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Author(s): Claire W. Varian-Ramos, Willow R. Lindsay, Jordan Karubian, and Michael S. Webster

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FEMALE RED-BACKED FAIRY-WRENS (*MALURUS MELANOCEPHALUS*) DO NOT APPEAR TO PAY A COST FOR HIGH RATES OF PROMISCUITY

CLAIRE W. VARIAN-RAMOS,^{1,3} WILLOW R. LINDSAY,¹ JORDAN KARUBIAN,² AND MICHAEL S. WEBSTER^{1,4}

¹*School of Biological Sciences, Washington State University, Pullman, Washington 99164, USA; and*

²*Department of Ecology and Evolutionary Biology, Tulane University, 400 Lindy Boggs Center, New Orleans, Louisiana 70118, USA*

ABSTRACT.—Males of monogamous species are expected to increase their overall fitness by engaging in extrapair copulations, but the fitness implications of this behavior for females are somewhat less clear. Numerous studies have examined the potential benefits of extrapair mating to females, but the costs of extrapair mating, which may be substantial, are less well studied. Quantifying these costs is critical to understanding the evolution of extrapair mating behavior in females. We examined the costs of extrapair paternity to female Red-backed Fairy-wrens (*Malurus melanocephalus*) using an 8-year data set that allowed us to examine both short-term and long-term costs. The variability of individual extrapair mating behavior in female Red-backed Fairy-wrens allowed us to compare the parental care, fecundity, and apparent survival of faithful and promiscuous females. We found no effect of the presence of extrapair offspring on the rate at which males provisioned broods. We also found that promiscuous and faithful females did not differ with respect to apparent annual survival and four indices of reproductive success. These findings suggest that there are few or no costs to extrapair mating in females in this population. Low costs, as documented here, may contribute to the evolution of high extrapair paternity rates observed in many species; thus, our results underscore the importance of both costs and benefits in explaining the evolution of extrapair mating behavior in females. *Received 6 October 2011, accepted 18 April 2012.*

Key words: direct costs, extrapair paternity, *Malurus melanocephalus*, paternal care, reproductive success, survival.

Las Hembras de *Malurus melanocephalus* no Parecen Pagar un Costo por Altas Tasas de Promiscuidad

RESUMEN.—Se espera que los machos de especies monógamas incrementen su aptitud al tener cópulas extrapareja, pero las implicaciones de este comportamiento para la aptitud de las hembras son menos conocidas. Numerosos estudios han examinado los beneficios potenciales de la cópula extrapareja para las hembras, pero los costos de la cópula extrapareja, que pueden ser sustanciales, han sido mucho menos estudiados. Cuantificar dichos costos es crítico para entender la evolución del comportamiento de cópula extrapareja en las hembras. Examinamos los costos de la paternidad extrapareja para las hembras de *Malurus melanocephalus* usando un conjunto de datos de 8 años que nos permitió examinar los costos tanto a corto como a largo plazo. La variabilidad del comportamiento de cópula extrapareja en la hembras de *M. melanocephalus* nos permitió comparar el cuidado parental, la fecundidad y la supervivencia aparente de hembras fieles y promiscuas. No encontramos efecto de la presencia de descendencia extrapareja en la tasa a la que los machos alimentaban a las camadas. Además encontramos que las hembras promiscuas y fieles no diferían con respecto a la supervivencia anual aparente y a cuatro índices de éxito reproductivo. Estos resultados sugieren que los costos de la cópula extrapareja son bajos o inexistentes para las hembras de esta población. Como se documenta aquí, los costos bajos pueden contribuir a la evolución de las altas tasas de paternidad extrapareja observada en muchas especies. De esta manera, nuestros resultados resaltan la importancia tanto de los costos como de los beneficios para explicar la evolución del comportamiento de cópula extrapareja en las hembras.

IT IS NOW clear that extrapair paternity (EPP) is common in many socially monogamous bird species, and also that the frequency of EPP varies widely across populations and species (Petrie and Kempenaers 1998, Griffith et al. 2002). Accordingly, there is considerable interest in determining the factors that account for this

variation (Griffith et al. 2002, Neudorf 2004). One possibility is that the variation in EPP rates is related to ecological factors, such as density and breeding synchrony, which may affect the opportunity for extrapair mating (e.g., Stutchbury and Morton 1995, Westneat and Sherman 1997, Weatherhead and Yezerinac 1998).

³Present address: Biology Department, The College of William and Mary, Williamsburg, Virginia 23187, USA. E-mail: cwramos@wm.edu

⁴Present address: Department of Neurobiology and Behavior, and Cornell Lab of Ornithology, Cornell University, 159 Sapsucker Woods Road, Ithaca, New York 14850, USA.

An alternative explanation, which is not mutually exclusive with the other, is that variation in EPP rates is determined by the costs, as well as the selective benefits, of extrapair mating to females. Given that fitness consequences of EPP are likely to shape female reproductive strategies (Gowaty 1996, Westneat and Stewart 2003), quantifying the costs and benefits of sexually promiscuous behavior by females would be a useful step toward improving our understanding of why EPP rates vary within and among species.

The costs of EPP to females are likely to be direct (see below), whereas the proposed benefits of EPP may be direct (e.g., fertility assurance, added paternal care from extra pair mates) or indirect (e.g., good or compatible genes for the offspring; Jennions and Petrie 2000). When the costs of EPP are high, there would need to be large benefits to females for extrapair mating to evolve as an adaptive female strategy. If benefits are modest and costs high, females should evolve behaviors to resist extrapair copulation attempts by males (Westneat and Stewart 2003), but conflict between extrapair males and females may maintain a low rate of extrapair copulations (Arnqvist and Kirkpatrick 2005). By contrast, when direct costs to females are low, we might expect relatively high rates of EPP, either because females have little reason to resist extrapair copulation attempts or because the benefits of EPP to females outweigh the costs (Cameron et al. 2003, Albrecht et al. 2006). Many studies have assessed the benefits that females gain from extrapair mating (reviewed in Akçay and Roughgarden 2007), but many fewer have examined the potential costs of extrapair mating, and fewer still consider measures of overall female fitness.

There are several potential costs of EPP to females. The most commonly examined cost in biparental species is reduction in paternal care by the social mate (e.g., Dixon et al. 1994, Chuang-Dobbs et al. 2001, Bouwman et al. 2005). Males are predicted to invest less in broods in which they have lower paternity, provided that they are able to assess their relationship to the offspring (Fishman and Stone 2004). This reduction in paternal care may result in reduced reproductive success for the female (e.g., Weatherhead et al. 1994; but see Dunn and Cockburn 1997). Alternatively, females of cooperatively breeding species may take advantage of auxiliary helpers to offset potential reductions in paternal care by cuckolded males (Dunn and Cockburn 1996). In some cooperatively breeding fairy-wrens (Maluridae), for example, females with auxiliary helpers have been found to produce more extrapair young (Mulder et al. 1994, Webster et al. 2004) and invest less in eggs (Russell et al. 2007) than females without auxiliaries. This suggests that the additional nest provisioning provided by auxiliaries allows females to compensate for reduced parental care from social mates (Mulder et al. 1994) and their own reduced investment in eggs (Russell et al. 2007). However, only a few studies have examined the relationships between EPP and offspring feeding by adult males or auxiliary helpers in cooperative species. In Superb Fairy-wrens (*Malurus cyaneus*), males reduce care only in response to lost paternity when auxiliary males are present (Dunn and Cockburn 1996), whereas in Brown Jays (*Psilorhinus morio*), the dominant male does not alter feeding rates on the basis of paternity (Williams and Hale 2008). Thus, the effects of male retaliation or compensation by auxiliaries in cooperative species remain unclear.

A related cost of EPP to females may be reduced survival. In particular, if females that engage in EPP are forced to offset reduction in male care by increasing their own reproductive effort, this may reduce physiological condition and survival of promiscuous

females. Another potential cost of EPP to females is the energetic investment needed to find a suitable extrapair mate (Dunn and Whittingham 2007), which may be particularly important in fairy-wrens because the female is thought to leave her territory to obtain extrapair copulations in the predawn period (Double and Cockburn 2000). Also, there may be costs associated with the actual act of mating with multiple partners, such as the risk of contracting a sexually transmitted disease (Thrall et al. 2000). Although it is extremely challenging to simultaneously measure each of these potential costs, it is possible to detect whether promiscuity per se is costly by examining female fecundity and survival in relation to EPP using a long-term data set.

We examined the costs of EPP to females in the Red-backed Fairy-wren (*M. melanocephalus*). These small Australian passerines are socially monogamous and breed cooperatively, with young males often remaining on the natal territory as auxiliaries to assist in raising subsequent broods (Schodde 1982, Rowley and Russell 1997). The female is solely responsible for nest construction and incubation, but both sexes and auxiliaries feed nestlings and fledglings (Schodde 1982, Rowley and Russell 1997). Like other members of their genus (Double et al. 1997, Webster et al. 2004), Red-backed Fairy-wrens have very high EPP rates; ~50% of offspring are sired by extrapair males, with 37% of broods containing entirely extrapair young and a similar proportion consisting of entirely within-pair young (Webster et al. 2008). Thus, there is also the possibility that the auxiliary males could mitigate the costs of reductions of paternal care in response to EPP (Mulder et al. 1994). These traits make the Red-backed Fairy-wren an ideal species in which to investigate the costs of extrapair paternity. We first assessed whether females suffer short-term fitness costs of EPP by examining whether males reduce their parental care in broods for which they have lower or no paternity, and whether promiscuous females suffer a reduction in several measures of reproductive success. We then assessed long-term fitness costs by testing whether promiscuous females have reduced apparent survival.

METHODS

Field methods.—We studied a population of Red-backed Fairy-wrens located in wet sclerophyll forest surrounding the reservoirs of the Herberton Shire in the Atherton Tablelands of Queensland, Australia (145°25'E, 17°22'S). Research was conducted during the breeding seasons (October–February) of 1998–2000 and 2003–2007 (breeding seasons are designated by the year in which they ended). Because Red-backed Fairy-wrens spend the majority of their time in the understory, we were able to capture them by chasing them into mist nets. From each captured individual, we collected a small (~30 µL) blood sample from the brachial vein for later genetic analysis. All captured individuals received a numbered aluminum band (Australian Bird and Bat Banding Scheme) and a unique combination of three colored leg bands to allow for identification in the field. We unambiguously determined group composition via repeated field observations. Red-backed Fairy-wrens are highly social, and adult members of groups spend the majority of their time in close association, which makes it easy to determine social groups. Most groups on our field site consisted of a breeding male and female, and a smaller number included one (~20%) or more (~2%) auxiliary males (Varian-Ramos et al. 2010). We monitored breeding

attempts for all identified groups. We monitored active nests by visiting them every third day. Nestlings grow rapidly in the first days after hatching and can be aged by observation of size. We banded nestlings on the sixth day after hatching, at which time we collected a small (30 μ L) blood sample from the tarsal vein. All blood samples were stored in lysis buffer (White and Densmore 1992) at 4°C until they were transported to Washington State University.

We measured parental provisioning rates when the nestlings were 7–9 days old. Most provisioning watches were conducted by an observer sitting in a blind 10–15 m from the nest. However, in 2006, a small number of provisioning watches ($n = 10$) were conducted with a video camera and later transcribed using the same protocols that were used by live observers. We set up the blind or video camera and then waited for 10–30 min before collecting provisioning data, to allow the birds to acclimate to the presence of the blind or camera. During the observation period, all visits to the nest were recorded, as well as the identity of the visitor and the type and size of food items brought to the nest. Adults were never observed entering the nest without a food item. All observations were conducted for at least 1 h (mean 3.1 ± 1.5 h). Observations were conducted during the morning and completed before 1000 hours.

Genetic methods.—We extracted DNA using a standard phenol-chloroform procedure (Westneat 1990), then genotyped all individuals using a panel of 10 highly polymorphic microsatellite loci (Webster et al. 2008). DNA was amplified using fluorescently labeled polymerase-chain-reaction primers; the products were visualized using an automated sequencer (model 3130; Applied Biosystems, Carlsbad, California), and alleles were sized using GENEMAPPER, version 3.7. The combined probability of excluding a random male in the population as the sire of a random offspring using this panel of microsatellites was 0.9998. The microsatellite genotypes of all offspring matched their social mother's genotype, indicating that there is little or no egg dumping in this study population. We assigned paternity to offspring following the procedure described in Webster et al. (2008). Briefly, we used CERVUS, version 2.0 (Marshall et al. 1998), to assign fathers to all sampled offspring, but also evaluated all paternity calls from CERVUS using other available data. We assigned paternity to a male ranked lower by CERVUS if (1) a lower-ranked male had fewer mismatches than the top-ranked male, (2) a lower-ranked male with the same number of mismatches as the top-ranked male was the social mate of the female or had sired other young in the brood, or (3) the mismatches of a lower-ranked male could be explained by the presence of a null allele (see Webster et al. 2008). We also did not assign paternity if no male sampled had fewer than two mismatches. In most cases, we accepted the paternity assignments made by CERVUS, but in ~13% of cases, the other sources of data led us to assign paternity to another male.

Statistical methods.—All statistics were performed in SAS, version 9.1 (SAS Institute, Cary, North Carolina). We report means \pm SE throughout. We used generalized linear mixed models (GLMMs) to analyze the parental investment of both males and females, as estimated by the number of provisioning trips made to the nest per hour. We constructed separate models for each sex using a normal distribution and an identity link. For each analysis, we included individual identity and year as random effects. We included proportion of extrapair offspring, presence of an auxiliary male, number of nestlings, and nest initiation date as fixed effects. A previous study in the same population of Red-backed Fairy-wrens

found that young, dull-colored males fed more frequently than older, brighter males (Karubian 2002). However, our data from the present study did not show this effect (results not shown) and, thus, we did not include plumage color as a factor in our analyses.

We also used GLMMs to analyze female reproductive success. Our measures of reproductive success were number of eggs per clutch, number of offspring fledged per successful nest, number of successful nests per year, and number of fledglings produced per year. We included only nests from which we had complete paternity information (i.e., all paternity was assigned for all eggs laid) to ensure that we had accurate measures of extrapair mating effort for females. Because all these data were counts, we used a Poisson distribution and a log link for all models of reproductive success. Each model included female identity and year as random effects and a measure of extrapair mating rate (see below) as a fixed effect.

For our measure of extrapair mating, we used the proportion of extrapair young produced by each female per brood and per year. A female with a large proportion of extrapair young was assumed to have engaged in more extrapair mating than a female with few or no extrapair young. However, because of a numerical artifact, the proportion of extrapair young is related to female reproductive success. On the basis of probability alone, assuming a constant rate of extrapair paternity among all females, females that produce few offspring are more likely to produce either all or no extrapair offspring than females that produce many offspring. For example, a female that produces only a single offspring can either produce all extrapair young or no extrapair young. As a result, analyses that relate reproductive success and the proportion of extrapair offspring tend to show lower reproductive success in females that produce either all or no extrapair offspring and higher reproductive success for intermediate females (Parker and Tang-Martinez 2005). To reduce this numerical artifact in our analysis, we categorized extrapair mating behavior such that the number of offspring would not be expected to be different between the categories based on probability alone. Specifically, we compared females that produced entirely extrapair young in a clutch or in a year with females that produced entirely within-pair young in a clutch or in a year (i.e., we excluded females that produced mixed broods either in a single clutch or in a year, ~30% of our samples). Additionally, it is likely that the extrapair mating behavior of these two categories differs, because females that produced no extrapair young probably engaged in fewer extrapair copulations and more within-pair copulations than females that produced entirely extrapair young. An alternative categorization that also eliminated the numerical artifacts but included more females (comparing females that produced >50% extrapair offspring with females that produced <50% extrapair offspring) produced nearly identical results (analyses not shown).

We compared survivorship rates between females with high or low EPP rates based on resightings of color-banded females between seasons. Females are highly sedentary after natal dispersal and rarely change territories between years (C. W. Varian-Ramos et al. unpubl. data). As in the reproductive-success analysis, we categorized females as having high extrapair mating effort if they produced only extrapair young in a single breeding season, and as having low extrapair mating effort if they produced only within-pair young in a breeding season. Females that produced both extrapair and within-pair offspring within the same year

TABLE 1. Frequency of extrapair young (EPY) in the Red-backed Fairy-wren from the Herberton Shire in the Atherton Tablelands of Queensland, Australia. Data from 1998 to 2005 are similar to those in Webster et al. (2008), but only complete broods are included here. Data from 2006 and 2007 represent additional paternity analyses.

Year	Number of young	Number of broods	Number of EPY (%)	Number of broods with EPY (%)	Number of broods entirely EPY (%)
1998	93	34	63 (68)	26 (76)	16 (47)
1999	131	44	64 (49)	30 (68)	15 (34)
2000	104	34	47 (45)	21 (62)	8 (24)
2003	23	9	13 (57)	5 (56)	4 (44)
2004	62	22	24 (39)	10 (45)	8 (36)
2005	116	38	72 (62)	29 (76)	15 (39)
2006	53	19	36 (68)	16 (84)	9 (47)
2007	91	31	43 (47)	20 (65)	9 (29)

were excluded from the analysis. However, the results were qualitatively unchanged if these females were included (results not shown) and, hence, we do not think that this introduced a bias. We used a GLMM with a binomial distribution and a logit link to test for differences in apparent survival between these two classes of female. Female identity and year were included as random effects, and extrapair mating category (high vs. low) was the fixed effect.

RESULTS

Paternity.—We determined the paternity of 673 young from 231 complete broods. Of these, 362 young (54%) were extrapair, and 158 broods (68%) included at least 1 extrapair offspring. Many females had multiple breeding attempts in a single season (females can produce up to two successful nests in a season, and may re-nest up to five times if nests are depredated), and 67% of females produced at least 1 extrapair offspring in a given breeding season. Extrapair paternity rates varied among years, ranging from 39% in 2004 to 68% in 2006 (Table 1).

Parental care and paternity.—We collected 291 h of provisioning data from 95 observation bouts. In groups without auxiliary helpers, males made 2.9 ± 0.38 provisioning trips h^{-1} (28% of all trips), compared with 7.6 ± 0.70 provisioning trips h^{-1} (72% of all trips) by females. In groups with auxiliary helpers, males made 1.1 ± 0.21 provisioning trips h^{-1} (10% of trips), females made 6.5 ± 0.54 provisioning trips h^{-1} (62% of trips), and auxiliaries made 2.9 ± 0.80 provisioning trips h^{-1} (28% of trips).

We examined factors that affected male parental care in nests for which we had both provisioning data and paternity data ($n = 87$). We found that males with auxiliaries provisioned at a lower rate than males without auxiliaries (Fig. 1; $F = 6.68$, $df = 1$ and 7 , $P = 0.04$) and that males fed less at later nests ($F = 9.10$, $df = 1$ and 7 , $P = 0.02$). Male provisioning rate showed a nonsignificant increase with brood size ($F = 4.03$, $df = 1$ and 7 , $P = 0.08$). However, the proportion of extrapair young in the nest had no effect on male feeding rates ($F = 0.25$, $df = 1$ and 7 , $P = 0.63$). Indeed, we found no difference in feeding rates even between males that raised broods that contained all within-pair young and those that raised broods with only extrapair young (Fig. 2).

Female provisioning rates showed patterns similar to those found in males, in that they were lower when auxiliaries were present (Fig. 1; $F = 6.52$, $df = 1$ and 10 , $P = 0.03$), declined with time

of season ($F = 7.39$, $df = 1$ and 10 , $P = 0.02$), and increased with brood size, although in females the latter pattern was significant ($F = 8.07$, $df = 1$ and 10 , $P = 0.02$). Again, the proportion of extrapair young in the nest did not affect the rate at which females visited the nest ($F = 0.14$, $df = 1$ and 10 , $P = 0.72$).

Female reproductive success and EPP.—We found no difference in the number of eggs in clutches that contained only extrapair young and clutches that contained only within-pair young (Fig. 3A; $F < 0.01$, $df = 1$ and 39 , $P = 0.97$, $n = 157$). Nor did we find a difference between the two groups in the number of young fledged from successful nests

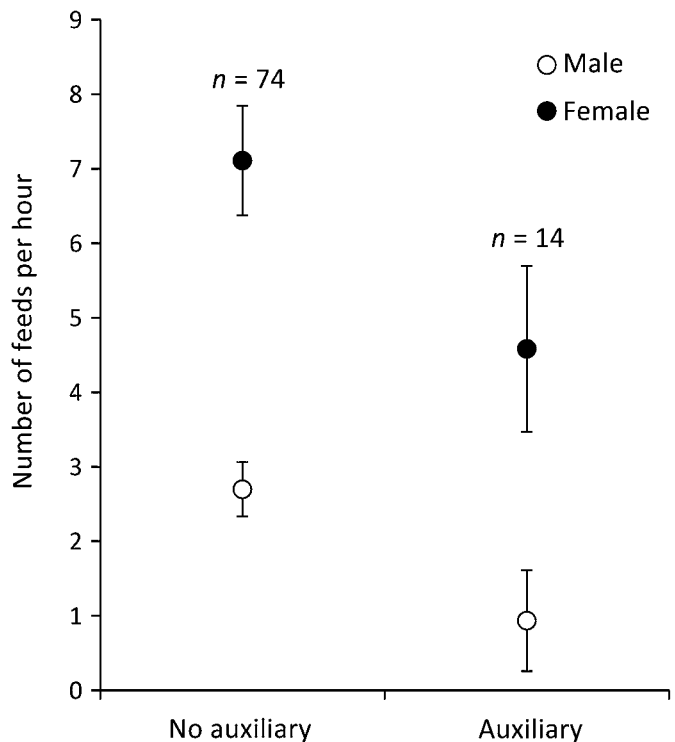


FIG. 1. Provisioning rates of male and female Red-backed Fairy-wrens from the Herberton Shire in the Atherton Tablelands of Queensland, Australia, with and without an auxiliary helper. Data presented are least square means \pm SE from the generalized linear mixed model.

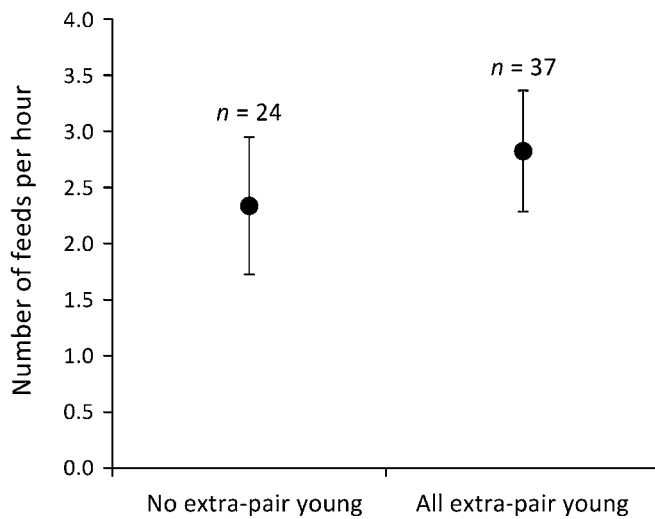


FIG. 2. Provisioning rate of male Red-backed Fairy-wrens from the Herberton Shire in the Atherton Tablelands of Queensland, Australia, to nests that contained either no extrapair young or all extrapair young (number of male visits to the nest per hour). Data presented are least square means \pm SE from the generalized linear mixed model comparing males that fed only extrapair young with males that fed only within-pair young. Provisioning rates do not differ between the two groups ($F = 0.59$, $df = 1$ and 1 , $P = 0.58$).

(Fig. 3B; $F = 0.20$, $df = 1$ and 13 , $P = 0.66$, $n = 75$). Nest predation rates are high in this species, and about half the nests were depredated between banding and fledging. Females that produced only within-pair young within a year did not have more successful nests per year than females that produced only extrapair young within a year (Fig. 3C; $F = 0.05$, $df = 1$ and 30 , $P = 0.82$, $n = 160$), nor did they produce more fledglings per year (Fig. 3D; $F = 0.36$, $df = 1$ and 29 , $P = 0.55$, $n = 160$).

Female apparent survival and EPP.—On average, $61.8 \pm 4.1\%$ of females survived between years. There was no difference in the apparent probability of surviving until the following year between females that produced only extrapair young ($63.5 \pm 6.0\%$) and those that produced only within-pair young ($60.1 \pm 5.7\%$; $F = 0.46$, $df = 1$ and 223 , $P = 0.50$, $n = 225$).

DISCUSSION

Our results indicate that there is little or no cost to producing extrapair young in female Red-backed Fairy-wrens. Males provisioned broods composed partly or wholly of extrapair young at the same rate at which they provisioned nests with no extrapair young. Intuitively, because providing parental care is costly, males should not provide parental care to young to which they are not related (Sheldon 2002). Although some studies have found that males reduced their level of care in response to their paternity (e.g., Dixon et al. 1994, Weatherhead et al. 1994, Chuang-Dobbs et al. 2001), most found no effect (e.g., Kempnaers et al. 1998, Bouwman et al. 2005, Rytönen et al. 2007). There are several possible reasons for males not to adjust their level of paternal care on the basis of their paternity (Westneat and Sherman 1993). First, males may lack reliable cues of their paternity and, thus, reducing the amount of care they provide to a brood would be costly to their

own offspring (Bouwman et al. 2005, Rytönen et al. 2007). Second, there may be other benefits of providing paternal care that encourage males to continue to feed at a high level. For example, males that feed at a high level may be demonstrating that they are of high quality and, thus, ensure more fertilizations in subsequent reproductive attempts with the same female (Freeman-Gallant 1997) or reduce the probability of divorce. Finally, paternal care may not be as costly as is commonly assumed, such that the benefit of providing care to broods of mixed paternity exceeds the cost (Bouwman et al. 2005). If the benefit of providing care to mixed broods is greater than the cost of providing that care, males would be expected to feed in all cases (Whittingham et al. 1992, Westneat and Sherman 1993).

In general, it is possible that the presence of auxiliary helpers liberates females to pursue EPP if these helpers compensate for reduced male parental care (Mulder et al. 1994). The results of our study, however, do not support this hypothesis. Male Red-backed Fairy-wrens do not adjust their feeding rates on the basis of the brood's paternity, and promiscuous females therefore do not require auxiliary males to compensate for reduced paternal care. In Superb Fairy-wrens, males without helpers do not appear to adjust parental care according to the proportion of extrapair young in the nest (Dunn and Cockburn 1996), and a population with relatively few auxiliaries appears to have similar levels of EPP to those found in a population with many auxiliaries (Colombelli-Negrel et al. 2009). On the basis of these findings, it is likely that another explanation underlies the association between high EPP rates and the presence of auxiliaries observed in the fairy-wrens (Mulder et al. 1994, Webster et al. 2004). One possibility is that another factor (e.g., age, territory quality, or local density) increases the chances of a female both engaging in extrapair copulations and having an auxiliary male on her territory. For example, if breeding density is high, females may have more opportunities to engage in extrapair copulations (Westneat and Sherman 1997). Simultaneously, young males may have fewer opportunities to acquire a breeding territory and, thus, may be more likely to remain as auxiliaries on their natal territories (Karubian et al. 2011). Alternatively, because auxiliary males are usually adult sons of the breeding female, females with auxiliary helpers are likely to be older than females without auxiliaries, and age may be a factor that can affect EPP rates in this and other species (Dietrich et al. 2004, Bouwman and Komdeur 2005). In any case, our results suggest that males do not impose a cost of reduced paternal feeding on unfaithful females and, thus, that auxiliaries cannot "liberate" females from those costs.

We also found little or no effect of promiscuity on several components of female fitness. Most studies of the costs of extrapair mating have focused on the potential loss of paternal care, probably because it is the most intuitively important and easiest to measure; other tangible costs are rarely addressed (Arnqvist and Kirkpatrick 2005). However, studies that have found no short-term costs of EPP in terms of nestling size or fledging success may have missed important costs, such as reduced female survival. We were able to address this in our study because female Red-backed Fairy-wrens are sedentary and we had repeated observations of the same females across multiple years but found no evidence that promiscuous females had lower apparent survival. Similarly, in all four of our measures

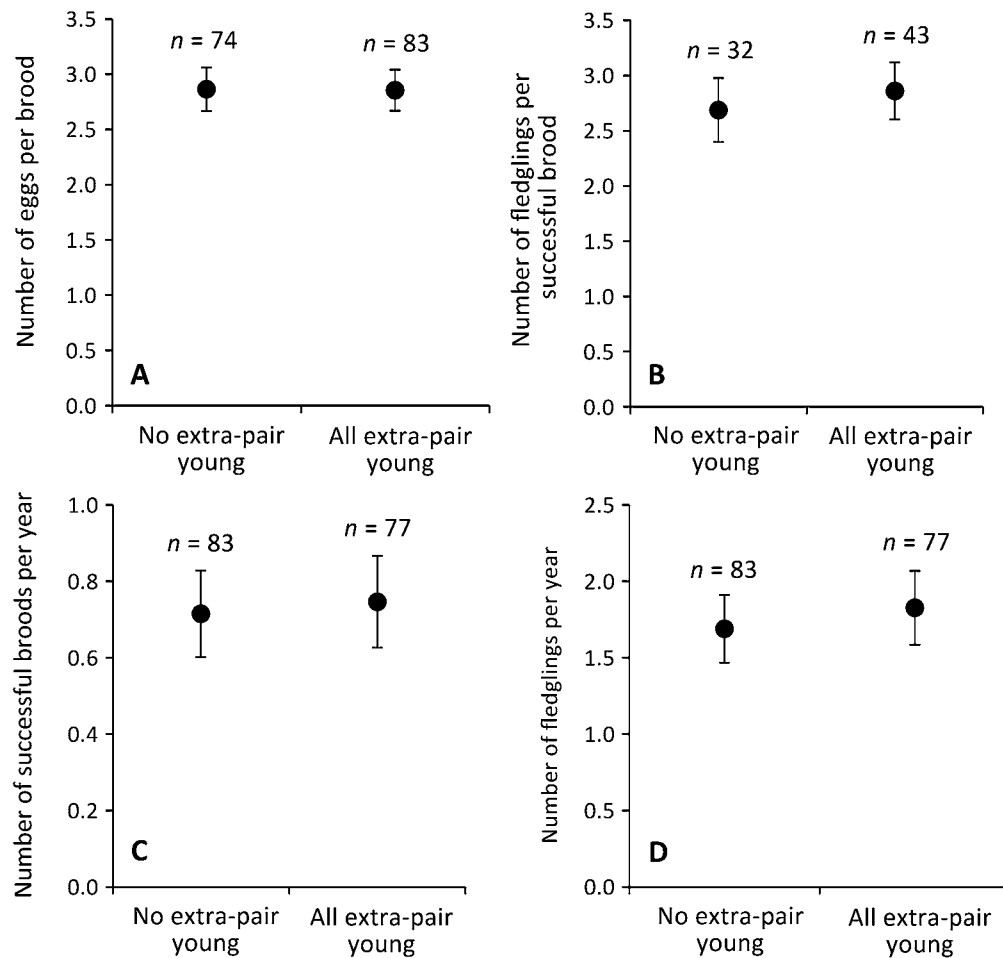


FIG. 3. A comparison of several measures of reproductive success of female Red-backed Fairy-wrens from the Herberton Shire in the Atherton Tablelands of Queensland, Australia, that produced broods containing either no extra-pair young or all extra-pair young. Data presented are least square means \pm SE from the generalized linear mixed model.

of reproductive success, the direction of the nonsignificant effects were all toward a negligible increase in reproductive success for females that produced extra-pair young. However, it must be noted that our study is correlational. It is possible that females in better condition or with more resources are more likely to produce extra-pair young. These females may be better able to withstand the costs associated with extra-pair mating behaviors or innately have higher fitness than females in poor condition that produce only within-pair young. Unfortunately, the experimental approach needed to tease apart these potentially confounding factors would be very challenging to implement in a wild population.

The degree to which engaging in extra-pair mating behavior is adaptive to females is determined by the relationship between the costs and benefits of this behavior (Arnold and Owens 2002, Albrecht et al. 2006). Our data suggest that direct fitness costs to females of extra-pair mating are weak or absent in the Red-backed Fairy-wren. In a previous study, we demonstrated one potential benefit: female Red-backed Fairy-wrens use extra-pair paternity as an inbreeding avoidance mechanism, and extra-pair offspring

are more heterozygous than their within-pair half siblings (Varian-Ramos and Webster 2012). On the basis of these findings, we propose that in the Red-backed Fairy-wren, low costs paired with inbreeding-avoidance benefits are likely to have contributed to the evolution of extra-pair mating as an adaptive female strategy. Considering the costs, as well as benefits, of EPP behavior for both males and females is necessary to obtain an accurate understanding of the adaptive significance of this widespread phenomenon in birds.

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