

THE EFFECTS OF SEX, AGE, AND SOCIAL STATUS ON ANNUAL SURVIVAL IN THE SPLENDID FAIRY-WREN

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Abstract. Survival is a critical life-history trait, and among cooperative breeders survival may be linked to the evolution of social organization. We used multi-state models in the program MARK to estimate apparent survival in the Splendid Fairy-wren (*Malurus splendens*), a cooperatively breeding species in which most pairs are assisted by male offspring from previous generations. We examined survival as it relates to sex, age, and social status (nestling, auxiliary, breeder), and quantified the probabilities of transition between social states. The best-supported model was one in which survival rates differed by social state, survival of auxiliaries and breeders varied annually in the same manner, and the effect of sex varied annually but influenced the survival rate of each group in the same manner. In both males and females overall survival estimates of auxiliaries were similar to those of breeders, whereas survival estimates of adult males were higher than those of females, although the effect of sex varied annually. The probability of transition between categories of social status varied in a manner expected for a cooperatively breeding species: nestling males were more likely than nestling females to become auxiliaries, whereas females were more likely to become breeders in the subsequent year. Similarly, among auxiliaries, females were more likely than males to become breeders. Survival of males being higher than that of females likely contributes to the male-biased sex ratio observed in adults of this species and, indirectly, the propensity of younger males to delay dispersal.

Key words: Australia, demography, survival, *Malurus splendens*, *Splendid Fairy-wren*.

Efectos del Sexo, la Edad y el Estatus Social sobre la Supervivencia Anual de *Malurus splendens*

Resumen. La supervivencia es un carácter de historia de vida importante y en las especies que presentan cría cooperativa la supervivencia puede estar relacionada a la evolución de la organización social. Usamos modelos de estado múltiple en el programa MARK para estimar la supervivencia aparente de *Malurus splendens*, una especie con cría cooperativa, en que la mayoría de las parejas son ayudadas por la progenie de sexo masculino de las generaciones previas. Examinamos si la supervivencia está relacionada al sexo, la edad o el estatus social (polluelo, auxiliar o reproductor) y cuantificamos la probabilidad de transición entre categorías sociales. El mejor modelo fue aquel en el que la tasa de supervivencia fue diferente entre los estatus sociales, en el que la supervivencia de los auxiliares y reproductores varió anualmente de la misma manera y en el que el efecto del sexo varió anualmente pero influyó la tasa de supervivencia de cada grupo de la misma manera. Tanto en los machos como en las hembras, las estimaciones de supervivencia de los auxiliares fueron similares a la de los reproductores, mientras que el estimado de supervivencia de los adultos fue mayor para los machos que para las hembras, a pesar de que el efecto del sexo varió anualmente. La probabilidad de transición entre categorías de estatus social varió de la manera esperada para una especie con cría cooperativa: los polluelos machos tuvieron una mayor probabilidad de convertirse en auxiliares que los polluelos hembra, mientras que las hembras tuvieron una mayor probabilidad de convertirse en reproductoras al año siguiente. De manera similar entre los auxiliares, las hembras tuvieron una mayor probabilidad de ser reproductoras que los machos. El hecho de que la supervivencia de los machos sea más alta que la de las hembras probablemente contribuye al cociente de sexo sesgado hacia los machos que se observa entre los adultos de esta especie y de manera indirecta, a que los machos jóvenes sean más propensos a retardar su dispersión natal.

INTRODUCTION

In all species, survival is a critical trait of life history, and trade offs between survival and other life-history traits, such as body size and age at first reproduction, are well known (Stearns 1992). For cooperatively breeding birds, survival is also potentially important as a factor leading to the basic social

organization of the species. High survival has been argued to be either a cause (Arnold and Owens 1998, 1999) or a consequence of cooperative breeding (Ligon and Burt 2004), but regardless of the exact relationship, it is clear that accurate estimates of survival are critical before such data can be used to examine evolutionary hypotheses. Although estimates of annual survival (return rates) are available for many species

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of cooperatively breeding birds (Woolfenden and Fitzpatrick 1984, Brown 1987, Koenig and Mumme 1987, Stacey and Koenig 1990, Rowley and Russell 1997), with the exception of McGowan et al. (2003) and Karubian et al. (2008) we could not find any study of cooperatively breeding birds in which survival was analyzed by capture–mark–recapture (Lebreton et al. 1992). By accounting for failure to detect individuals that are actually present and temporary movement in and out of a study area, robust analytical techniques of capture–mark–recapture provide more accurate estimates of true survival than do traditional “return rates” (Sandercock 2006).

In this study we use a multi-state model in program MARK to estimate survival of the Splendid Fairy-wren (*M. splendens melanotus*) over a 13-year study in South Australia. The Splendid Fairy-wren is a common passerine in arid habitats in southern and western Australia. Four subspecies are recognized (*splendens*, *musgravi*, *melanotus*, and *emmottorum*; Rowley and Russell 1997, Schodde and Mason 1999), but a recent phylogeographic analysis found only three distinct genetic clades (*splendens*, *musgravi*, and *melanotus* combined with *emmottorum*; Kearns et al. 2009).

The biology of the Splendid Fairy-wren was extensively reviewed by Rowley and Russell (1997). In brief, Splendid Fairy-wrens are nonmigratory and reside on permanent territories during the breeding season, from August to January. Both males and females are capable of breeding at one year of age. In general, one-year-old females disperse or are evicted from their natal territory by the breeding female, as observed in our population, but in western populations yearling females are more often tolerated as auxiliaries (Rowley and Russell 1997). One-year-old males may disperse or may continue to reside on their natal territory as auxiliaries, assisting the social pair in rearing additional offspring. Thus most family groups consist of a breeding pair plus one or more auxiliary males. The frequency of groups with auxiliary females varies by subspecies (geographically). In the western subspecies (*M. s. splendens*) up to 68% of one-year-old females remain on their natal territory as auxiliaries (Russell and Rowley 1993). In the eastern subspecies (*M. s. melanotus*), the focus of our study, auxiliary females are rare and seldom breed (Van Bael and Pruett-Jones 2000).

Splendid Fairy-wrens are socially monogamous and reproductively promiscuous (Brooker et al. 1990, Webster et al. 2004, 2007). In our population an average of 55.4% of broods contained extra-pair offspring, and an average of 42.2% of nestlings resulted from extra-pair fertilizations (Webster et al. 2004). Of the extra-pair offspring, approximately 75% were sired by a dominant male in another group, 10% by an auxiliary male from the same group, and 14% by an auxiliary male in a different group. The rate of extra-pair paternity increased with group size, at least for groups with two or more auxiliary males (Webster et al. 2004).

From a long-term study by Rowley et al. (1991), survival rates (return rates) of *M. s. splendens* are available as follows: return rates of juveniles from fledging to one year of age

average 31.2%; annual return rates of breeding males average 69.5% and those of breeding females average 59.3%. In this study our objectives were to estimate for *M. s. melanotus* annual survival as it relates to age, sex, and social status (nestling, auxiliary, breeder), as well as to quantify probabilities of transition between social states. No estimates of actual survival have previously been published for *M. s. melanotus* or any species of fairy-wren.

MATERIALS AND METHODS

FIELD METHODS

We studied Splendid Fairy-wrens at Brookfield Conservation Park in South Australia during October, November, and December each year from 1992 to 1999 and again from 2004 to 2008. Habitat at the study area consists of chenopod scrub and mallee eucalyptus scrub. Details of the site and the long-term study there can be found in Van Bael and Pruett-Jones (2000), Webster et al. (2004, 2007), and Tarvin et al. (2005). The Splendid Fairy-wren is common in the mallee areas of Brookfield Conservation Park, where it occurs sympatrically with the Variegated Fairy-wren (*M. lamberti*). These two species are often seen in the same areas and overlap extensively in habitat choice and nesting sites (Tibbetts and Pruett-Jones 1999). The White-winged Fairy-wren (*M. leucopterus*) occurs in the chenopod scrub, and both the Splendid and more often Variegated Fairy-wrens are occasionally found and breed in this area.

Within the core research area, we captured and monitored every Splendid Fairy-wren each year and quantified the composition of all social groups. The number of groups and details of the population are listed in Table 1. Birds were captured with mist nets set in breeding territories. Each bird was banded with a metal permanent band and three plastic colored bands. Nestlings were banded at 5–7 days of age, approximately 1 week before they fledged. Nestlings (and juveniles captured after fledging) were banded with just a permanent metal band. If they survived to one year of age, they were recaptured and color banded. Small blood samples were taken from all birds captured and stored in either a lysis buffer or an ethanol/salt solution. The sex of nestling birds was determined by a now standard molecular technique (Griffiths et al. 1998).

In our analyses we include all birds that received a metal band (1184 birds total), either as a nestling ($n = 592$) or as an adult ($n = 592$). Over the 13 years, 61 adults that were captured and banded were never seen again, so details of their social group or social status were unavailable; most of these birds were at the edge of the study area and likely on territories not in our core area; they are not included in the analysis. For our analyses, we consider survival as survival from the time of banding to the start of next breeding season (first week in October) or, for birds already banded, as survival from the start of one breeding season to the start of the next breeding season. We do not specifically analyze survival during the breeding season, in part because it was rare for an adult alive at

TABLE 1. Summary of banded population of the Splendid Fairy-wren at Brookfield Conservation Park, South Australia.

	1992	1993	1994	1995	1996	1997	1998	1999	2004	2005	2006	2007	2008
Number of family groups	35	42	60	64	69	54	45	41	25	46	54	53	48
Mean group size	2.4	3.1	3.3	2.4	2.7	2.3	2.4	2.5	2.2	2.2	2.5	2.2	2.3
New adult males	50	27	36	11	30	8	8	10	29	23	25	12	4
New adult females	33	30	37	16	29	22	12	13	28	26	26	25	22
New hatch-year males	13	29	3	41	40	28	28	12	10	25	18	35	15
New hatch-year females	10	17	1	39	43	29	21	12	18	38	24	35	8
Banded birds included in analysis	106	176	201	226	240	178	148	122	87	163	176	186	136

the beginning of the season (early October) not to survive to the conclusion of our field work (mid-December). As regards nestlings, our estimate of first-year survival is an estimate of survival from 6 days of age (the time of banding) to 1 year of age (or rather to the start of the next breeding season).

ANALYSIS

We used the multi-state recaptures-only model in program MARK to estimate a Splendid Fairy-wren's probability of survival (S), detection (p), and transition (ψ) between social states (nestling, auxiliary, breeder). We also estimate the influence of sex on state-specific annual survival and transition between social states. We use multi-state models to partition estimates of apparent survival (ϕ) into two subcomponents: state-specific apparent survival between encounter periods (S) and the probability an individual transitions to a different state (ψ) (Cooch and White 2008). Multi-state models facilitate estimation of S and p for each state of the model while concurrently estimating the movement between these states (Sandercock 2006). The probability of movement or transition (ψ) may represent movement among physical locations as well as transition between social or reproductive states such as the transition from nonbreeder to breeder (Cooch and White 2008).

We used data on banded birds resighted 1992–1999 and 2004–2008 to assign individuals to a social state by year. We treat the 1999–2004 gap as a single interval, allowing us to combine data from the two periods into a single analysis. Only three birds banded in 1999 were encountered in 2004, so we ignored all parameter estimates associated with the gap. Each encounter occasion represented detection during a single breeding season (October–December), and we modeled two groups: (1) birds first banded as nestlings and of known age and (2) birds first banded as adults and of unknown age. Individuals in group 1 necessarily began in the social state of nestlings and had the opportunity to transition into auxiliaries or breeders in subsequent years. Individuals in group 2 began as either auxiliaries or breeders. We did not model a nestling state separately from an auxiliary state because doing so results in nonsensical estimates of p (“nestling resighting” does not exist because an individual is no longer a nestling the year after it hatches). Despite this aspect of our model, both nestlings and auxiliaries had independent opportunities to transition into breeders since

fairy-wrens do not breed until they are at least 1 year old. We assigned each wren a sex covariate of 0 (male) or 1 (female).

We began modeling with a global model that recognized annual variation in state-specific apparent survival of adults ($S_{g \times t}$) and resighting rates ($p_{g \times t}$) but no annual variation in transition rates (ψ_g). The subscript g denotes the group and recognizes unique parameter estimates for birds first banded as nestlings (n) or first banded as adults (a) and auxiliaries (x) or breeders (b) in any given year; t denotes time and identifies unique parameter estimates for each year of study. Our model with the most parameters ($S_{g \times t}, p_{g \times t}, \psi_g$) therefore included 63 parameters, comprising 33 unique survival rates ($S_{g \times t} = 12$ nestling + 11 auxiliary + 11 breeder), 24 unique resighting rates ($p_{g \times t} = 12$ auxiliary + 12 breeder), 3 unique transition rates, and 2 confounded estimates of survival in the final year multiplied by the rate of resighting in the final year (i.e., $\phi_{t-1} \times p_t$; Lebreton et al. 1992). We used this global model to test for overdispersion (\hat{c}) by using a bootstrap goodness-of-fit test (Cooch and White 2008); we divided observed deviance by theoretical deviance. Our estimate of mean empirical deviance was based on 1000 bootstrap simulations of the global model [$S(t \times g_{(n,x,b)}), p(t \times g_{(x,b)}), \psi(\cdot)$] (Cooch and White 2008). As our estimate of \hat{c} was 0.99, we chose not to correct Akaike's information criterion for overdispersion (QAIC_c), and we used model weight (w_i) to rank all tested models.

Assumptions regarding the constancy of resighting probabilities (p) influence estimates of apparent survival, potentially obfuscating detection of annual variation in S . As our prime objective was to derive annual estimates of survival, we first concentrated on simplified models for resighting rate (Lebreton et al. 1992). We built models sequentially, beginning with the global model. To reduce the model's complexity, we fit separate intercepts for auxiliaries and breeders in the design matrix and allowed p to vary annually but constrained the two social states to the same slope. Additionally, as females, if they were not breeding (because of either permanent emigration or death), were not likely to be observed in the years after hatching, we included sex in our model for transition rate [$S(t \times g_{(n,x,b)}), p(\text{sex} + t \times g_{(x,b)}), \psi(\cdot)$]. Our simplification resulted in a savings of 10 estimable parameters and a net reduction of 75.48 AIC_c units.

We used this simplified model to investigate how survival varied by year, age, sex, and social status. We built each model specified in our a priori set of candidate models (Table 2).

TABLE 2. Set of a priori models used to estimate apparent survival, S , in Splendid Fairy-wrens as a function of sex and breeding status. Parameters having independent (i.e., factorial) relationships are joined by \times , whereas parameters having parallel (additive) relationships are joined by $+$; t specifies that survival varied by year. The designation $g_{(n,a)}$ represents a grouping based on age class (n = hatch-year, a = adult); $g_{(n,x,a)}$ represents a grouping based on social state (n = nestling, x = auxiliary, b = breeder). For all a priori models, $p = g_{(x,b)} \times t$ and $\psi = \text{age} \times g_{(n,a)} \times \text{sex}$. The best-supported model, before sex was added as a covariate, is printed in bold.

Model (S)	Description
$g_{(n,x,b)}$	Survival rates vary by social state but not by year
t	Survival rates vary by year but not by social state
$g_{(n,x,b)} + t$	Survival rates vary by social state and by year, all states following the same pattern
$[g_{(x,b)} + t], [g_{(n)} \times t]$	Survival rates vary by state; rates of auxiliaries and breeders vary by year in the same pattern
$g_{(n,x,b)} \times t$	Survival rates vary by state and by year, each state following a different pattern
$t \times g_{(n,a)}$	Survival rates vary by year and by age class, each age class following a different pattern
<i>Models in which sex was added as a covariate to the best-supported model above (bold)</i>	
Top + sex	Sex effect on survival constant
Top + sex $\times g_{(n,a)}$	Sex effect on survival varies by age class but not by year
Top + sex $\times g_{(n,x,b)}$	Sex effect on survival varies by social state but not by year
Top + sex $\times t$	Sex effect on survival varies by year but not by social state or age class

We estimated S and p only from top models with an evidence ratio greater than 2.0 (Cooch and White 2008); otherwise, we averaged the set of top-ranking models having $\Sigma w_i \geq 0.9$. We took the arithmetic mean of model-averaged estimates of S and p , with standard errors generated by the delta method (Powell 2007). We excluded S_{1994} from our estimate of the arithmetic mean for nestling S because only four nestlings survived to be banded during that year. We also excluded estimates of S for the final year of each period (S_{1999} and S_{2008}) for both nestlings and adults because they were not fully resolvable because we were not able to fit a temporally reduced model of p (Cooch and White 2008). We excluded estimates of p_{1995} for birds hatched in 1994 for the same reasons mentioned above as well as estimates of p_{1999} and p_{2008} .

RESULTS

APPARENT SURVIVAL

Over our study, annual apparent survival of Splendid Fairy-wrens varied greatly (Fig. 1, 2). The best-supported initial model (before sex was added as a covariate) was one in which the birds' survival rates differed by social status but the survival of auxiliaries and breeders varied annually in the same manner (Table 2). Adding sex as a covariate to the initial model improved it greatly (Table 3). In the new best-supported model, survival rate varied by social status and the effect of sex, which fluctuated annually (i.e., there was a separate intercept for each year), was of the same magnitude for all social states.

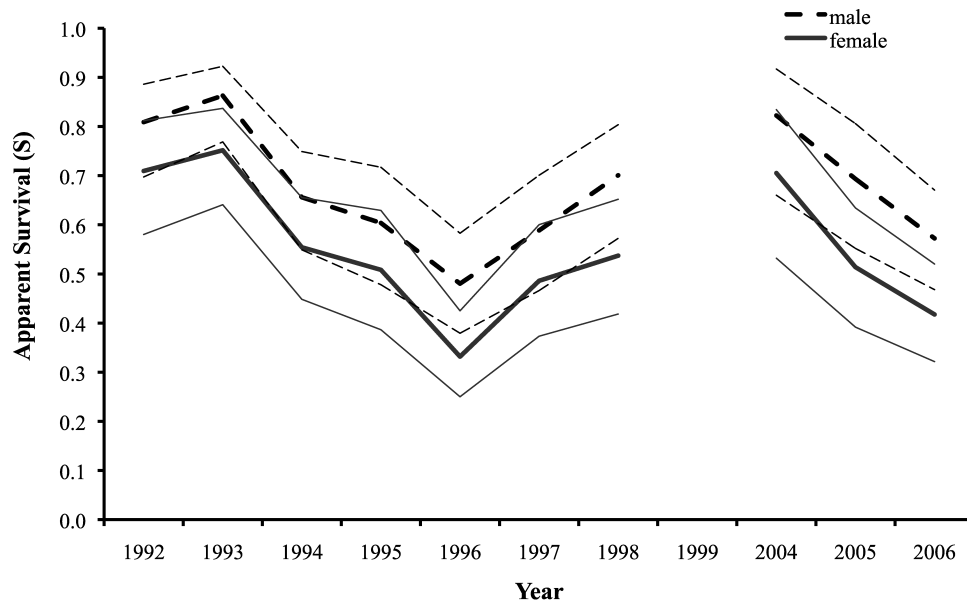


FIGURE 1. Annual apparent survival (S) of adult Splendid Fairy-wrens based on model-averaging the best-supported models (see Table 3). Lighter lines (dashed or solid) represent the 95% confidence intervals.

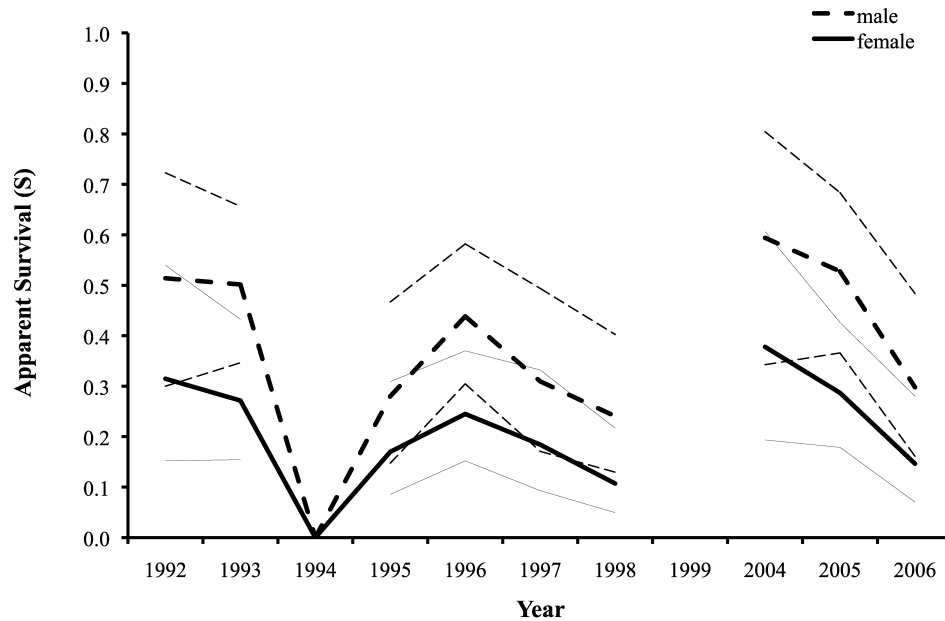


FIGURE 2. Annual apparent survival (*S*) of nestling Splendid Fairy-wrens based on model-averaging the best-supported models (see Table 3). Lighter lines (dashed or solid) represent the 95% confidence intervals.

Throughout the study, apparent survival of adults was consistently higher and less variable than that of nestlings (Fig. 1, 2). In addition, nestlings experienced several years of noticeably low survival (Fig. 2). The mean apparent survival rates of nestling, auxiliary, and breeding males were higher than those of females of the same status (Table 4). The ranges of apparent survival rates for males were 0.24–0.59 (nestlings), 0.50–0.87 (auxiliaries), and 0.48–0.86 (breeders); for females, they were 0.11–0.38 (nestlings), 0.34–0.76 (auxiliaries), and 0.33–0.75 (breeders). There was strong support for apparent survival of females being lower than that of males during 4 of the 10 years for which we generated estimates (Table 5).

LIKELIHOOD OF RESIGHTING

The likelihood of a Splendid Fairy-wren being resighted was influenced by year and breeding status (Table 3). In general, once an adult (male or female) became a breeder, it remained on that territory throughout its life. Therefore, throughout the study, the likelihood of adults being resighted was essentially 1.0 (Table 4), and annual variation was driven largely by fluctuations in the likelihood of resighting auxiliaries. The most parsimonious model (lowest AIC) lacked an effect of sex on the detection of breeders and auxiliaries, so we do not estimate the likelihood of resighting of males and females separately (Table 4).

TABLE 3. Best-supported models used to estimate apparent annual survival (*S*), detection probability (*p*), and probability of transition between breeding states (ψ) for the Splendid Fairy-wren. Values of Akaike’s information criterion (AIC) were corrected for small sample size (AIC_c); Δ AIC_c values and model weights (*w*_{*i*}) were used to rank the models according to social status (b = breeder, x = auxiliary, and n = nestling), age class (a = adult and n = nestling), and annual variation (*t* specifies variation by year). Parameters (*K*) having independent (i.e., factorial) relationships are joined by \times ; those having parallel (additive) relationships are joined by +. For all models, $p = g_{(x,b)} + t$ and $\psi = ag_{(n,a)} \times \text{sex}$.

Rank	Model (<i>S</i>)	Δ AIC _c	<i>w</i> _{<i>i</i>}	<i>K</i>	Deviance
1 ^a	$[g_{(x,b)} + t], [g_{(n)} \times t] + \text{sex} \times t$	0.00	0.48	56	3133.74
2	$[g_{(x,b)} + t], [g_{(n)} \times t] + \text{sex} \times g_{(n,a)}$	1.11	0.28	46	3155.93
3	$[g_{(x,b)} + t], [g_{(n)} \times t] + \text{sex}$	2.60	0.13	45	3159.52
4	$[g_{(x,b)} + t], [g_{(n)} \times t] + \text{sex} \times g_{(n,x,a)}$	3.15	0.10	47	3155.88

^aTop model; AIC_c = 3249.1.

TABLE 4. Means and 95% confidence intervals for estimates of apparent survival (S_b , S_x , S_n) and detection (p_x and p_b) generated by model-averaging the best-supported models (see Table 3). Survival (S) estimates for nestlings excluded 1994. We also excluded estimates of S and p for the final year of each period of mark–recapture (S_{1999} and S_{2007} ; p_{1999} and p_{2008}).

	Survival (S)			Detection (p)	
	Nestling	Auxiliary	Breeder	Auxiliary	Breeder
Male	0.392 (0.234–0.574)	0.683 (0.552–0.788)	0.669 (0.548–0.768)		
Female	0.218 (0.115–0.373)	0.546 (0.377–0.704)			
All adults				0.606 (0.289–0.882)	0.929 (0.71–0.99)

Despite the very high likelihood of adults being resighted, there were a few instances of birds (23 total, 12 males and 13 females) leaving the study area and then moving back to the core area and being detected again. That is, the bird was counted one year, not observed the next year, and reappeared the third year.

TRANSITION PROBABILITY

Transition probability as applied to this study is the probability of an individual fairy-wren (given that it is alive) becoming an auxiliary or a breeder after being a nestling or becoming a breeder after having first been an auxiliary. Probabilities of

transition between these social states differed substantially by sex (Table 6). The magnitude of this sex effect varied with the particular transition (Table 5). For example, by their second year, male nestlings were more likely to become auxiliaries than breeders, while female nestlings were more likely to become breeders (Table 6). Once becoming an auxiliary, a male was slightly more likely to breed in the following season than to remain an auxiliary. However, a female that did not breed in her second year had only a slim chance of remaining an auxiliary the following year. In most cases, breeding birds remained breeders throughout their lives (Table 6). We did, however, observe 24 “reverse” transitions, where a bird was a breeder one year and an auxiliary the next (19 males, 5 females).

TABLE 5. Magnitude and direction of the effect of sex on annual apparent survival estimates (S) and transition probabilities (ψ) for the Splendid Fairy-wren. Sex effects are represented by estimates of β generated by the top model, $S([g_{(x,b)} + t], [g_{(n)} \times t] + \text{sex} \times t)$, $p[g_{(x,b)} + t]$, $\psi[\text{age} \times g_{(n,a)} \times \text{sex}]$. A negative value indicates that the value for females was lower than that for males; a positive value indicates that the value for females was higher than that for males.

	Sex effect (β)		95% confidence limits	
	Estimate	SE	Lower	Upper
S_{1992}	-0.54	0.45	-1.43	0.35
S_{1993}^a	-1.10	0.39	-1.87	-0.32
S_{1994}	-0.13	0.32	-0.76	0.50
S_{1995}	0.02	0.32	-0.60	0.64
S_{1996}^a	-0.75	0.28	-1.31	-0.20
S_{1997}	-0.09	0.32	-0.73	0.54
S_{1998}	-1.01	0.38	-1.75	-0.27
S_{2004}	-0.84	0.57	-1.94	0.27
S_{2005}^a	-1.19	0.35	-1.87	-0.51
S_{2006}^a	-0.81	0.32	-1.44	-0.18
ψ_{n-x}^a	-0.56	0.21	-0.97	-0.16
ψ_{x-b}	0.13	0.17	-0.21	0.47
ψ_{b-x}^a	-2.65	0.24	-3.12	-2.18

^a Strong support for an effect of sex on either survival or transition between categories of status (n = nestling, x = auxiliary, and b = breeder).

DISCUSSION

In ornithological studies, standard estimates of survival (return rates, or the percentage of birds marked at time x and still alive at time $x + 1$) are minimal estimates of actual survival because return rates are actually the product of four separate probabilities: true survival, site fidelity, site propensity, and true detection (Sandercock 2006). In brief, true survival is the probability that an individual survives between two periods of sampling, site fidelity is the probability that an individual returns to the same sampling area (if it is alive), site propensity is the probability that an individual is available for encounter (detection) in the same sampling area the next year, and true detection is the probability that an observer detects the individual.

TABLE 6. Probabilities (ψ) of transition among social states of male and female Splendid Fairy-wrens. Estimates, with 95% confidence intervals, are based on the top model, $S([g_{(x,b)} + t], [g_{(n)} \times t] + \text{sex} \times t)$, $p[g_{(x,b)} + t]$, $\psi[\text{age} \times g_{(n,a)} \times \text{sex}]$.

	Male	Female
Hatch-year to auxiliary	0.64 (0.27–0.46)	0.28 (0.53–0.82)
Hatch-year to breeder	0.36 (0.27–0.46)	0.72 (0.53–0.82)
Auxiliary to breeder	0.53 (0.44–0.61)	0.91 (0.55–0.97)
Breeder to auxiliary	0.07 (0.04–0.10)	0.02 (0.01–0.06)

In fairy-wrens, the probabilities of site fidelity, site propensity, and true detection may be large, given the short distances of dispersal (at least of males) and the sedentary nature of individuals residing on traditional territories. Therefore, in fairy-wrens return rates may reflect true survival more accurately than in other species, though this hypothesis remains to be tested. Given the availability of more accurate methods of analysis (reviewed by Sandercock 2006), it will be important to re-examine earlier published values of return rates, especially with regard to testing hypotheses about the importance of survival in the evolution of cooperative breeding (Arnold and Owens 1998, 1999). We chose multi-state models in program MARK because they permit estimation of survival of individuals in different states, such as age, sex, and social state, in our case. Multi-state models also permit estimation of the probabilities of transitions between states, as seems particularly relevant for cooperative breeders.

Our estimates of annual survival of males were generally higher than those of females of all ages, but both the estimates of survival and the differences between the sexes varied by year. In some years survival estimates were high for all birds regardless of sex or social state (e.g., 1993 and 2004; Fig. 1, 2), whereas in other years (e.g., 1996; Fig. 1, 2) survival estimates varied considerably by sex and social state. Whether this variation was due to environmental conditions (rainfall and temperature) or biological factors (reproduction) is not yet known, but any such relationships are likely to be complex. For example, the study area experienced a severe drought in 1994, when only three family groups (of 60 monitored) produced offspring. None of these offspring survived to the following year, but estimates of adults' survival were not particularly low (Fig. 2). In contrast, another drought in 1996 affected survival of adults dramatically, but the population as a whole still produced many offspring. The possible influences of rainfall or other environmental conditions on reproduction and survival may also be temporally separated, at least in our study, considering how our data were gathered. Reproduction (October to December) may be influenced by rainfall during the previous winter (April to June), whereas annual survival estimates as we have quantified them may be influenced by rainfall during the subsequent winter.

Our estimates of annual survival for hatch-year females must be regarded as minima. In our population, as in other species of fairy-wrens, most one-year-old females disperse, whereas most one-year-old males remain on their natal territory as auxiliaries. If yearling females dispersed into a territory in our study area, we would detect them during that breeding season, but if they dispersed farther, off the study site, we would not. We do not know the maximum distance females disperse from our study site, but we have found banded females (but not males) up to 5 km away from the core study site. There is habitat suitable for Splendid Fairy-wrens up to 6–8 km away from our core area at Brookfield Conservation

Park, and it is possible that some females disperse this far. Farther dispersal distances are unlikely as the park is surrounded by properties heavily grazed by sheep and we have never seen Splendid Fairy-wrens residing in the surrounding areas.

The high probability of detection of adults (0.929; Table 4) was expected, given the sedentary nature of adults and the rarity of a bird breeding in the study area, moving off the site, and then returning at a later date: only 11 (1.86%) of the 592 adults we analyzed. Of course, our study site is continuous with other suitable habitat, so these birds could have been just one or two territories away from our core area without our detecting them. In contrast, the probability of detecting auxiliaries (0.682) is undoubtedly influenced by the detection of auxiliary females, which are more likely to disperse than auxiliary males. As described under Methods, the model we used was constrained in its estimation of detection probabilities so that the results were not separated by sex.

Hatch-year males were almost twice as likely to transition to an auxiliary as to a breeder in the following year, whereas for females the ratio was reversed (Table 6). This difference was expected, as the dispersal of hatch-year females is greater than that of hatch-year males. Similarly, for a bird remaining on the territory as an auxiliary, a female was much more likely than a male to become a breeder the following year (Table 6). It was rare for a bird to transition to an auxiliary once it was breeding, but this did occasionally happen. These cases, however, had no consistent features in common. For example, in the cases where a male breeder later became an auxiliary, it was as likely that it became an auxiliary to a social relative (brother or son) as to an unrelated individual that dispersed into the territory.

In our population, the values of apparent survival for breeding males (68.3%) and for breeding females (54.61%) (Table 4) are similar to the published return rates for the western population of the Splendid Fairy-wren (*M. s. splendens*: 69.5% for males and 59.3% for females; Rowley et al. 1991, Rowley and Russell 1997). The return rates reported by Rowley and Russell and our survival estimates were calculated differently, and their estimates included auxiliary males and females, whereas our estimates do not. Nevertheless, Rowley and Russell's values taken as reflecting survival in *M. s. splendens* accurately, the comparison with our data is striking because of life-history differences between these two populations that have led us, at least, to expect that the survival of the birds we studied would be lower survival than that of those in the western population. Those differences are extensive, as virtually every aspect of the habitat and population biology of the western population (as studied by Rowley and Russell in Perth, Western Australia) and our population differ. In comparison with that of the western population (and study area), the habitat in our area is drier (consisting of dry mallee eucalyptus scrub), rainfall is less, family group size is smaller, clutches are smaller (on average 3 rather than 4 eggs),

the proportion of groups with auxiliary females is lower, and the density of breeding birds is less (Rowley and Russell 1997 and references therein; Van Bael and Pruett-Jones 2000; Pruett-Jones, unpublished data). We anticipated that these differences were the result of survival in our population being lower. Either our expectation is correct, and the return rates published by Rowley and Russell are lower than true survival in that population, or other factors are influencing the demography of these two populations.

Rowley and Russell (1997) listed survival values (return rates) for a number of species of fairy-wrens. Without exception, and as we found, the survival of males is higher than that of females. In all species of fairy-wrens both males and females are capable of breeding at one year of age, although more females than males actually begin breeding at one year of age because many one-year-old males become auxiliaries. On average, therefore, the age of first breeding is lower for females than for males, and this difference is likely the cause of females' generally lower survival rates. Besides age at first breeding, reproduction may also be costly to females, given the energy demands of laying multiple clutches during a season. Predation of nests of all species of fairy-wrens is common, and females often lay multiple clutches each year before rearing offspring successfully.

Another hypothesis, difficult to disprove, is that apparent survival of adult females is lower than that of adult males because the probability of females dispersing is higher at all ages, not just as fledglings. Indeed, on the basis of data in Table 4, survival of females is lower than that of males at all life stages by approximately the same amount (13–17%), even though above we argued that the difference for nestlings is due to differences in detection whereas the difference for adults is due to real differences in survival. Although we cannot disprove this hypothesis, higher female mortality has been observed in all species of fairy-wrens (Rowley and Russell 1997), even though not all species disperse in the same patterns as the Splendid Fairy-wren. Additionally, if lower apparent survival of adult females were due to dispersal, we would expect to occasionally see females banded as adults off the study area in the surrounding habitat. We have, in fact, seen banded females off the main study area, but in every case it was a female first banded as a nestling that dispersed away from the core area, not a female that bred in the core area and subsequently dispersed elsewhere.

Higher survival of males is one of the likely causes of sex ratios biased toward adult males in the Splendid and other species of fairy-wrens (Rowley and Russell 1997). In our population, the sex ratio of adults has been biased toward males in every year of our study. In the Superb Fairy-wren (*M. cyaneus*), male-biased sex ratios interact with habitat limitation to promote delayed dispersal of young males (Pruett-Jones and Lewis 1990). In that species, auxiliary males

disperse into suitable habitat if a female is residing in the habitat, but they do not disperse into suitable habitat without a female (Pruett-Jones and Lewis 1990). Our field observations suggest similar behavior of the Splendid Fairy-wren. Females moving through (dispersing) the study site should cause auxiliary males to leave their social group and pair with the dispersing female. If the female stays in the area, a new pair is formed. If the female leaves or disappears, the auxiliary male returns to his previous group.

We acknowledge that this study is a first step in understanding the dynamics of survival in the Splendid Fairy-wren. We have shown that age, sex, and social status all contribute importantly in determining annual survival. Nevertheless, in both absolute and relative terms, survival of both males and females varied considerably from year to year. Sex was an important influence on annual survival in fewer than half of the years of the study, and in one year survival of females was higher than that of males. Understanding the environmental and ecological factors influencing survival will require an understanding of how the population as a whole responds to a particular factor as well as how males and females respond differently. Additionally, the striking annual differences in survival estimates and the influence of sex illustrate the importance of long-term data for accurate estimates of survival. Such data will be critical before survival data can be used to critically examine hypotheses on the evolution of cooperative breeding in birds.

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