JUVENILE AND ADULT SURVIVAL IN THE SOCIABLE WEAVER (*PHILETAIRUS SOCIUS*), A SOUTHERN-TEMPERATE COLONIAL COOPERATIVE BREEDER IN AFRICA

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Abstract.—We used capture–recapture analyses to describe juvenile and adult survival from 1993 to 2001 in a population of Sociable Weavers (*Philetairus socius*), a colonial, cooperatively breeding passerine of southern Africa. We examined temporal variation in survival and the role that the breeding season's length and environmental factors play in determining survival patterns in the population. Annual survival probability (mean ± SE) was 0.66 ± 0.02. In contrast to most passerines, juveniles and adults had similar survival probabilities; survival rates did not vary significantly between years. We found no relationship among temperature, rainfall, and survival. Relatively high survival rates in Sociable Weavers probably result from a benign climate and easy access to food in winter. Juvenile survival may also be enhanced by prolonged parental care and delayed dispersal. *Received 1 April 2003, accepted 24 June 2004.*

Resumen.—Utilizamos análisis de captura y recaptura para describir la supervivencia de juveniles y adultos entre 1993 y 2001 en una población de *Philetairus socius,* una especie de ave paserina colonial con cría cooperativa del sur de África. Examinamos la variación temporal en la supervivencia, y la importancia de la longitud del período de apareamiento y de los factores ambientales para la supervivencia de los individuos de la población. La probabilidad de supervivencia anual (media ± EE) fue de 0.66 ± 0.02. En contraste con la mayoría de los Passeriformes, los individuos juveniles y adultos mostraron probabilidades de supervivencia similares, y las tasas de supervivencia no variaron significativamente entre años. No encontramos relación alguna entre la temperatura, la cantidad de lluvia y la supervivencia. La relativamente alta probabilidad de supervivencia observada se encuentra probablemente relacionada con un clima benigno y fácil acceso al alimento durante el invierno. La supervivencia de los juveniles puede además estar influenciada positivamente por un período de cuidado parental prolongado y por la dispersión retardada de las crías.

Comparative study of life-history evolution requires knowing how survival varies with age and environmental conditions (Stearns 1992, Charlesworth 1994). Studying survival, however, is often difficult, because individuals must be marked and monitored for multiple years. In birds, we know especially little about annual survival rates of populations in the tropics and the Southern Hemisphere, where relatively few long-term population studies have been conducted. Because birds in southern regions generally have smaller clutches, longer developmental periods, and higher adult survival than their northern-temperate counterparts (Rowley and Russell 1991, Martin 1996, Ghalambor and Martin 2001), parents may invest more energy in fewer young (Williams 1966, Martin 1996, Russell 2000). As a result, juvenile (i.e. post-fledging) survival may be higher at southern latitudes than in more temperate locations (Martin 1996, Martin et al. 2000, Russell 2000).

Recent work has shown that adult survival in some southern populations is higher than in similar taxa in northern-temperate regions (Johnston et al. 1997, Ghalambor and Martin 2001, Peach et al. 2001). How survival at southern latitudes varies between years and how it may be affected by environmental factors is largely unknown. Passerine survival can be affected by food availability (Jansson et al. 1981, Newton 1998) and winter severity (McNamara and Houston 1990,

Cuthill and Houston 1997). However, most tropical and southern-temperate regions experience mild winters—which probably support relatively high food levels (Oatley 1982, Rowley and Russell 1991)—and less extreme weather conditions than more northerly areas. Knowing how survival of southern-temperate species is affected by food availability and weather conditions would help in understanding the mechanisms that regulate survival at southern latitudes.

Here, we investigate juvenile and adult survival in the Sociable Weaver (*Philetairus socius*), a colonial cooperative passerine endemic to the semi-arid savannas of southern Africa. The latitudinal trend in avian life histories predicts higher adult survival in Sociable Weavers than in most northern-temperate passerines. High juvenile survival should also occur because—besides benefiting from factors that might increase adult survival—young in this sedentary species receive extended parental care and remain in the natal colony for at least four months (Covas 2002, R. Covas and C. Doutrelant unpubl. data). Sociable Weavers are suitable for study of environmental factors and survival because they inhabit a highly fluctuating environment, where rainfall, which is variable and often low, is the main determinant of food availability and reproductive effort (Maclean 1973c, Lloyd 1999). In our study area, winters are usually sunny, with mild daytime temperatures. However, night-time temperatures can drop to several degrees below zero, representing a potential cost in terms of thermoregulation (White et al. 1975, du Plessis and Williams 1994). The present study aims to (1) estimate juvenile and adult survival in the Sociable Weaver and (2) investigate temporal variation in survival—in particular, how survival is affected by winter temperature, rainfall, and duration of the breeding season.

METHODS

Study site.—The study was conducted at Benfontein Game Farm, situated ~6 km southeast of Kimberley, in the Northern Cape Province, South Africa (~28°53′S, 24°89′E). Vegetation consists of open savanna and is dominated by *Stipagrostis* grasses and camelthorn tree (*Acacia erioloba*). Study area is semi-arid, experiencing low and unpredictable rainfall (average 431 ± 127 mm year^{-1}; Weather Bureau, Pretoria), with most of the precipitation falling during the summer months from September to April. Daily temperature ranges are

typically high, with hot days and cool–warm nights from October to March (approximately 8–40°C) and mild days and very cold nights from May to September (approximately –8 to 25°C)

Study species.—The Sociable Weaver is endemic to southern Africa, with its distribution centered in the Northern Cape and Namibia in strong association with southern Kalahari vegetation (Maclean 1973a; Mendelsohn and Anderson 1997). Sociable Weavers weigh between 26 and 32 g, and sexes are indistinguishable in the field. Sociable Weavers feed predominantly on insects, but also on seeds and other plant products (Maclean 1973d). Colonial cooperative breeders, they show great variation in colony size (2–500 individuals per colony; Maclean 1973b) and in number of helpers attending a brood (up to nine helpers per brood; Maclean 1973c). Sociable Weavers build a huge nest (1–4 m wide) with separate chambers in which a pair (with their offspring or other birds) roost and breed. The nest is built on a variety of sturdy structures, from *Acacia* trees to telephone poles (Maclean 1973b, Mendelsohn and Anderson 1997). At Benfontein, nests are constructed on *Acacia erioloba* trees or, occasionally, on *A. tortilis*. The colony can remain active for several decades, being occupied by successive generations of birds, which continually add to the structure (Maclean 1973b).

Sociable Weavers breed aseasonally in response to rainfall (Maclean 1973c). Rainfall is also a major determinant of duration of the breeding period, number of broods (1–8), and clutch size (2–6; Maclean 1973c). In our study area, Sociable Weavers usually start breeding in September or October, and the breeding season can last between three and nine months (Covas et al. 2002).

Field methods.—From August 1993 to November 2000, we conducted a capture–mark–recapture study at Benfontein. The study area contained 25 Sociable Weaver colonies. At 16–18 of those colonies, residents were captured twice a year. During the first five years, the capture effort was distributed throughout the year (capturing the birds in 1–2 colonies each month). Beginning in mid-1998, we concentrated our capture efforts during 1–2 consecutive months at the beginning and end of the breeding period. Birds were captured with mist nets placed around the nesting tree before dawn. 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 most individuals present were caught. 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. Birds were marked with a unique numbered ring from the South African Bird Ringing Unit (SAFRING) and, in recent years, with an additional individual color-combination. Juvenile birds molt into adult plumage when they are approximately four months old; before that, their age

can be estimated through the development of a black patch on the face and throat (Maclean 1973c, R. Covas unpubl. data).

During the first five years of the study, the breeding activity of the birds was not directly monitored. To determine when the breeding season took place, we used development of the black patch on captured juveniles to estimate month of hatching. Presence or absence of a brood patch also provided an indication of the breeding season. In total, we considered eight breeding periods (there was no breeding activity in the summer of 1994–1995): August 1993 (beginning of the study), October 1993 to April 1994, October 1995 to April 1996, October 1996 to March 1997, June 1997 to May 1998 (no capture during that period), October 1998 to January 1999, September 1999 to May 2000, and September 2000 to January 2001.

Statistical methods.—We estimated annual survival probabilities and tested hypotheses using the general methods of Lebreton et al. (1992) and Burnham and Anderson (2002). We used MARK (Cooch and White 1998, White and Burnham 1999) to generate maximum-likelihood estimates of survival and recapture probabilities. A software package that computes survival and recapture parameters using encounter histories of individually marked birds, MARK compares and tests the fit of different statistical models, allowing one to evaluate the plausibility of different biological hypotheses (Lebreton et al. 1992).

We use the general notation of Lebreton et al. (1992), in which annual survival probability is denoted as ϕ and recapture probability as p. Subscripts indicate whether parameters in a model are time-dependent (e.g. ϕ_{time}, p_{time}), vary with age (and if so, with how many age classes; for example, ϕ_{age2}, p_{age2} for two age classes), are constant over time (e.g. $\phi_{constant}$, $p_{constant}$), are group-specific (e.g. ϕ_{group}, p_{group}), or describe an interaction between group and time (e.g. $\phi_{group\times time}$, $p_{group\times time}$).

We compared the fit of competing models with the Akaike Information Criterion (AIC; Akaike 1973, Lebreton et al. 1992, Burnham and Anderson 2002) corrected for sample size (AIC_c) 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 criterion used to select among competing models; the currently accepted convention (Burnham and Anderson 2002) is that models with AIC_c that differ by <2 are indistinguishable in terms of their fit to the data. We also present normalized AIC_c weights, a measure of a model's relative probability of being the best model for the data as compared with alternative models (Burnham and Anderson 2002). We assessed potential differences in survival among groups of birds (e.g. age classes) by comparing various models, some of which modeled the effect of each group, whereas others considered the groups as a common pool. If a model with a group effect provided a better

fit (judging by AIC_c values and weights) than one without it, survival was considered to differ among the groups. We devised a candidate set of models *a priori* that tested legitimate survival hypotheses, and those are the ones presented in the tables. Number of estimable parameters in our models was provided by MARK on the basis of the chosen model structure and statistical information provided by our data.

Before comparing the fit of the candidate set of models, we performed a goodness-of-fit test for each dataset, using RELEASE (Burnham et al. 1987). That program evaluated how well the data met variance assumptions inherent in the binomial distribution used in mark–recapture analysis. When a data set does not meet the assumptions, it is usually because the data are overdispersed, reflecting lack of independence or some heterogeneity among observations and often brought about by the presence of transients or trap-dependence. We assessed goodness-of-fit by first calculating a combined chi-square value on the basis of tests 3m, 2ct, and 2cl in RELEASE. That subset of tests can incorporate age-dependence in determining goodness-of-fit (Pradel et al. 2004); our most highly parameterized models (for which goodness-of-fit was assessed) all contained age-dependence. The total chi-square value allowed estimation of a variance inflation factor, ĉ, as chi-square divided by degrees of freedom (χ^2/df). The ĉ value was used in MARK to adjust the AIC_c through quasi-likelihood, resulting in a $QAIC_c$ whenever ĉ departed from 1.0. In our case, model selection and parameter estimation was based on the model with the lowest $QAIC_c$ value as described above for AIC_c. That variance inflation adjustment allowed use of data that departed from the assumptions of the binomial distribution. In such cases, after adjustment, maximum likelihood can still provide optimal point estimators of model parameters (Wedderburn 1974, Burnham and Anderson 2002).

Because Sociable Weavers are unpredictable, aseasonal breeders, time intervals in-between our capture occasions were not constant (see above). Each interval was defined as time from the start of the nonbreeding period until the end of the successive breeding period. Thus, as in most mark–recapture studies, the breeding season was considered to take place in an instant in time, with zero mortality during that breeding season. For the eight capture occasions, corresponding to the eight breeding periods that occurred between July 1993 and January 2001, the intervening intervals consisted of 0.67, 2, 0.92, 1.2, 0.58, 1.4, and 0.67 years. However, we standardized all survival estimates to intervals of 1 year, using the set-time-intervals utility in MARK. That made all survival probabilities comparable (and consistent with other studies), being estimated for a period of the same length. Program MARK uses the actual time interval as an exponent of the estimated survival probability to correct for the length of the time interval. Although some birds were

caught during nonbreeding periods, those captures were not used in constructing individual encounter histories; a bird had to be caught during a breeding period to be designated as surviving to that period.

Because of the variation in length of intervals between breeding periods, we checked to see if those different intervals might have affected our survival estimates. We compared the best-fitting time-dependent model (model 2; Table 1) with a structurally similar model that had survival linearly constrained on the length of the breeding season (using the log-link function in MARK). The model with an effect of breeding-season length had a QAIC$_c$ that was only 0.25 less than that for model 2, which indicates that it did not provide a better fit to our data. For that reason, and also because we found no strong effect of time in our analyses (below), we conclude that the differing breeding-season lengths did not affect our results or conclusions.

Juveniles were birds younger than four months upon initial capture, and adults those with a fully developed black throat-patch (older than four months). Juveniles were caught at different ages; we initially assigned each individual to one of four classes based on its approximate age upon first capture: 24–40 days old, 40–60 days old, 60–90 days old, and 90–120 days old. To determine if survival may have varied across birds in the different age classes, we compared a model that treated each age class as the same ($\phi_{constant}$, p_{time}; model 10; Table 2) with one that treated each age class as a separate group (ϕ_{group4}, p_{time}). The one treating all juveniles the same regardless of age at first capture was a much better fit to our data (QAIC$_c$ = 576.94, AIC$_c$ weight = 0.9347) than the one treating survival among the four age classes as different (AIC$_c$ = 582.26, AIC$_c$ weight = 0.0652). Thus, all juveniles were pooled for analysis, regardless of age at first capture.

We tested for survival differences between juveniles and adults in two ways. (1) We treated birds banded as adults and those banded as juveniles as separate groups, with first-year survival of juveniles constant but different from all other cohorts; yearly survival of adults and juveniles in their later years was otherwise modeled as the same. That approach also tested for other differences among birds marked as adults versus those marked as juveniles, such as a greater proportion of transients in one age class. Such analysis used the entire data set, with all those banded as adults designated as one group and those banded as juveniles designated as the second group (models 3 and 8; Table 1). (2) We then repeated the age analysis using only juveniles (known-age birds) and modeled first-year versus later-year survival for that set of birds (models 11 and 13; Table 2).

Total summer rainfall (October–March) and minimum and average winter temperatures (May–August) were modeled as linear constraints on survival, using the log-link function in MARK. Winter temperature was chosen because passerines are often vulnerable to food shortage brought about by climatic severity during winter (e.g. Newton 1998). Weather data were obtained from the Weather Bureau, Pretoria, South Africa.

Results

Goodness-of-fit.—The variance inflation factor, ĉ, was calculated as 2.41 for the full data set and 1.69 for the subset of birds first banded as juveniles. We thus used quasi-likelihood (e.g. QAICc) for survival estimation and model fitting. The lack of fit was caused principally by trap-dependence among birds banded as adults (RELEASE test 2ct; χ^2 = 24.56, df = 5, P < 0.001). There may also have

Table 1. Models to assess effects of period ($_{time}$), minimum ($_{mintemp}$) and average ($_{avgtemp}$) winter temperatures, and rainfall ($_{rain}$) on survival and recapture probabilities in Sociable Weavers, using all data (n = 1,486 birds). Birds first banded as adults and as juveniles were treated as separate groups ($_{group2}$) in some models; first-year survival of juveniles were treated as separate ($_{age2}$) in others. All models, except (9), had full time-dependence in recapture probability.

Model	QAIC$_c$	ΔQAIC$_c$	QAIC$_c$ weight	Number of estimable parameters
(1) $\phi_{constant}$, p_{time}	1226.9	0.0	0.4608	8
(2) $\phi_{time,modified}$, p_{time} [a]	1228.9	2.0	0.1760	10
(3) $\phi_{group2age2}$, p_{time}	1229.0	2.1	0.1693	9
(4) $\phi_{mintemp}$, p_{time}	1229.9	3.0	0.1022	11
(5) $\phi_{avgtemp}$, p_{time}	1232.0	5.1	0.0371	12
(6) ϕ_{time}, p_{time} [a]	1232.2	5.3	0.0367	12
(7) ϕ_{rain}, p_{time}	1233.2	6.3	0.0199	11
(8) $\phi_{time \times group2age2}$, p_{time}	1255.8	28.9	0.0000	13
(9) $\phi_{constant}$, $p_{constant}$	1443.2	216.2	0.0000	2

[a] In model (6), survival varied with each period (full time-dependence); whereas model (2) treated the first, fourth, and fifth breeding periods as the same, and the remaining ones as separate.

TABLE 2. Models to assess effects of age on survival and recapture probabilities in Sociable Weavers using only the subset of birds first banded as juveniles ($n = 473$ birds). The two age classes used were the first year and all older ages ($_{age2}$), and time-dependent models ($_{time}$) treated all periods as separate. All models with an effect of time ($_{time}$) for either survival or recapture were fully time-dependent.

Model	QAIC$_c$	ΔQAIC$_c$	QAIC$_c$ weight	Number of estimable parameters
(10) $\phi_{constant}$, p_{time}	576.9	0.0	0.8566	8
(11) ϕ_{age2}, p_{time}	581.1	4.2	0.1089	9
(12) ϕ_{time}, p_{time}	583.4	6.5	0.0343	12
(13) $\phi_{time \times age2}$, p_{time}	593.1	16.2	0.0003	17
(14) ϕ_{time}, $p_{constant}$	633.5	56.6	0.0000	8
(15) $\phi_{constant}$, $p_{constant}$	662.0	85.1	0.0000	2

been some trap-dependence among birds marked as juveniles (test 2ct; $\chi^2 = 8.14$, df = 4, $P = 0.09$).

Effect of time.—Our data set consisted of 1,013 adults and 473 juveniles. Of those, 348 adults (34.4%) and 173 juveniles (36.6%) were recaptured during at least one subsequent breeding period. There was no strong effect of time (i.e. interval between breeding periods) on survival probabilities in Sociable Weavers (Table 1). A fully time-dependent model (model 6; Table 1) was a poorer fit to our data than one with survival constant across all time periods (model 1; Table 1). A model in which survival was treated as the same for the first, fourth, and fifth breeding periods and separately for the remaining ones (model 2; Table 1) was a better fit than the fully time-dependent one (model 6; Table 1); but even the modified time-dependent model did not provide a better fit than one with constant survival (model 1; Table 1). The time-constant model was 12.5× more likely than the fully time-dependent one and 2.6× more likely than the modified time-dependent model, as judged from QAIC$_c$ weights (Table 1).

We found a similar result when confining the analysis to only known-age birds (those first banded as juveniles). A model without an effect of time (model 10; Table 2) was 25× more likely than a similar model with time-dependence (model 12). Recapture probabilities did vary with time, however (Tables 1 and 2); all models with constant recapture probabilities (e.g. models 9, 14, and 15) had substantially worse fit. That is consistent with the fact that our field effort varied between different periods.

Model 1 (Table 1) was used to derive the average annual-survival probability using the total data set ($n = 1,486$ birds), which yielded an annual survival probability (mean ± SE)

of 0.662 ± 0.019 for Sociable Weavers in the Kimberley population. Recapture probabilities (mean ± SE) estimated from that model were 0.600 ± 0.057, 0.476 ± 0.064, 0.144 ± 0.030, 0, 0.106 ± 0.035, 0.827 ± 0.073, and 0.596 ± 0.047, respectively, for the seven intervals between the observed breeding periods.

Effects of winter temperature and rainfall.—There was little evidence that Sociable Weaver survival was affected by either temperature or rainfall in winter. A model with minimum winter temperature as a linear constraint on survival (model 4; Table 1) did not fit as well as one without an effect of temperature (model 1). Similarly, a model using average winter temperature as a constraint on survival (model 5; Table 1) was far less plausible than one without an effect, and a model with an effect of rainfall (model 7; Table 1) was even less likely.

Effects of age.—We found little evidence that survival differed between adult and juvenile Sociable Weavers. A model treating birds banded as adults and juveniles as separate groups, with first-year survival of the juvenile group different from that of older classes (model 3; Table 1), was less plausible than the more parsimonious model without an age effect that treated the groups the same (model 1). Similarly, using only the subset of known-age juvenile birds ($n = 473$), a model with constant survival across time and age (model 10; Table 2) was the best fit. In the case of the full data set (Table 1) and the known-age subsample (Table 2), the best-fitting model without an age effect was 2.7× and 7.9× more likely, respectively, than the next best one that included an age effect, based on the QAIC$_c$ weights. Using only the known-age birds, model $\phi_{constant}$, p_{time} (model 10; Table 2) estimated average (mean ± SE) annual-survival probability of Sociable Weavers

as 0.659 ± 0.028, which is similar to the estimate from the total data set.

Discussion

Adult and juvenile survival.—We found relatively high adult and juvenile survival in the Sociable Weaver. The annual survival estimate obtained for our population (0.66) was higher than estimates for European passerine populations, which are mostly around or below 0.5 (Sæther 1989, Peach et al. 2001); but it was lower than some estimates obtained for other southern African passerines by Peach et al. (2001). However, our estimate may be an underestimate, if there is any permanent dispersal away from the study area. As in virtually any survival study of an open population using recaptures or resightings, permanent emigration is confounded with mortality, leading to underestimates of true survival (Cilimburg et al. 2002). That might be particularly true for some weaver species in southern Africa, which were found to have higher tendency for dispersal than other passerines (Peach et al. 2001). Thus, our results are better termed "apparent" or "local" survival. Still, Sociable Weavers in and around Kimberley appear to be highly sedentary. Of 164 individuals ringed in the nest and recaptured one year later, only 6% had moved to another colony (Covas 2002). The trend is similar when also considering the adult population: only 6.9% of the birds ringed (n = 2,094) were recaptured at other colonies (Covas et al. 2002). Moreover, we monitored 18 colonies out of 25; thus, many of the birds that dispersed were recaptured.

The most unusual result was the finding that juvenile survival was the same as that of adults. Juvenile survival in small birds is often thought to be about half the adult survival rate (e.g. Gill 1995; cf. Baillie and McCulloch 1993), though that generalization is based mostly on studies of northern-temperate species and relatively few studies have estimated juvenile survival in songbirds using mark–recapture statistics. Postfledging survival at southern latitudes is not well studied, but work on cooperatively breeding passerine species from Australia and South America (though not based on mark–recapture statistics) reported first year survival probabilities ranging from 0.35 to 0.76 (Stacey and Koenig 1990, Rowley and Russell 1991). In some of those studies (e.g. *Campylorhyncus*

wrens; Rabenold 1990), first-year survival estimates overlapped with adult estimates, which suggests that our result could be found in other species.

The relatively high juvenile survival reported here could be related to prolonged parental care and delayed dispersal. Young Sociable Weavers can be fed for up to six weeks after fledging, which may enhance survival by reducing risks taken during development of foraging skills (Langen 2000, Russell 2000; cf. Sullivan 1989). Delayed dispersal was shown to promote juvenile survival in Siberian Jays (*Perisoreus infaustus*; Ekman et al. 2000) and Brown Thornbills (*Acanthiza pusilla*; Green and Cockburn 2001). In a study conducted over three breeding seasons and involving intensive color-banding of nestlings, young Sociable Weavers never left the natal colony in their first four months of life and seldom did so in their first year (Covas 2002). Spending that period in the company of parents or helpers and communally roosting in the nest chamber is likely to provide extra protection from potential causes of mortality, such as predators and cold nights. Still, it is possible that the apparently higher juvenile survival for species with delayed dispersal is a spurious result, because in these species local survival estimates approach the true figure, which would not happen in species with higher juvenile dispersal.

The relatively high juvenile survival in Sociable Weavers could also appear to have resulted because we measured survival for some juveniles that, when first marked, were up to 120 days old. That could lead to inflated survival estimates if we had missed a period just after fledging when mortality could have been higher. That seems unlikely, however, because we found no differences in survival among juveniles first marked at different ages, from 24 to 120 days. The youngest birds were ones that had just fledged, and if there was a period of unusually high mortality just after fledging, we should have detected differences in survival among the juvenile age classes.

Interannual survival.—Our data indicated constant survival during the study period. That was unexpected, because arid environments are considered to be highly fluctuating. Moreover, several studies have reported temporal variation in survival of passerines (e.g. Newton 1998), though again that is mainly based on the study of northern-temperate species. Temporal variations

in survival are most commonly attributed to environmental fluctuations affecting food levels, exposure to bad weather, or density-dependent mechanisms. It seems, therefore, that the environmental variation experienced by our population does not place any obvious constraints on survival. In addition, survival in Sociable Weavers was not affected by variation in reproductive effort, as measured by duration of the breeding season (which varied from one year when no breeding activity was detected to a continuous nine-month breeding season). That result is interesting, because it is contrary to the predominant view of avian life histories, which suggests that survival is mainly a consequence of reproductive effort through the reproduction–survival trade-off (e.g. Lack 1968, Martin 1987, Stearns 1992). Hence, contrary to our findings, survival should have decreased after years of prolonged breeding activity. Of course, a problem with correlative studies such as the present one is that the probability of detecting reproductive costs based on natural variation is low, if individuals adjust reproductive effort to environmental conditions. Therefore, further work is needed to establish the real relationship between reproductive effort and survival in this species.

Environmental factors.—Survival in Sociable Weavers did not seem to be affected strongly by winter temperature. Winter severity is often thought to be the main survival constraint for birds (e.g. Newton 1998), because persistent bad weather may decrease foraging opportunities (Cuthill and Houston 1997) and food availability (Jansson et al. 1981, Brittingham and Temple 1988, Newton 1998) or increase energetic demands for thermoregulation (McNamara and Houston 1990, Cuthill and Houston 1997). One of the main food sources for Sociable Weavers, the harvester termite (*Hodotermes mossambicus*; Maclean 1973d), increases its daily activity in winter when temperatures are cooler (Richardson 1985, R. Adam pers. comm.). Moreover, Sociable Weavers inhabit an area where winter days are usually sunny, with temperatures >15°C. Therefore, an effect of bad weather on foraging opportunities may be negligible. Hence, it is possible that variations in winter temperature do not play a significant role in limiting food availability in our study area. However, cold winter nights (that can reach –8°C), could affect survival through increased

energetic demands for thermoregulation. Still, the Sociable Weaver's nest mass and its habit of communal roosting help the birds cope with cold night-time temperatures by reducing the metabolic cost of thermoregulation (White et al. 1975).

That rainfall did not affect survival in the population was surprising, because rainfall, through its effect on insect abundance and production of seeds, is believed to be the main determinant of food availability in semi-arid regions (Maclean 1973c, Harrison et al. 1997, Lloyd 1999, Dean and Milton 2001), including our study area (M. Picker pers. comm.). Thus, our results contrast with studies on northern-temperate birds, in which food availability during winter has been shown to influence survival (Jansson et al. 1981, Brittingham and Temple 1988, Newton 1998). The absence of a rainfall effect suggests that, though food levels can vary greatly in the region, they do not represent an important constraint on survival. Relatively high food levels outside the breeding season have also been suggested as being responsible for high adult survival of birds in southern Africa (Peach et al. 2001) and Australia (Ford et al. 1988, Rowley and Russell 1991).

That we did not find significant effects of age, time, or environmental conditions on survival could indicate that our data set either was too small or had other characteristics (such as not enough recaptures) to enable a strong test of those effects. In classical statistical terms, this could be a case in which failure to reject a null hypothesis might not necessarily mean that the null hypothesis was supported. Whether this is a serious issue—both for our study and others—is unknown, because there is no sort of power analysis available for mark–recapture modeling. However, we note that our total sample size and percentage of individuals recaptured at least once were relatively large for studies of passerine survival, which suggests that the present study was at least as likely as most others to detect any effects on survival if they existed.

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