between-year movement probabilities of breeders were clearly affected by breeding-colony size and by colony site. All models with constant movement probability had relatively high AIC_c values (e.g., model 17; Table 2) and thus did not describe our data well. All of the better-fitting models for breeders incorporated both an effect of colony size and site-usage history (i.e., six states) on movement probabilities (Table 2). We tried several models that combined different pairs of our colony-size classes in estimating movement (e.g., as model 10 did for survival), and none of these provided as good a fit as the model that kept the three size and site-usage classes. We also found that models that did not take site usage into account (e.g., models 15–17; Table 2) were a much poorer fit.

From the best-fitting model (10; Table 2), we estimated the transition probabilities among the three breeding-colony size classes and the two possible site-usage histories (Table 3). These data show that sociable weavers remain relatively faithful to both a breeding-colony size from year to year and to a particular site. Because colony size at a site tends to be similar between breeding episodes, as measured by the intraclass correlation coefficient (Zar, 1999) for colony size by site ($r_I = .897$; $p < .0001$), size and site are confounded for birds

Table 2

Multistate models to assess the effect of three breeding-colony-size classes on survival, recapture, and movement probabilities in sociable weavers

Model	AIC_c	AIC_c weight	Number of estimable parameters	Deviance
(10) ϕ_{cc2}, $p_{cc3 \cdot t}$, $\psi_{cc3/suh3}$	1945.9	0.467	53	472.1
(11) ϕ, $p_{cc3 \cdot t}$, $\psi_{cc3/suh3}$	1947.0	0.268	52	475.5
(12) ϕ_{cc3}, $p_{cc3 \cdot t}$, $\psi_{cc3/suh3}$	1948.2	0.154	54	472.0
(13) ϕ_{cc2}, $p_{cc3 \cdot t}$, $\psi_{cc3/suh3}$	1949.0	0.103	53	475.1
(14) ϕ_{cc3}, p_t, $\psi_{cc3/suh3}$	1980.4	0.000	40	535.8
(15) ϕ, $p_{cc3 \cdot t}$, ψ_{cc3}	2008.4	0.000	31	583.5
(16) ϕ_{cc2}, $p_{cc3 \cdot t}$, ψ_{cc3}	2009.6	0.000	32	582.6
(17) ϕ, p_t, ψ	2592.7	0.000	9	1214.1

Models with three colony size classes are indicated with a subscript cc3. Some models used only two colony-size classes (subscript cc2). Movement probabilities modelled both the effect of colony size (subscript cc3) and site-usage history (subscript suh3). See text for definition of colony-size classes and site-usage histories. Models 10 and 16 used two colony-size classes of small + medium and large; model 13 used two classes of small and medium + large.

that occupy the same physical location between breeding periods. However, by examining the probability of movement from one colony size to another only for birds that switched colony sites, we could determine the effect of colony size independent of site. Considering *only* birds that moved between different sites, we found (Table 3) that birds were likely to use a site of size similar to that they had used the previous season. For example, birds using small colonies in year t generally moved only to other small colonies and were unlikely ever to use medium or large colonies (Table 3), even though the larger colonies were often nearby (Figure 1). Individuals occupying large colonies also tended to occupy other large colonies when moving (Table 3) despite the proximity of many small colonies (Figure 1). Thus, sociable weavers maintained a preference for the colony-size class they used at time t even when changing physical sites at time $t + 1$; this preference was particularly strong for birds in small colonies.

We also examined whether natal-colony size affected the dispersal decisions of birds during their first year and thus asked whether birds might be using different decision rules in their first year than those used in later years. For this analysis, we used the sample of all birds first banded as juveniles, and classified their natal and subsequent breeding colonies into the three size classes described above (but we could not also model site-usage history because of sparseness of data). There would be age dependence in the movement probabilities if the birds' first choice of breeding-colony size differed from later choices they made as breeders. However, we found no evidence of any age dependence in movement probabilities. Multistate models with an age effect on movement were markedly poorer fits to the data than models with a simple colony-size effect (Table 4), owing mainly to the extra parameters required and no improvement in fit. We thus conclude that sociable weavers' movement probabilities during their first season were not different from their subsequent movement probabilities, although our power to detect any age-related difference was limited.

DISCUSSION

This study is the first to estimate survival and movement probability explicitly in relation to colony size for any species.

Table 3

Between-season movement (transition) probabilities (± SE) for sociable weavers from small, medium, and large colonies (S, M, L) that used a colony site they had not been known to use the previous breeding season ("first-time site," denoted by $_f$) and that occupied the same site they were known to have used the previous breeding season ("previous-use site," denoted by $_r$)

	To first-time site			To previous-use site		
From	Small (S_f)	Medium (M_f)	Large (L_f)	Small (S_r)	Medium (M_r)	Large (L_r)
Small, first-time site (S_f)	**0.038** ± 0.082	**0.026** ± 0.018	**0.051** ± 0.034	0.719 ± 0.056	0.166 ± 0.046	0.000 ± 0.000
Medium, first-time site (M_f)	**0.027** ± 0.019	**0.022** ± 0.031	**0.000** ± 0.000	0.000 ± 0.000	0.951 ± 0.024	0.000 ± 0.000
Large, first-time site (L_f)	**0.000** ± 0.000	**0.000** ± 0.000	**0.048** ± 0.052	0.000 ± 0.000	0.077 ± 0.032	0.875 ± 0.041
Small, previous-use site (S_r)	**0.536** ± 0.084	**0.000** ± 0.000	**0.000** ± 0.000	0.464 ± 0.084	0.000 ± 0.000	0.000 ± 0.000
Medium, previous-use site (M_r)	**0.203** ± 0.056	**0.414** ± 0.099	**0.073** ± 0.054	0.000 ± 0.000	0.310 ± 0.126	0.000 ± 0.000
Large, previous-use site (L_r)	**0.000** ± 0.000	**0.294** ± 0.074	**0.367** ± 0.091	0.000 ± 0.000	0.000 ± 0.000	0.339 ± 0.117

Colony-size classes are defined in the text. Movement probabilities were estimated by using model 10 in Table 2. Those in bold show transition probabilities for birds moving to a site different from the one they used the previous season, and those not in bold are probabilities for birds remaining at the same colony site. Each transition is theoretically possible, because sites can change in size between breeding periods.

Both were influenced by colony size, although movement probabilities were more strongly affected. For survival, both natal-colony size and breeding-colony size apparently had only weak effects. However, in each case, it appeared that survival varied positively with colony size, with both breeders and the birds raised in the largest colonies showing higher probabilities of survival. Movement probabilities illustrated that individuals preferred colonies of particular sizes, even when controlling for site-usage history. We found little evidence of time or age dependence in our analyses in general, suggesting that colony-size effects tended not to vary with breeding period or age. In the case of time dependence, this might have reflected our not having enough data over time to model time effects rigorously, given the increased numbers of parameters that must be estimated in time-dependent models. Alternatively, it could have been that colony-size effects in sociable weavers were of sufficient magnitude to mask any annual variation in ecological conditions.

Table 4

Models to assess the effect of age on movement probabilities in sociable weavers for birds first banded as juveniles

Model	AIC_c	AIC_c weight[a]	Number of estimable parameters	Deviance
(18) ϕ, $p_{cc3 \cdot t}$, ψ_{cc3}	1038.7	0.371	28	200.2
(19) ϕ_{a2}, $p_{cc3 \cdot t}$, ψ_{cc3}	1040.0	0.200	29	199.2
(20) ϕ_{cc3}, $p_{cc3 \cdot t}$, ψ_{cc3}	1041.8	0.081	30	198.7
(21) ϕ, $p_{cc3 \cdot t}$, ψ	1044.7	0.019	23	217.2
(22) ϕ, $p_{cc3 \cdot t}$, ψ_{a2}	1046.8	0.006	24	217.2
(23) ϕ_{a2}, $p_{cc3 \cdot t}$, ψ_{a2}	1048.7	0.003	25	216.8
(24) ϕ, $p_{cc3 \cdot t}$, $\psi_{cc3 \cdot a2}$	1050.7	0.001	34	198.5
(25) ϕ_{a2}, $p_{cc3 \cdot t}$, $\psi_{cc3 \cdot a2}$	1052.1	0.000	35	197.6
(26) ϕ_{cc3}, $p_{cc3 \cdot t}$, $\psi_{cc3 \cdot a2}$	1053.9	0.000	36	197.1
(27) $\phi_{cc3 \cdot a2}$, $p_{cc3 \cdot t}$, $\psi_{cc3 \cdot a2}$	1057.3	0.000	39	193.4

Some models contained an effect of colony-size class (subscript cc3), which represented the natal-colony size at the time of banding and breeding-colony size at later encounters. Colony-size classes are defined in the text. The age classes used were the first year and all older ages combined. The data set was not large enough to model an effect of site-usage history.

[a] Weights do not sum to 1.000 because some models tried are not presented here.

Colony size and survival

Any increase in survival associated with larger natal colonies was likely brought about by benefits to fledglings from living in large groups. Larger colony sizes in sociable weavers tend to have a negative effect on fledging mass, at least in some years (Covas R and Doutrelant C, unpublished data; Marsden, 1999), so the enhanced postfledging survival of birds that hatched at large colonies cannot be owing to advantages experienced during the nestling phase. However, the postfledging period is a particularly critical time when, for example, the young birds need to learn how to forage and avoid predators. Predation by Gabar goshawks (*Micronisus gabar*) is a survival risk for this species (Covas R and Anderson MD, personal observation; Maclean, 1973; Marsden, 1999), and it is likely that larger groups provide extra protection through increased vigilance. We noticed, for example, that goshawks could sometimes catch single weavers immediately upon release from our mist nets, whereas they rarely captured birds when we released them as a group.

In addition, there may be thermal benefits of large colonies that influence survival of adults and juveniles. The large multicompartmented nest is thought to be important in helping sociable weavers to thermoregulate during cold winter nights in the Kalahari region (Marsden, 1999; White et al., 1975; Williams and du Plessis, 1996). Other analyses (Covas R, Brown CR, Anderson MD, and Brown MB, unpublished data) show that weaver survival can be higher when winter temperatures are warmer, implying that these small birds are indeed sensitive to the thermal environment. Because the colony sites are occupied year-round in most cases, large colonies may be particularly advantageous during cold winters when the large nest allows the birds to stay warmer.

Survival rates also reflect the costs of occupying groups of a given size. Some of the potential costs of coloniality for sociable weavers include increased parasite load, food depletion around the colonies, and higher nest predation rates. Adult sociable weavers at larger colonies had significantly greater ectoparasite loads in a study in Namibia (Marsden, 1999). Lower fledging weights in larger colonies in some years (Marsden, 1999; Covas R and Doutrelant C, unpublished data) suggest that food depletion might increase with colony size, and food depletion around colonies is probably common in colonial birds in general (Brown and Brown 1996, 2001a). Larger sociable weaver colonies may also attract more predators; nest predation was higher at larger colonies in Namibia (Marsden, 1999). Although the cost of nest predation in terms of adult survival is not clear, in Marsden's

(1999) study, nests in larger colonies had a greater per capita risk of predation, primarily by snakes, than those in small colonies. Our analyses, however, suggest that all of these costs of coloniality are either not important or are balanced by benefits of colonial nesting in sociable weavers.

If we assume that the colony-size effects described by models 2 (Table 1) and 10 (Table 2) are real, even these relatively small differences in annual survival probabilities for sociable weavers translate into relatively large effects on lifespan. For example, the variation in natal colony size in our population led to an estimated range in survival probabilities of 0.62–0.71. Converting these survival probabilities into mean lifespan with the formula of Brownie et al. (1985: 208), there is a difference of almost 10 months (or about 39%) in mean lifespan for birds raised in the smallest versus largest colonies. The increase in adult survival probabilities for birds living in the large colonies (0.66–0.75) translates into an increase of over 1 year (or about 45%) in mean lifespan. Because sociable weaver breeding seasons are unpredictable and sometimes closely spaced in time, an increase of only a few months in average survival can in some situations lead to an individual's surviving to an additional breeding period and thus potentially greatly increasing its lifetime reproductive success. For small passerines such as sociable weavers, even minor differences in survival tend to result in relatively large fitness gains (see Bryant, 1988; McCleery and Perrins, 1988; Newton, 1989; Smith, 1988; van Noordwijk and van Balen, 1988). We should not discount small apparent differences in survival, even when models suggesting these differences are not unambiguously the best (as in this study). Small but meaningful differences in survival will usually be difficult to detect statistically, because survival may often vary over time and only "average" survival probability is constant. Thus, in general, sampling error and annual variability can hamper our ability to "prove" differences among classes of individuals.

These results on survival complement those studies using annual reproductive success to infer the net fitness effect of different group sizes. Many studies on colonial birds have not found strong effects of colony size on reproductive success (Brown and Brown, 2001a), and at least statistically speaking, we did not find a strong effect of colony size on survival. The consequence may be relatively equivalent fitness for individuals in groups of different sizes. This pattern is thought to result from tradeoffs between costs and benefits in some species (Brown and Brown, 1996). The range in colony sizes seen in sociable weavers and other species may be maintained whenever no one group size confers a reproductive advantage over another. We emphasize, however, that complete estimates of fitness are not yet available for birds occupying colonies of different sizes in our population, and we thus do not know whether the costs and benefits associated with colonies of different sizes affect weavers in all colonies in the same way or to the same degree.

Colony size and movement

Movement probabilities, in which an animal's likelihood of moving from one site to another is estimated, can be useful in developing management strategies (Spendelow et al. 1995) and in understanding metapopulation biology. Unfortunately, essentially no studies have used multistate statistical methods (e.g., with distance from initial capture site as a continuous covariate) to generate quantitative estimates of dispersal, despite the need for unbiased, quantitative measures of movement in animal populations (Koenig et al., 1996). Among colonial species, movement probabilities may also reflect colony choice and provide relative measures of how

likely an individual occupying one colony (perhaps of a particular size) is to move to another colony. In some species, colony settlement decisions are based on a moderate degree of heritable variation in social-group preference (Brown and Brown, 2000; Møller, 2002), and thus, colony choice may reflect the attributes of (and the expected payoffs for) individuals settling at different colony sites.

Sociable weavers show strong between-year fidelity to both the colony size and the colony site they used the previous year. The probabilities of birds staying at the same colony location, irrespective of colony size, from breeding period to breeding period were relatively high, ranging from 0.310–0.951 depending on the class of individuals considered (Table 3). However, the most striking result was the between-year fidelity to breeding-colony size class shown by birds that moved between colony sites. For all classes of colony size, dispersing birds were more likely to settle in a colony of size similar to the one they had occupied the previous year. Strong fidelity to particular colony sizes could come about if the birds are sensitive to colony size in making settlement decisions, as in cliff swallows (*Petrochelidon pyrrhonota*; Brown and Brown, 2000), and actively choose the colony size to which they are behaviorally or physiologically best suited. Our data are consistent with the hypothesis, for which data are accumulating in a variety of species (Brown and Brown, 1996, 2001a), that variation in colony size reflects phenotypic sorting of individuals into colonies of different sizes and that variation in colony size is maintained by individuals' preferences for groups of particular sizes. Sociable weavers in this study, and cliff swallows and barn swallows (*Hirundo rustica*) in Brown and Brown's (2000) and Møller's (2002) cross-fostering experiments, are the only species for which site choice based on colony size has so far been demonstrated.

One caveat is in order. Demonstrating a greater likelihood of a bird using a colony of a particular size class does not necessarily rule out random choice of sites. Depending on how colonies of different sizes are distributed in space (Figure 1), dispersing individuals could be more likely to use a given colony size simply because they are more likely to encounter sites with colonies of that size. This is a difficult problem to resolve, requiring simulations to ascertain the expected multistate movement probabilities under the assumption of random (or other spatially-dependent) movement rules. These sorts of simulations have not been done for any species to our knowledge. However, regardless of whether movement contains a random component, in sociable weavers, colony settlement results in birds tending to remain in colonies of similar size between years.

In the absence of similar multistate movement estimates for other colonial birds, direct comparison to other species is difficult; however, the relatively low probabilities of movement of birds between colonies of different sizes suggest that each colony-size class is relatively closed with respect to emigration and immigration. One consequence can be higher levels of within-colony relatedness in the smaller colonies (Brown and Brown, 2001b). Preliminary results from Namibia suggest a greater degree of within-colony relatedness among males in sociable weavers (Marsden, 1999). Our observation that birds dispersing between colonies are often females (Anderson MD and Covas R, unpublished data) and the colony-size-specific movement probabilities reported here are consistent with higher levels of relatedness in smaller colonies.

Multistate models and studies of coloniality

Although still seldom used, the application of multistate methods has great promise for evolutionary ecology, being the only way to examine how an individual's changing attributes

sequentially affect its probability of survival or movement. The principal limitation of multistate analysis at present is the large number of parameters that are generated in any meaningful model and the large amount of data needed to test such heavily parameterized models. One consequence is that researchers often must restrict their analyses to relatively simple models that contain manageable numbers of parameters. However, even when this is done, as we had to in our study, the resulting parameter estimates can yield unexpected insight and reveal information about fitness components that would not have been possible from more traditional studies on particular aspects of coloniality. We would not have predicted the positive effect of colony size on juvenile and adult survival in sociable weavers using measures of fledging success or from behavioral observations alone (see Marsden, 1999). Similarly, the multistate movement probabilities that separated the effects of site and size may be a viable alternative to more laborious cross-fostering experiments (see Brown and Brown, 2000; Møller, 2002) in studying colony choice in some species. We urge increasing use of multistate methods, as they should add considerably to our ability to measure reproductive success in colonial birds, now regarded as a priority for future studies of coloniality (Brown and Brown, 1996, 2001a; Danchin and Wagner, 1997).

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