Subtle benefits of cooperation to breeding males of the Red-backed Fairywren

Author(s): Ahva L. Potticary , Jenélle L. Dowling , Douglas G. Barron , Daniel T. Baldassarre , and Michael S. Webster

RESEARCH ARTICLE

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Ahva L. Potticary,[1,a]* Jenélle L. Dowling,[2#] Douglas G. Barron,[3,b#] Daniel T. Baldassarre,[2,c#] and Michael S. Webster[2#]

[1] Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana, USA
[2] Department of Neurobiology and Behavior, and Cornell Lab of Ornithology, Cornell University, Ithaca, New York, USA
[3] School of Biological Sciences, Washington State University, Pullman, Washington, USA
[a] Current address: University of Arizona, Tucson, Arizona, USA
[b] Current address: Psychology Department, University of South Florida, Tampa, Florida, USA
[c] Current address: Department of Biology, University of Miami, Coral Gables, Florida, USA
[#] These authors contributed equally to the paper
* Corresponding author: apotticary@email.arizona.edu

ABSTRACT
Cooperative breeding is a phenomenon whereby breeding and nonbreeding individuals collectively provision young. Nonbreeding group members ("helpers") may gain indirect and/or direct fitness benefits by breeding in a group, but there has been conflicting evidence regarding the benefits to breeders. In fact, the presence of helpers may sometimes be detrimental to aspects of breeder fitness. For example, in some species of the chiefly Australian genus *Malurus,* breeding males with helpers have lower within-pair paternity than do males without helpers. Additionally, indirect benefits to breeding males are often limited by low relatedness to their helpers due to high extrapair paternity rates, and helpers often appear to have minimal impact on breeder reproductive success. However, the presence of helpers may allow breeding males to shift their behaviors from guarding and provisioning young to alternative behaviors that affect other components of fitness, such as extraterritory forays (which might increase extrapair mating success) and self-maintenance (which might increase survival). We investigated these possibilities in the facultatively cooperative Red-backed Fairywren (*Malurus melanocephalus*). Males with helpers spent significantly less time engaging in guarding behaviors and provisioning of young than did those without helpers, but there was no difference in the frequency of extrapair forays nor the number of young sired by males with vs. without helpers. Additionally, the decreased investment in nesting behaviors did not result in consistently higher survival, but may have increased survival in some years. Overall, the results of this study did not suggest any strong direct fitness benefits to breeding males, which may indicate that the costs of retaining helpers are negligible relative to the indirect benefits of helping a potentially related male.

Keywords: bird, mate-guarding, foray behavior, age-dependence, tradeoff

Beneficios sutiles de la cooperación para los machos reproductivos en *Malurus melanocephalus*

RESUMEN
La cría cooperativa es un fenómeno en el que individuos reproductivos y no reproductivos aprovisionan colectivamente a las crías. Los miembros del grupo que no se reproducen ("auxiliares") podrían tener beneficios directos o indirectos en su aptitud al reproducirse como un grupo, pero existe evidencia contradictoria en relación con los beneficios percibidos por los individuos reproductivos. De hecho, a veces la presencia de los auxiliares podría ser perjudicial para algunos aspectos de la aptitud de los individuos reproductivos. Por ejemplo, en algunas especies del género australiano *Malurus* los machos reproductivos con auxiliares tienen menores valores de paternidad intrapareja que los machos sin auxiliares. Además, los beneficios indirectos para los machos reproductivos frecuentemente son limitados por causa del bajo parentesco con sus auxiliares debido a las altas tasas de paternidad extra pareja y los auxiliares frecuentemente parecen tener un impacto mínimo en el éxito reproductivo de los individuos reproductivos. Sin embargo, la presencia de los auxiliares podría permitir que los machos reproductivos cambien su comportamiento de cuidar y abastecer a los jóvenes por comportamientos alternativos que afectan otros componentes de la aptitud, como las incursiones extra territoriales (que podrían incrementar el éxito de las cópulas extra pareja) o el auto mantenimiento (que podría incrementar la supervivencia). Investigamos estas posibilidades en *Malurus melanocephalus*, una especie que presenta cría cooperativa facultativa. Los machos con auxiliares invirtieron significativamente menos tiempo en comportamientos de cuidado y abastecimiento de los jóvenes que los machos sin auxiliares, pero no hubo diferencia en la frecuencia de las incursiones extra pareja ni en el número crías engendradas por machos con o

sin auxiliares. Además, esta disminución en la inversión del comportamiento de anidación no resultó consistentemente en mayor supervivencia, pero podría incrementar la supervivencia en algunos años. En general, los resultados de este estudio no encontraron evidencia de algún beneficio directo considerable sobre la aptitud darwiniana de los machos reproductivos, lo que podría indicar que los costos de retener los auxiliares son despreciables en relación con los beneficios indirectos de ayudar a un macho potencialmente relacionado.

Palabras clave: ave, comportamiento de incursión, compromiso, dependencia de edad, vigilancia de pareja

INTRODUCTION

Cooperative breeding, in which nonbreeding individuals ("helpers") aid breeders to raise young (Cockburn 2006), is by definition a collaboration between multiple individuals, requiring selection for cooperative behavior in both breeding and nonbreeding individuals to facilitate its evolution. Accordingly, determining how helpers and breeders benefit may provide insight into the evolution and maintenance of cooperative breeding strategies (Stacey and Ligon 1991, Clutton-Brock 2002).

There are numerous potential benefits that helpers may gain from delaying dispersal and cooperating (for reviews see Emlen 1991, Cockburn 1998). Similarly, breeders with helpers may benefit directly through increased reproductive success within a season (Heinsohn 1991, Covas Monteiro 2002) or by increased survival as a result of aid provided by helpers (Magrath and Yezerinac 1997, Russell et al. 2007). Breeders may also benefit indirectly if retained offspring are subsequently more likely to survive and reproduce themselves (Cockburn 1998). However, many cooperative systems do not exhibit clear reproductive or survival benefits of helper retention to breeding individuals (Dunn et al. 1995, Eguchi et al. 2002, Cockburn et al. 2008, Varian-Ramos et al. 2010). Paradoxically, helper retention can be detrimental to breeder fitness in some cases (Mulder et al. 1994, Dierkes et al. 1999, Double and Cockburn 2003, Webster et al. 2004). This is particularly true for breeding males, as the presence of helpers can sometimes lead to increased rates of cuckoldry (Green et al. 1995), and male helpers are potential reproductive competitors with the breeding male (Double and Cockburn 2003, Webster et al. 2004). Moreover, the breeding males of promiscuous species are less assured of high kinship with helpers (Dunn et al. 1995), and therefore may gain few indirect benefits from increased helper fitness (Hamilton 1964). For these reasons, it is often unclear why breeding males tolerate the presence of potentially unrelated male helpers in their territories.

Helpers may benefit breeding males by increasing fitness in ways that do not directly affect within-pair reproductive output. First, decreased provisioning or guarding effort could translate into increased survival for breeding males as a result of a lowered cost of reproduction (see Russell et al. [2007] for similar benefits to females). It is already known that, in many cooperatively breeding species, breeding males make fewer provisioning trips to the nest when a helper is present (e.g., Green et al. 1995, Varian-Ramos et al. 2012). Similarly, mate-guarding entails a tradeoff between paternity assurance and self-maintenance (Westneat 1994) that may be mitigated if helpers assist with guarding females (Welbergen and Quader 2006). Second, breeding males who spend less time provisioning nestlings or guarding females may have more time to seek extrapair copulations (Green et al. 1995).

Cooperatively breeding Red-backed Fairywrens (*Malurus melanocephalus*) are an ideal species to investigate the potential benefits of cooperation to breeding males. First, this species is a facultative cooperative breeder, meaning that some pairs breed with helpers whereas others do not, allowing for comparison across group compositions. Second, breeding males are cuckolded by extragroup males at a higher rate than are males without helpers (Varian-Ramos 2008), representing a fitness cost to retaining helpers that may be a common pattern in *Malurus* species (see Mulder et al. 1994, Webster et al. 2004). Helpers also sometimes sire offspring within the group at the breeding male's expense (Webster et al. 2004, Varian-Ramos 2008) and may similarly parasitize extrapair breeding opportunities (Double and Cockburn 2003). Moreover, while helpers in *Malurus* are almost always the male offspring of the breeding female (Varian-Ramos 2008, Ligon et al. 2010), they are often unrelated to the breeding male due to high extrapair paternity rates (~51%, with only ~21% of helpers related to the breeding male; see below and Webster et al. 2008), indicating that kin-selected benefits to breeding males are likely to be low. Lastly, in Red-backed Fairywrens, helpers seem to have a limited impact on breeder reproductive output, as pairs breeding with helpers do not produce more or higher-quality fledglings relative to those without helpers (Varian-Ramos et al. 2010).

These indications of lower breeding male fitness in the presence of a helper are contradictory to current thinking and provide an opportunity to test for subtle direct benefits of cooperative breeding to breeding males. We therefore investigated the hypothesis that breeding males tolerate the presence of helpers because it permits a behavioral shift from parental investment and guarding to increased extrapair mating effort and/or self-maintenance. We further tested whether such behavioral shifts confer

fitness benefits to breeding males through increased extrapair reproductive success and/or survival.

METHODS

Study Species and General Field Methods

The Red-backed Fairywren is a small, insectivorous passerine that ranges across northern and eastern Australia, inhabiting open woodlands and grasslands (Schodde 1982, Rowley and Russell 1997). The species is socially monogamous, with some pairs remaining together in the same territory for multiple breeding seasons (M. S. Webster personal observation). Red-backed Fairywrens often breed cooperatively in groups consisting of a breeding male and female with 1–2 male helpers (Rowley and Russell 1997), although few breeding groups have more than a single helper and the majority of pairs breed without helpers (Varian-Ramos et al. 2010). Most breeding males in the population display red and black nuptial coloration, whereas females, helpers, and some breeding males display cryptic brown plumage (Webster et al. 2008). Males that bred in brown plumage were excluded from all analyses reported here, because these males are known to differ in their mating and parental behaviors and have significantly different total reproductive success from males breeding in nuptial plumage (Karubian 2002, Webster et al. 2008, Barron et al. 2015). Helper males generally disperse from their natal territory to become breeders by their second breeding season (Varian-Ramos et al. 2010). However, all males, regardless of social status, are capable of fertilizing females (Rowe et al. 2010). Females are responsible for nest building, incubation, and brooding, but breeding and helper males assist with the feeding of nestlings and fledglings (Varian-Ramos et al. 2010).

Our field research was conducted during the breeding season (October–February) of 2011–2012 on 2 color-banded populations of Red-backed Fairywrens near Herberton, Queensland, Australia. These populations have been monitored each breeding season since 2003. Our field sites included the forests surrounding the Moomin Reservoir (145°26′E, 17°22′S) and Kalinvale Farm (145°22′E, 17°27′S), where 80 and 115 groups of breeding Fairywrens were observed, respectively. In the 2011–2012 field season, 10% (8/80) of pairs at Moomin and 27% (31/115) of pairs at Kalinvale had helpers (i.e. bred in groups). We defined a group as a breeding pair with ≥1 helper (i.e. more than one male was observed consistently with the group and provisioning at the nest; Cockburn 2006, Koenig and Dickinson 2004). For groups, we defined the dominant breeding male as the male who spent the most time with, and sang with, the group's breeding female and was also in nuptial breeding plumage; other males in the group were defined as helpers (per Webster et al. 2008).

Pairs that had a helper for at least 1 reproductive attempt were classified as a group for the season for the purpose of season-wide analyses. All successful and most unsuccessful nesting attempts were monitored, and individuals were resighted at least once a week. Active nests were visited at least once every other day to determine nesting stage, laying date, clutch size, hatching date, and to band and collect a small blood sample from nestlings at pin-break (about day 6 after hatching).

Adult birds in each population were captured using mist nets, and banded with an Australian Bird and Bat Banding Scheme (ABBBS) numbered aluminum band and a unique combination of colored bands for visual identification. At the time of banding, we also collected a small blood sample (∼20–50 µL for nestlings, 40–75 µL for adults) for the purposes of genetic paternity analyses. Blood samples were collected from the wing or tarsus of nestlings and from the jugular vein of adults. All blood samples were stored in lysis buffer. Unbanded adult males were aged as either hatch-year (age 1) or after-hatch-year (age ≥1) based upon skull pneumatization at time of first capture. All males were included in survival analyses due to the small sample size of males whose age was precisely known. Because males that were first aged as after-hatch-year were included in analyses, males were categorized as "young" (<3 yr old) and "old" (≥3 yr old) for behavioral analyses in order to include males for whom exact age was not known and to increase sample size. The age of 3 yr was delineated as the cutoff point between "old" and "young" males because this represents the mean life expectancy for these birds (mean life expectancy = 2.51 ± 0.08 SE yr, $n = 379$). For the purpose of better illustrating age trends in figures, males were classified by age categories, in which males originally captured as after-hatch-year were categorized as age 1. When these males were resighted in subsequent years, males originally banded as after-hatch-year were putatively called age 2 if resighted the next year, age 3 if resighted the year after that, etc., which likely underestimated the true age of some males. However, due to the high capture rate of individuals in our population and very low dispersal of males older than 1 yr, the majority of males aged as after-hatch-year at first capture were likely 1 yr old. Males for whom age was precisely known (either banded as nestlings or captured as hatch-year birds) were placed into the age category that corresponded to their true age.

Assessment of Display Behavior

Red-backed Fairywren males engage in forays and courtship displays that are directed primarily at extrapair females (see Mulder 1997, Green et al. 1995, Karubian 2002). Males have been observed making forays to display to females at least 60 days prior to the onset of nest building and throughout the extrapair females' breeding

cycle, even late in the season when females have fledglings and are unlikely to breed again until the next year (A. L. Potticary personal observation). We defined a foray as a male departing from his own territory and entering, alone, onto another male's territory. A common display is the "puff-back," in which males erect the red scapulars and back feathers over the wings (Rowley and Russell 1997), sometimes accompanied by a vigorous head-bobbing motion (M. S. Webster personal observation). Males also carry red or pink petals from *Banksia* sp. and *Lantana* sp., or red seeds from *Gahnia* sp.; these ornaments are reddish in coloration and match the red backs of males in nuptial plumage, and thus are thought to increase male attractiveness to potential extrapair mates (see Karubian and Alvarado 2003). During forays, males also carry food into other territories for the purpose of feeding extrapair mates (A. L. Potticary personal observation). Additionally, we observed "female sexual chases," in which males chased the female for prolonged bouts. Group members respond aggressively to intruding males through chasing, duetting (a territory defense behavior; Dowling and Webster 2013), countersinging, and alarm calling. All displays were recorded, during both focal behavioral observations and opportunistic observations.

Behavioral Observations

We quantified behavior by observing focal males for 60 min. These focal observations were performed during the incubation ($n = 29$) and nestling periods ($n = 25$) on pairs both with and without helpers. Observations during the nestling period were performed when the nestlings were 3–5 days old. During focal observation periods, we collected data on guarding, nesting behaviors, and foray rates of breeding males to estimate male time allocation. We quantified guarding as the amount of time that a male spent: (1) <10 m from a female, (2) performing sentinel behavior (when a male was perched vigilantly near a female, not foraging or preening for >60 sec, and continued vigilant behavior until he resumed other activities), and (3) <20 m from the nest. Criterion distances for guarding were selected as the upper limits of distance between birds moving dynamically as a group in the field; in practice, birds were often much closer together and guarding could be easily inferred from reciprocal movements, contact calling, and cohesive responses of group members to intruders. These data were collected continuously, with times measured using a stopwatch. We also recorded the number of male extraterritorial forays, mating displays, vocalizations, and nestling feeding rates, and counted the number of intrusions into the focal territory by other males. We were able to determine when males left and returned to a territory because males used long, direct flights when making forays or returning (see Mulder 1997, Rowley and

Russell 1997, Karubian 2002). Behavioral data were calculated as rate per 60 min (with the exception of the time that a male was <10m from a female, which was calculated as a proportion of the time that the female was not incubating or brooding), and these rates were used in subsequent analyses.

Additional data on extraterritorial forays were collected opportunistically throughout the season whenever we encountered a male in another's territory. For opportunistic observations of forays, we recorded the intruding male's identity, breeding status, age, whether he was breeding with or without a helper at his social nest, and the displays performed. Opportunistic foray data were collected in the daily process of population monitoring, and effort was approximately equal across the site, reducing potential observer bias in the dataset.

Survival Analyses

Survival was estimated from long-term data collected at both the Moomin and Kalinvale sites during the 2005–2012 breeding seasons, including a total of 515 males. In order to analyze the influence of helper presence on the survival of breeding males, survival probabilities were calculated using multistate capture–recapture models (see Varian-Ramos 2008, Pruett-Jones et al. 2010) in program MARK (White and Cooch 2008) and RMark (Laake 2013). This method simultaneously estimates the probabilities of survival (S), resighting (p), and state change (ψ; in this case, the probability of changing from being a breeding male with helpers to one without, and vice versa). Breeding males were categorized into 3 groups: (1) male breeding without helper, (2) male breeding with helper, and (3) male resighted, but breeding status unknown. Only breeding males in the first 2 groups (i.e. males of known breeding status) were included in survival analyses. Each of the 3 probabilities (survival, resighting, and state change) can be modeled as a function of year, helper presence, year*helper presence, and as a constant, giving a total of 64 possible candidate models. We tested for overdispersion in the global model using the U-CARE goodness-of-fit test for the Jolly-Movement (JMV) model ($\hat{c} = 0.923$, $\chi^2 = 73.869$, df = 80), in which a $\hat{c} < 1$ does not require adjustment for overdispersion (White and Cooch 2008). For the purpose of analyses, $\hat{c}$ was set to the standard value of 1. Later analyses of the most parsimonious model displayed an estimated $\hat{c} = 1.04$ when modeled using Markov chain Monte Carlo (MCMC) estimation (White and Cooch 2008), which is within theoretical confines. The number of models run was constrained by making a priori assumptions based on the biology of the birds and project study methods. We assumed that p varied with year and group composition because of differences in field personnel, bird behavior across years, and the potential for some group compositions to be more detectable than others. S was

TABLE 1. Based on a priori assumptions, these models were selected to estimate the survival (S), detection probability (p), and probability of transitioning between breeding states (with nonbreeding helper and without; ψ) for male Red-backed Fairywrens near Herberton, Queensland, Australia, from the 2005 to 2012 breeding seasons. Differences in Akaike's Information Criterion corrected for small sample sizes (ΔAIC_c) and model weights (w_i) were used to rank models. Parameters (K) were modeled as either dependent or independent, or as a factorial (i.e. gt = helper presence*year, where "g" is the presence or absence of a helper and "t" is year). The model deviance (Dev) is also shown. The global model $S(gt)p(gt)\psi(gt)$ is included as the last model.

Model	K	Dev	ΔAIC_c	w_i
$S(gt)p(gt)\psi(g)$	47	482.71	0.00 [a]	0.99
$S(t)p(gt)\psi(g)$	33	523.07	9.65	0.01
$S(.)p(gt)\psi(g)$	28	543.80	19.66	0.00
$S(g)p(gt)\psi(g)$	30	540.91	21.05	0.00
$S(t)p(gt)\psi(gt)$	70	462.82	32.79	0.00
$S(.)p(gt)\psi(gt)$	64	490.70	46.65	0.00
$S(g)p(gt)\psi(gt)$	66	490.08	50.68	0.00
$S(gt)p(gt)\psi(.)$	42	552.48	58.68	0.00
$S(gt)p(gt)\psi(t)$	49	545.04	66.79	0.00
$S(t)p(gt)\psi(.)$	28	597.76	73.62	0.00
$S(t)p(gt)\psi(t)$	34	590.25	78.99	0.00
$S(.)p(gt)\psi(.)$	23	625.47	90.73	0.00
$S(g)p(gt)\psi(.)$	25	621.36	90.84	0.00
$S(.)p(gt)\psi(t)$	29	620.04	98.03	0.00
$S(g)p(gt)\psi(t)$	31	616.26	98.54	0.00
$S(gt)p(gt)\psi(gt)$	80	433.82	27.62	0.00

[a] The lowest AIC_c value = 2216.26.

modeled as constant over time and as a function of year. S was also modeled as either dependent or independent of breeding male group composition (no helper, helper, or breeding status unknown). The probability of state change (ψ) was modeled as constant, and dependent on helper presence, year, and a factorial combination of year*helper. This resulted in 16 candidate models (Table 1). The relative likelihood of each model was estimated with second-order Akaike's Information Criterion values, or AIC_c (White and Cooch 2008).

Paternity Analyses
DNA was extracted from the red blood cells of samples collected from captured adults and nestlings, and individuals were genotyped using a panel of highly polymorphic microsatellite loci to examine parentage and relatedness within and across groups (see Webster et al. 2008, Baldassarre and Webster 2013). In brief, we PCR-amplified 7 microsatellite loci from the DNA extracted from each individual sample, and size-separated the amplified fragments (alleles) on an ABI Prism 3730 automated sequencer (Applied Biosystems, Foster City, California, USA). Allele sizes were scored for each individual at each locus using the program GeneMapper (Applied Biosystems), and these genotypes were compared across

individuals to determine the parentage of nestlings using CERVUS 3.0 (Kalinowski et al. 2007). Across all years in which paternity analyses were performed, the average percentage of offspring to which we were able to assign a sire was ~82% (range: ~67–93%). All males that were actively monitored within the field sites were captured to collect a blood sample. Of 317 active males across 5 yr of paternity data, 315 candidate sires were tested, meaning that we tested ~99% of candidate sires. However, there may have been unsampled candidate sires that held territories around the periphery of the study sites. Thus, for paternity analyses, we set the percentage of candidate sires included in the analyses at 85%, which was likely a conservative estimate.

Statistical Analyses
Behavioral observations were analyzed to determine the amount of time that breeding males with and without helpers spent guarding, making forays, and engaging in nesting behaviors in the postfertile stage (incubation and nestling periods). All proportions from behavioral observations were arcsine-root transformed, assessed for normality using a Shapiro-Wilk W test, and analyzed using ANOVA and Student's t-tests if normally distributed. If transformation failed to normalize the distribution, nonparametric tests (Wilcoxon rank-sum and Spearman's rank correlation coefficient tests) were applied. All statistics were performed using JMP 8 software (SAS Institute, Cary, North Carolina, USA). All measures of male time allocation and the opportunistic foray data were also analyzed using mixed-effects models, with male age as a categorical variable (old vs. young due to low sample size of known-age males), the presence or absence of a helper and male age*helper presence as fixed effects, and accounting for replication between groups by using group identifier as a random effect. Helper presence or absence was included as a categorical variable because the vast majority of groups had only 1 helper (1/182 groups had >1 helper). Paternity analyses were conducted using mixed-effects models, including the presence or absence of a helper, male age (as a continuous variable), and male age*helper presence as fixed effects, and accounting for replication between groups by using male identifier as a random effect. For paternity analyses incorporating male age, only males of known age were included. Data are presented as means ± standard error unless otherwise stated. Some opportunistic foray data were analyzed using contingency tables and chi-square tests for observed vs. expected numbers of males making forays from each age category, mean number of forays and number of displays observed for males of each age, and group composition (presence or absence of a helper). Expected values were derived using the relative proportion of old vs. young males in the overall population and assuming that males
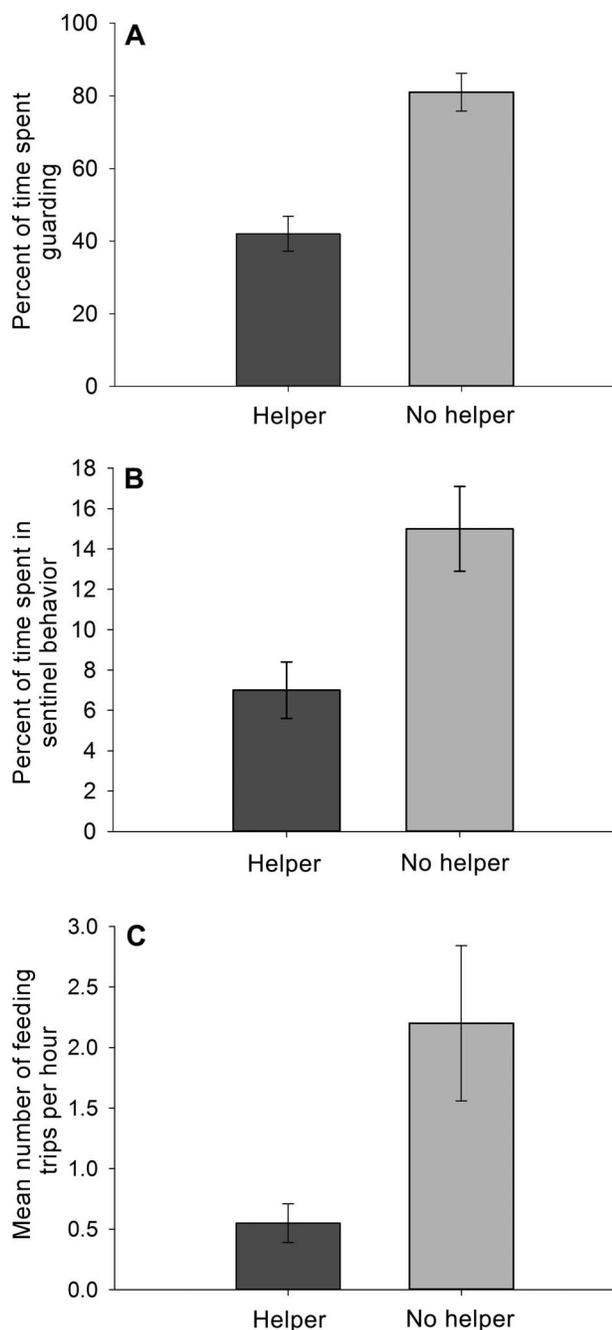
FIGURE 1. (A) Mean percentage of time of the observation period that breeding Red-backed Fairywren males with and without nonbreeding helpers engaged in guarding behavior (time that the male was <10 m from the female, <20 m from the nest, or both; $P < 0.001$); (B) Percentage of observation time that breeding males with and without helpers performed sentinel behavior ($P < 0.01$); and (C) Mean number of feeding trips per hour ($P = 0.05$) of breeding males near Herberton, Queensland, Australia, from October 2011 to January 2012. Error bars represent ±1 SE.

should be observed making forays at a frequency similar to their representation in the population. Mixed-effects models including male age, helper presence, and male age*helper presence as fixed effects and male color band combination as a random effect were also applied to opportunistic foray data.

RESULTS

Time Allocation of Breeding Males

Breeding males without helpers spent more time guarding their mates (81 ± 5% vs. 42 ± 5% of observation time; $F = 27.10$, df = 1 and 20, $P = <0.001$; Figure 1A) and performing sentinel behavior (15 ± 2% vs. 7 ± 1% SD; Wilcoxon rank-sum test: $Z = -2.96$, $P < 0.01$; Figure 1B) than did males with helpers. Breeding males without helpers also provisioned nestlings more often than males with helpers (2.20 ± 0.64 vs. 0.55 ± 0.16 trips per hour; Wilcoxon rank-sum test: $Z = -1.67$, $P = 0.05$; Figure 1C). Neither male age category ($F = 0.31$, df = 1 and 22, $P = 0.58$) nor its interaction with helper presence ($F = 1.35$, df = 1 and 22, $P = 0.26$) predicted guarding or feeding behavior.

In contrast, in the systematic focal observations, male foray frequency and duration were unrelated to helper presence (frequency: $F = 1.20$, df = 1 and 31, $P = 0.28$; duration: $F = 2.74$, df = 1 and 18, $P = 0.11$), and in the opportunistic foray sampling, frequency was similarly unrelated to helper presence (frequency: $F = 0.11$, df = 3 and 32, $P = 0.75$). Focal observations showed that males made more forays during the incubation stage (1.02 ± 0.21 departures per observation hour) than during the nestling period (0.41 ± 0.21 departures; $F = 4.91$, df = 1 and 28, $P = 0.04$), with an average foray duration across both stages of 4.81 ± 0.85 min.

Male foray behavior did appear to be associated with male age. Although systematic observations showed no relationship between male age and foray behavior ($F = 3.16$, df = 1 and 25, $P = 0.10$), opportunistic sampling indicated that older breeding males made considerably more forays within the breeding season (10.00 ± 1.56 forays) than did younger breeding males (1.70 ± 3.06 forays; $F = 6.93$, df = 3 and 32, $P = 0.01$; Figure 2). Additionally, in opportunistic observations, a greater percentage of older males than younger males were observed making forays (71% vs. 14% of total males in the population of each age group, respectively; $\chi^2 = 18.38$, $P < 0.001$). Finally, older males were responsible for the majority of displays observed during opportunistic observations within the season (97% of petal carries, $n = 44$; 95% of food carries, $n = 44$; and 94% of puff-back displays, $n = 83$), which is more than expected based upon their relative proportion in the population (χ^2 tests, petal carries: $P =$
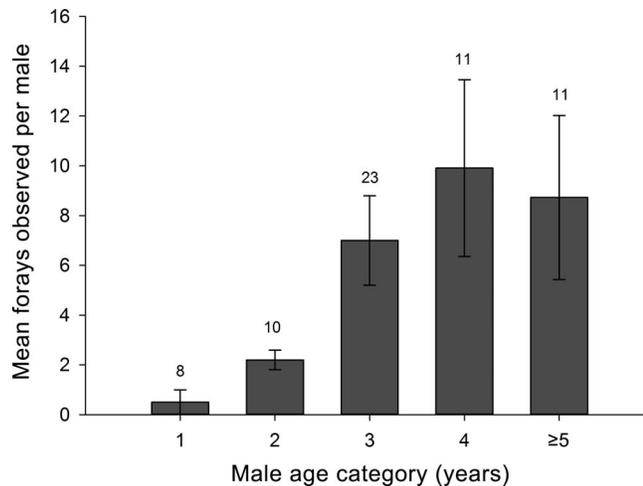
FIGURE 2. Mean number of forays opportunistically observed per male of each estimated age group of Red-backed Fairywrens at the Kalinvale site near Herberton, Queensland, Australia, from October 2011 to January 2012 ($P < 0.001$). Error bars represent standard error with significant differences. The numbers over the bars represent the sample size of males observed foraging from each age category.

0.05; food carries: $P = 0.05$; and puff-back displays: $P = 0.05$).

Paternity Analyses

Males with helpers did not sire more extrapair young than males without helpers (1.07 ± 1.39 SD and 1.00 ± 1.35 SD mean offspring, respectively; $F = 0.16$, df $= 1$ and 307, $P = 0.69$), nor was there a significant interaction between male age and helper presence ($F = 0.85$, df $= 1$ and 165, $P = 0.36$). Likewise, within-pair paternity for males breeding with and without helpers did not differ (0.65 ± 0.83 SD and 0.94 ± 1.08 SD mean offspring, respectively; $F = 1.66$, df $= 1$ and 230, $P = 0.20$). However, taken together, males with helpers sired fewer total offspring (extrapair + within-pair) within a season than did males without helpers (2.25 ± 1.00 SD and 2.61 ± 1.68 SD total offspring, respectively; $F = 2.82$, df $= 1$ and 66, $P = 0.03$; Figure 3A). Male age did not affect the number of extrapair offspring sired ($F = 1.62$, df $= 1$ and 163, $P = 0.21$), but was negatively correlated with loss of within-pair paternity, with older males being cuckolded less frequently than younger males (Spearman rank correlation coefficients, $r_s = -0.18$, $P = 0.04$; Figure 3B). Overall, male age did not affect the total number of offspring produced ($F = 0.99$, df $= 1$ and 121, $P = 0.43$). Lastly, helpers were found to be helping their genetic father only 21% of the time, whereas helpers were helping their genetic mother 77% of the time.

Survival Analyses

The best model included survival as a function of an interaction between year and helper presence and the
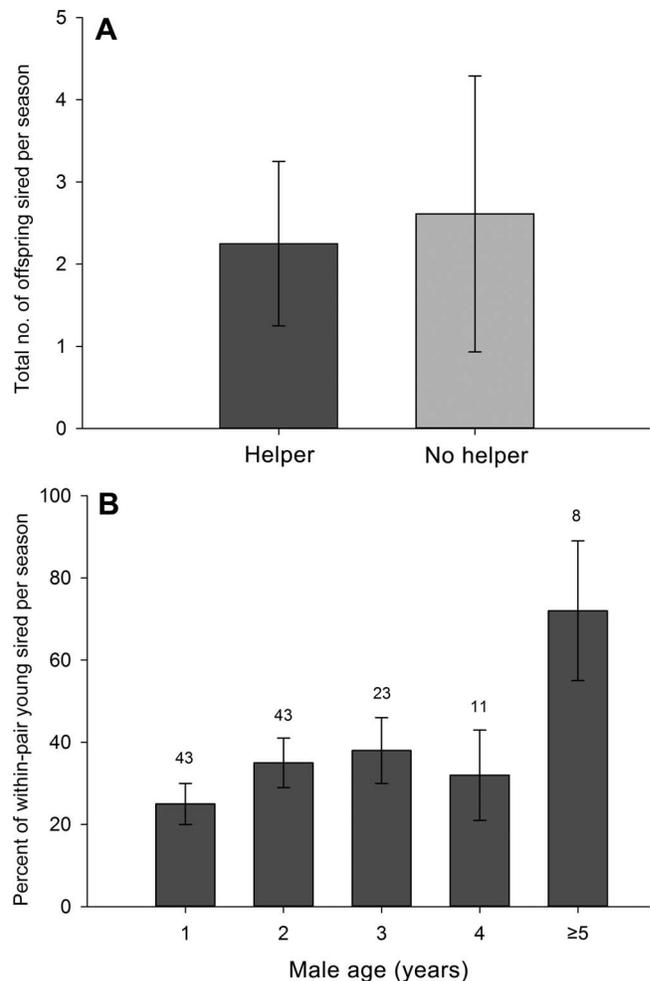
FIGURE 3. (**A**) Total number of offspring (including all extrapair and within-pair offspring) sired within a breeding season by Red-backed Fairywren males with and without nonbreeding helpers ($F = 2.82$, df $= 15$ and 66, $P = 0.03$); and (**B**) Older males were cuckolded less frequently relative to younger males (Spearman rank correlation coefficient, $r_s = -0.17$, $P = 0.04$) near Herberton, Queensland, Australia, in the 2005–2012 breeding seasons. Error bars represent ± 1 SE. The numbers over the bars are sample sizes.

probability of state change as a function of helper presence (Table 1 and Appendix Table 2). The average survival probability was ~64% and ~59% for males with and without helpers, respectively, with yearly fluctuations in survival probability demonstrated in Figure 4. The probability of state change (ψ), or the probability of a breeding male gaining or losing a helper, depended on male group composition. The probability of a male gaining a helper from one breeding season to the next was 19 ± 2%, whereas the probability of a male losing a helper was 54 ± 6%. The probability of detection (p) for males with helpers was >99% and for males without helpers was 95%.
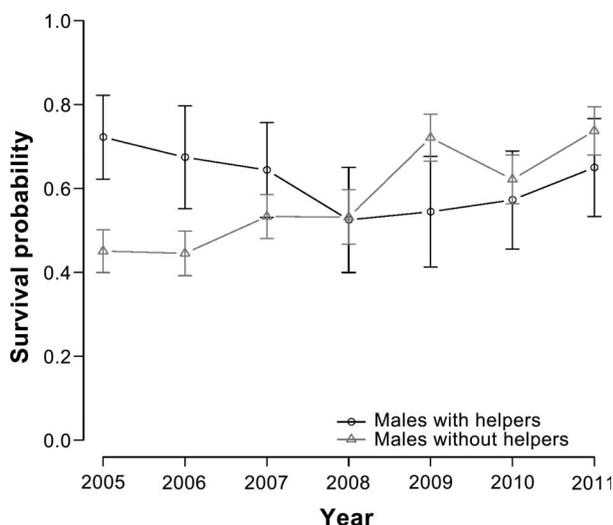
FIGURE 4. Annual survival probability of breeding Red-backed Fairywren males to the subsequent breeding season near Herberton, Queensland, Australia, from the 2005 to 2012 breeding seasons, as graphed from the best-fit model that included year*helper presence.

DISCUSSION

The presence of social offspring from previous nests (helpers) may allow breeding males to shift their behavior in order to gain fitness benefits that might offset the potential costs associated with helper retention. Such behavioral shifts may decrease the costs of within-pair reproduction, resulting in increased survival or extrapair reproductive success. We found that breeding males with helpers altered their behavior in several ways, including investing less time in guarding behaviors and feeding nestlings less frequently (Figure 1). Yet, even though breeding males decreased their within-pair reproductive investment in the presence of a helper, these behavioral differences did not translate into clear survival or reproductive benefits.

Breeding males substantially changed their guarding behavior when breeding in a group (i.e. with a helper), which has several potential implications. Lower within-pair paternity is thought to result because assistance provided by helpers frees females to choose extrapair partners without the risk of reduced parental assistance (Mulder et al. 1994), although other explanations are possible. For example, lower within-pair reproductive success of males with helpers (Varian-Ramos 2008) may simply follow from decreased mate-guarding. Fairywrens perform repeated, conspicuous displays throughout the breeding season (Rowley and Russell 1997, Karubian and Alvarado 2003), and mate-guarding may prevent the female from seeing and responding to extrapair displays. This would be particularly likely if helpers exhibit poor or

inconsistent female guarding behaviors (Welbergen and Quader 2006). These ideas are not mutually exclusive; helpers may free females to choose alternative partners, and decreased mate-guarding may allow females to be courted by many potential partners.

Behavioral shifts away from within-pair breeding efforts may benefit breeding males if extra time is allocated to increasing extrapair reproduction (Green et al. 1995). However, despite differences in time allocation between males with and without helpers, we found no relationship between helper presence and foray behavior once male age was taken into account. Older males made forays more often and performed a greater proportion of all display types to extrapair females, regardless of helper presence (see also Barron et al. 2015). However, although foray rates were used as a proxy for investment in extrapair reproductive effort, the relationships between foray rate and subsequent paternity were complex. First, breeding males with helpers were found to have lower total reproductive success (extrapair plus within-pair offspring) within a season than males without helpers (Figure 3A). The lack of evidence for increased foray rates of breeding males with helpers is concordant with this result, but it is surprising because it appears that males do not offset loss of within-pair paternity (Varian-Ramos 2008) with increased extrapair success. Second, older males were cuckolded less frequently than younger males (Figure 3B), which is perplexing because older males did not have higher extrapair success, despite a disproportionately greater investment in extrapair reproductive effort. The reasons for this are not clear, but it corroborates evidence that high foray rates do not necessarily lead to high extrapair success (Green et al. 2000), indicating that other factors, such as display quality, likely determine male extrapair reproductive success.

These results may be a corollary of the strong reproductive skew in the population. The majority of offspring were sired by a small number of males, regardless of male age or whether the male had a helper, with more than half of the paired males in the population siring no offspring at all (see also Webster et al. 2008). That there is reproductive skew is perhaps unsurprising, given the wide variety of sexual traits (morphological and behavioral) in this species (Karubian 2002, Karubian and Alvarado 2003). Moreover, the presence of strong reproductive skew may indicate that the costs to breeding males of having helpers are negligible, given that the majority of males sire very few offspring anyway. Overall, the results of our study indicate that the relationships among mate-guarding, helper presence, male age, and subsequent paternity are complicated and most likely driven by female choice (Mulder et al. 1994, Double and Cockburn 2000) and possibly other cryptic factors.

Alternatively to increasing reproductive success, breeding males with helpers may decrease parental investment in order to allocate more time to self-maintenance, potentially resulting in higher annual survival. Overall, there was no difference in annual survival between males with and without helpers, but models incorporating both year and helper presence were best supported, indicating that helpers influenced breeding male survival in some years but not in others. This result is unlikely to have arisen from a purely demographic effect, as the numbers of males breeding with and without helpers were remarkably consistent across all years sampled. One adaptive explanation is that the survival benefits of helpers are only discernible in years of greater hardship. Cooperative breeding is most common in highly variable environments and has been hypothesized to reduce variation in reproductive success across years of varying uncertainty (Jetz and Rubenstein 2011, Rubenstein 2011). Males with helpers decrease within-pair reproductive effort without a concurrent increase in extrapair effort, and this decrease in effort may act to increase survival in difficult years. Anecdotal support for this idea comes from the fact that many males did not breed in one of the study years (2008), in which there was a negligible difference in survival between males with and without helpers, while higher survival was observed in other years. However, when proxies for environmental harshness, such as breeding season rainfall or temperature, were included in analyses, the foremost model was still one that included group and year without either of the environmental variables. While season-wide averages likely do not represent the environmental variance in conditions that males may experience during individual breeding attempts (e.g., breeding early vs. late in the season), this does indicate that weather per se may not provide a mechanistic understanding of this result.

Alternatively, this pattern could be an emergent property of complex interactions between multiple aspects of a breeding males' environment, including ecological factors (Webster et al. 2010, Rubenstein 2011), social environment, age structure, and sex ratio (Pruett-Jones et al. 2010). As such, the strength of selection on the expression of cooperative behavior may vary across years, with fitness benefits being most apparent over a longer time frame and in particular contexts. These potentially interesting mechanisms remain conjecture and are beyond the scope of this study to determine, yet merit future research.

This study found little evidence that breeding males had higher reproductive success or consistently higher survival in the presence of helpers. There are several explanations for these findings. While the indirect benefits of retaining helpers are likely to be low given that helpers are seldom related to the breeding male, it is possible that the costs of evicting a potential son outweigh the benefits of evicting a potentially unrelated male. Accidental eviction of sons would be particularly costly if sons benefit greatly from remaining with the family group, either through increased survival or future reproductive success. Further, this scenario would be especially likely if males are unable to distinguish between sons and extrapair young and males do not have additional cues of female infidelity. Moreover, the cost (decreased within-pair paternity) of retaining helpers may be fundamentally negligible given the strong reproductive skew in the population. Lastly, it is possible that the costs and benefits of helper presence change according to ecological context among years, perhaps only becoming evident in certain years. Overall, the interactions between breeding investment, survival, and cooperative breeding strategies in populations are complex, with the relevant costs and benefits perhaps only being discernible across time and in various ecological contexts (Webster et al. 2010, Rubenstein 2011).

LITERATURE CITED

Baldassarre, D. T., and M. S. Webster (2013). Experimental evidence that extra-pair mating drives asymmetrical introgression of a sexual trait. Proceedings of the Royal Society of London, Series B 280:20132175. http://dx.doi.org/10.1098/rspb.2013.2175

Barron, D. G., M. S. Webster, and H. Schwabl (2015). Do androgens link morphology and behavior to produce phenotype-specific behavioral strategies? Animal Behaviour 100:116–124.

Clutton-Brock, T. (2002). Breeding together: Kin selection and mutualism in cooperative vertebrates. Science 296:69–72.

Cockburn, A. (1998). Evolution of helping behavior in cooperatively breeding birds. Annual Reviews in Ecology and Systematics 29:141–177.

Cockburn, A. (2006). Prevalence of different modes of parental care in birds. Proceedings of the Royal Society of London, Series B 273:1375–1383.

Cockburn, A., R. A. Sims, H. L. Osmond, D. J. Green, M. C. Double, and R. A. Mulder (2008). Can we measure the benefits of help in cooperatively breeding birds: The case of Superb Fairy-Wrens Malurus cyaneus? Journal of Animal Ecology 77:430–438.

Covas Monteiro, R. (2002). Life-history evolution and cooperative breeding in the Sociable Weaver. Ph.D. dissertation, Percy FitzPatrick Institute, University of Cape Town, Rondebosch, Cape Town, South Africa.

Dierkes, P., M. Taborsky, and U. Kohler (1999). Reproductive parasitism of broodcare helpers in a cooperatively breeding fish. Behavioral Ecology 10:510–515.

Double, M., and A. Cockburn (2000). Pre-dawn infidelity: Females control extra-pair mating in Superb Fairy-Wrens. Proceedings of the Royal Society of London, Series B 267:465–470.

Double, M. C., and A. Cockburn (2003). Subordinate Superb Fairy-Wrens (Malurus cyaneus) parasitize the reproductive success of attractive dominant males. Proceedings of the Royal Society of London, Series B 270:379–384.

Dowling, J. L., and M. S. Webster (2013). The form and function of duets and choruses in Red-backed Fairy-Wrens. Emu 113:282–293.

Dunn, P. O., A. Cockburn, and R. A. Mulder (1995). Fairy-Wren helpers often care for young to which they are unrelated. Proceedings of the Royal Society of London, Series B 259:339–343.

Eguchi, K., S. Yamagishi, S. Asai, H. Nagata, and T. Hino (2002). Helping does not enhance reproductive success of cooperatively breeding Rufous Vanga in Madagascar. Journal of Animal Ecology 71:123–130.

Emlen, S. T. (1991). Evolution of cooperative breeding in birds and mammals. In Behavioural Ecology: An Evolutionary Approach, third edition (J. R. Krebs and N.B. Davies, Editors). Blackwell Publishing, Oxford, UK. pp. 301–337.

Green, D. J., A. Cockburn, M. L. Hall, H. Osmond, and P. O. Dunn (1995). Increased opportunities for cuckoldry may be why dominant male fairy-wrens tolerate helpers. Proceedings of the Royal Society of London, Series B 262:297–303.

Green, D. J., H. L. Osmond, M. C. Double, and A. Cockburn (2000). Display rate by male fairy-wrens (Malurus cyaneus) during the fertile period of females had little influence on extrapair mate choice. Behavioral Ecology and Sociobiology 48:438–446.

Hamilton, W. D. (1964). The genetical theory of social behaviour. Journal of Theoretical Biology 7:1–52.

Heinsohn, R. G. (1991). Slow learning of foraging skills and extended parental care in cooperatively breeding White-winged Choughs. American Naturalist 137:864–881.

Jetz, W., and D. R. Rubenstein (2011). Environmental uncertainty and the global biogeography of cooperative breeding in birds. Current Biology 21:72–78.

Kalinowski, S. T., M. L. Taper, and T. C. Marshall (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Molecular Ecology 16:1099–1106.

Karubian, J. (2002). Costs and benefits of variable breeding plumage in the Red-backed Fairy-Wren. Evolution 56:1673–1682.

Karubian, J., and A. Alvarado (2003). Testing the function of petal-carrying in the Red-backed Fairy-Wren (Malurus melanocephalus). Emu 103:87–92.

Koenig, W., and J. Dickinson (Editors) (2004). Ecology and Evolution of Cooperative Breeding in Birds. Cambridge University Press, Cambridge, UK.

Laake, J. L. (2013). RMark: An R Interface for Analysis of Capture–Recapture Data with MARK. AFSC Processed Report 2013-01, Alaska Fisheries Science Center, NOAA National Marine Fisheries Service, Seattle, WA, USA.

Ligon, J. D., S. H. Ligon, and H. A. Ford (2010). An experimental study of the bases of male philopatry in the cooperatively breeding Superb Fairy-Wren Malurus cyaneus. Ethology 87:134–148.

Magrath, R. D., and S. M. Yezerinac (1997). Facultative helping does not influence reproductive success or survival in cooperatively breeding White-browed Scrubwrens. Journal of Animal Ecology 66:658–670.

Mulder, R. A. (1997). Extra-group courtship displays and other reproductive tactics of Superb Fairy-Wrens. Australian Journal of Zoology 45:131–143.

Mulder, R. A., P. O. Dunn, A. Cockburn, K. A. Lazenby-Cohen, and M. J. Howell (1994). Helpers liberate female fairy-wrens from constraints on extra-pair mate choice. Proceedings of the Royal Society of London, Series B 255:223–229.

Pruett-Jones, S., E. I. Greig, M. Rowe, and E. A. Roche (2010). The effects of sex, age, and social status on annual survival in the Splendid Fairy-Wren. The Condor 112:369–377.

Rowe, M., J. P. Swaddle, S. Pruett-Jones, and M. S. Webster (2010). Plumage coloration, ejaculate quality and reproductive phenotype in the Red-backed Fairy-Wren. Animal Behaviour 79:1239–1246.

Rowley, I., and E. Russell (1997). Fairy-Wrens and Grasswrens. Oxford University Press, Oxford, UK.

Rubenstein, D. R. (2011). Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. Proceedings of the National Academy of Sciences USA 108:10816–10822.

Russell, A. F., N. E. Langmore, A. Cockburn, L. B. Astheimer, and R. M. Kilner (2007). Reduced egg investment can conceal helper effects in cooperatively breeding birds. Science 317:941–943.

Schodde, R. (1982). The Fairy-Wrens: A Monograph of the Maluridae. Lansdowne Editions, Melbourne, Australia.

Stacey, P. B., and J. D. Ligon (1991) The benefits-of-philopatry hypothesis for the evolution of cooperative breeding:

Variation in territory quality and group size effects. American Naturalist 137:831–846.

Varian-Ramos, C. W. (2008). Reproductive strategies of females in the Red-backed Fairy Wren (*Malurus melanocephalus*). Ph.D. dissertation, Washington State University, Pullman, WA, USA.

Varian-Ramos, C. W., J. Karubian, V. Talbott, I. Tapia, and M. S. Webster (2010). Offspring sex ratios reflect lack of repayment by auxiliary males in a cooperatively breeding passerine. Behavioral Ecology and Sociobiology 64:967–977.

Varian-Ramos, C., W. R. Lindsay, J. Karubian, and M. S. Webster (2012). Female Red-backed Fairy-Wrens (*Malurus melanoce-phalus*) do not appear to pay a cost for high rates of promiscuity. The Auk 129:529–536.

Webster, M. S., J. Karubian, and H. Schwabl (2010). Dealing with uncertainty: Flexible reproductive strategies by a tropical passerine in an unstable ecological and social environment. Advances in the Study of Behavior 42:123–153.

Webster, M. S., K. A. Tarvin, E. M. Tuttle, and S. Pruett-Jones (2004). Reproductive promiscuity in the Splendid Fairy-Wren: Effects of group size and auxiliary reproduction. Behavioral Ecology 15:907–915.

Webster, M. S., C. W. Varian, and J. Karubian (2008). Plumage color and reproduction in the Red-backed Fairy-Wren: Why be a dull breeder? Behavioral Ecology 19:517–524.

Welbergen, J. A., and S. Quader (2006). Mother guarding: How offspring may influence the extra-pair behaviour of their parents. Proceedings of the Royal Society of London, Series B 273:2363–2368.

Westneat, D. F. (1994). To guard mates or go forage: Conflicting demands affect the paternity of male Red-winged Blackbirds. American Naturalist 144:343–354.

White, G. C., and E. G. Cooch (Editors) (2008). Program Mark: A Gentle Introduction, seventh edition. http://www.phidot.org/software/mark/docs/book/

APPENDIX TABLE 2. Model outputs for estimates of mean survival (S), detection probability (p), and the probability of transitioning between breeding states (with nonbreeding helper and without; ψ), standard deviation (SD), and 95% confidence limits per year for Red-backed Fairywren males with helpers (Helper), without helpers (No helper), and males of unknown group composition (Unknown) as determined by the top model, $S(gt)p(gt)\psi(g)$ (Table 1).

Parameters		Mean	SD	Lower 95% CL	Upper 95% CL
1: S	1: No helper	0.449	0.051	0.353	0.549
2: S	1: No helper	0.439	0.052	0.342	0.542
3: S	1: No helper	0.553	0.057	0.441	0.660
4: S	1: No helper	0.509	0.063	0.386	0.630
5: S	1: No helper	0.717	0.055	0.598	0.812
6: S	1: No helper	0.614	0.056	0.500	0.716
7: S	1: No helper	0.919	161.626	1.118 E−303	1.000
8: S	2: Helper	0.722	0.100	0.495	0.874
9: S	2: Helper	0.674	0.123	0.409	0.860
10: S	2: Helper	0.663	0.117	0.412	0.846
11: S	2: Helper	0.516	0.125	0.286	0.740
12: S	2: Helper	0.545	0.132	0.297	0.773
13: S	2: Helper	0.573	0.117	0.345	0.774
14: S	2: Helper	0.794	139.582	3.792 E−304	1.000
15: S	3: Unknown	0.873	0.085	0.604	0.969
16: S	3: Unknown	0.575	0.132	0.319	0.796
17: S	3: Unknown	0.296	0.111	0.129	0.545
18: S	3: Unknown	0.298	0.097	0.146	0.513
19: S	3: Unknown	0.799	0.376	0.039	0.997
20: S	3: Unknown	0.762	0.122	0.461	0.923
21: S	3: Unknown	0.386	67.814	1.383 E−244	1.000
22: p	1: No helper	1.000	0.000	1.000	1.000
23: p	1: No helper	1.000	1.159 E−08	1.000	1.000
24: p	1: No helper	0.828	0.086	0.594	0.940
25: p	1: No helper	1.000	3.611 E−08	0.999	1.000
26: p	1: No helper	1.000	4.196 E−08	0.999	1.000
27: p	1: No helper	1.000	1.027 E−08	1.000	1.000
28: p	1: No helper	0.747	131.368	2.910 E−304	1.000
29: p	2: Helper	1.000	2.662 E−07	0.999	1.000
30: p	2: Helper	1.000	2.518 E−07	0.999	1.000
31: p	2: Helper	1.000	2.857 E−08	0.999	1.000
32: p	2: Helper	1.000	1.375 E−06	0.999	1.000
33: p	2: Helper	1.000	2.104 E−07	0.999	1.000
34: p	2: Helper	1.000	2.138 E−07	0.999	1.000
35: p	2: Helper	0.920	161.839	1.137 E−303	1.000
36: p	3: Unknown	0.841	0.140	0.403	0.976
37: p	3: Unknown	0.620	0.221	0.207	0.911
38: p	3: Unknown	1.000	1.645 E−07	0.999	1.000
39: p	3: Unknown	0.108	0.113	0.012	0.545
40: p	3: Unknown	0.526	0.215	0.170	0.858
41: p	3: Unknown	0.617	0.174	0.276	0.872
42: p	3: Unknown	0.706	124.088	2.363 E−304	1.000
43: ψ	ψ 1 to 2	0.190	0.022	0.150	0.238
44: ψ	ψ 1 to 3	0.136	0.023	0.097	0.189
45: ψ	ψ 2 to 1	0.536	0.058	0.423	0.646
46: ψ	ψ 2 to 3	0.147	0.044	0.079	0.256
47: ψ	ψ 3 to 1	0.558	0.062	0.436	0.674
48: ψ	ψ 3 to 2	0.101	0.034	0.051	0.191