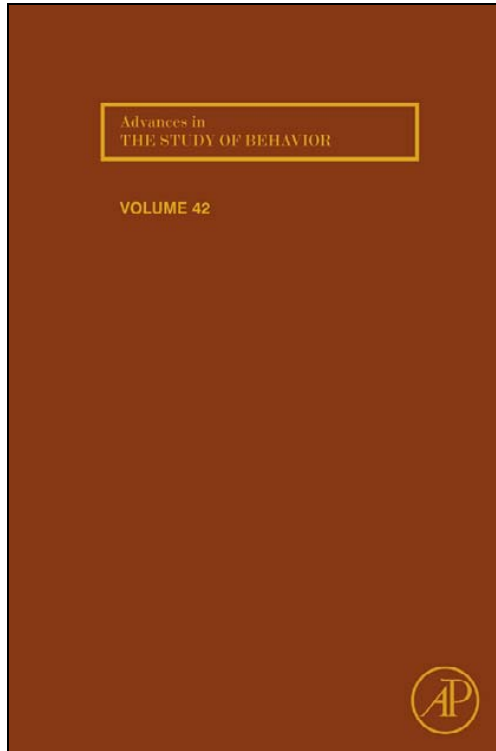


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Dealing with Uncertainty: Flexible Reproductive Strategies by a Tropical Passerine Bird in an Unstable Ecological and Social Environment

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I. INTRODUCTION

In contrast to temperate regions, the tropics are commonly perceived to be relatively aseasonal, benign, and climatically stable, and this in turn has led to a series of assumptions and predictions about life history, reproductive, and behavioral differences between tropical and temperate organisms. For example, tropical species are generally thought to be longer-lived and aseasonal, invest less in each reproductive effort, exhibit lower rates of sexual promiscuity, and show limited differences in hormonal status across the annual cycle (Stutchbury and Morton, 2001). Indeed, many of these broad assumptions and predictions about tropical species have been supported by empirical studies (Stutchbury and Morton, 2008). At the same time, however, it has become increasingly apparent that there is an impressive range of life history variation among tropical species (Macedo et al., 2008; Martin, 1996; Stutchbury and Morton, 2001, 2008), and that the ecological and social environments of tropical organisms are less stable and less predictable than previously perceived.

Variable and unpredictable environments may occur in tropical regions for three reasons. First, the tropics lack the large, seasonal changes in day length that accompany seasonal change in environmental conditions, and which are used by higher latitude organisms as a reliable environmental cue

to prepare for transitions between life history phases (Dawson, 2008). An example is the transition from the nonreproductive phase, when the gonads are shut down and sexual signals are suppressed, to the reproductive phase, when the gonads and sexual signals develop for anticipated reproduction. Because seasonal change in day length may not be a reliable cue in the tropics, supplementary ecological cues such as rainfall or plant growth may be of greater importance for tropical than temperate organisms to time the onset of reproduction (Wingfield, 1980, 2008).

Second, the tropics encompass a diverse array of habitat types, ranging from tropical rainforests (typically between about 10° S and 25° N) with heavy rain during much of the year, through monsoon climates with rainfall concentrated in the hottest parts of the season, to highly seasonal regions (e.g., most tropical savannas), where there are pronounced wet and dry periods, and finally to desert biomes (generally between 18° and 28° in both hemispheres), where rainfall is highly limited. As in the temperate zone, ecological conditions in the tropics can also be affected strongly by altitude and topography. Movement and breeding behavior of animal populations living in tropical habitat types is often synchronized closely with seasonal patterns of rainfall (i.e., the timing and amount of rain), and this in turn can vary considerably within and across years in many tropical habitats (e.g., Rubenstein and Lovette, 2007; Shine and Brown, 2008; Taylor and Tulloch, 1985). Accordingly, we might expect to see high variability in the onset, duration, and level of breeding for animal species living in many tropical habitats (see below).

Third, as in the temperate zone, tropical animals that live in social groups encounter another potentially important source of environmental uncertainty: social instability. That is, in addition to the need to respond to ecological conditions, group-living animals also face the added challenge of living in an inherently unstable social environment where relative dominance and/or breeding status may shift unpredictably. This may occur at the level of individuals, for example when a dominant breeding individual in the group dies, or at the population level, as when variable ecological conditions across years lead to changes in the social environment (e.g., through changes in population density or breeding sex ratio). While the degree of sociality varies substantially across taxa, there are several taxa well represented in the tropics that live predominantly in social groups, including most primates, cooperatively breeding birds and mammals, and social insects. For these and other tropical group-living animals, access to resources and/or reproductive success may depend as much on the ability to respond to changes in relative dominance and group composition as to changes in ecological conditions.

This raises the question: to what extent do tropical species adaptively modify behavior and physiology to match unpredictable conditions in the ecological and social environment, and how does this compare with better-studied patterns from temperate species? In this chapter, we address this question by reviewing our own studies of a small tropical passerine bird, the red-backed fairy-wren (*Malurus melanocephalus*). Our objective is to characterize the degree to which red-backed fairy-wrens use flexible behavioral and physiological strategies to negotiate the uncertain ecological and social environment that they experience, and to compare and contrast this reproductive flexibility with other tropical and temperate species, many of which may face similar levels of uncertainty.

II. THE FOCAL STUDY SPECIES

The red-backed fairy-wren is found primarily in the northern tropical regions of Australia (Rowley and Russell, 1997), ranging across a landscape that includes open forests, savannahs, and seasonal wetlands. This species is a small (~8 g) insectivorous passerine bird that inhabits open woodlands and grasslands, females building domed nests in tall grass (Schodde, 1982). Red-backed fairy-wrens breed cooperatively, with sons often staying on their natal territory to assist parents in raising subsequent broods (Rowley and Russell, 1997). Genetic studies have shown that extra-pair paternity (EPP) is very common in this species (Karubian, 2002; Webster et al., 2008), similar to all other *Malurus* studied to date (Rowe and Pruett-Jones, 2006). This high level of EPP differentiates the red-backed fairy-wren from many other tropical birds studied to date (see Stutchbury and Morton, 2008), though few studies have focused on tropical species, and it is therefore possible that EPP may be more common in the tropics than currently perceived (Macedo et al., 2008).

Much of the range of the red-backed fairy-wren falls within the monsoon belt of northern Australia, a region marked by long periods with little or no rain (~9 months per year) punctuated with monsoonal rains associated with cyclones in the Pacific and Indian Oceans (~3 months per year). The ecological environment of red-backed fairy-wrens is unpredictable as well as variable, as they are obligate insectivores that depend on the insect flush associated with the onset of rains for successful reproduction, but the timing and extent of these rains is unpredictable across years (see below). In addition, the habitats occupied by these birds are influenced strongly

by fire. Indeed, fire, both natural and also anthropogenic, has played a major role in shaping the Australian biota for at least the last 40,000 years (Kershaw et al., 2002).

Perhaps even more than ecological instability, red-backed fairy-wrens face an unstable and unpredictable social environment. These birds live in cooperatively breeding groups in which male offspring from previous breeding seasons often delay dispersal from their natal territory and assist their parents with subsequent reproductive efforts as auxiliary males (Rowley and Russell, 1997; Schodde, 1982). Groups are therefore often composed of a dominant, breeding male and female and one or more socially subordinate, nonbreeding auxiliary males (females typically disperse before their first breeding season). Interestingly, there are two basic types of breeding males: those that breed in red-black plumage and invest heavily in traits associated with mating effort, and those that breed in brown female-like plumage and show higher levels of parental effort (Table I). Auxiliary males are socially subordinate and reproductively suppressed relative to breeding males: they exhibit weak or no expression of sexual signals and phenotypic traits associated with reproduction (Table I and references therein), and sire young only rarely (Webster et al., 2008). Yet auxiliary males can and often do switch from helping to breeding within a single breeding season (Karubian, 2008; Karubian et al., 2008), typically when a breeding male dies to create a breeding vacancy, or when a young unpaired female immigrates into the area (see below). Males that change from auxiliary to breeder undergo a switch in breeding status (from unpaired to paired) as well as social status (from socially subordinate auxiliary to socially dominant breeder).

Thus, red-backed fairy-wrens experience a profoundly unstable ecological and social environment, in which conditions suitable for breeding depend on ecological factors such as rainfall and fire as well as (for males) social factors influencing social rank and status. Here, we report on our research, conducted with several colleagues, on the behavioral and physiological adaptations that allow these birds to adjust to an ever-changing environment.

III. GENERAL METHODS

We studied populations of red-backed fairy-wrens at two study sites near the town of Herberton on the Atherton Tablelands in Queensland, Australia (145°25' E, 17°22' S). One study site was located in open forests surrounding the Moomin Reservoir, where we have monitored the

TABLE I
SUMMARY OF SIGNALS, REPRODUCTIVE TRAITS, AND TESTOSTERONE LEVELS CHARACTERISTIC OF THREE PHENOTYPIC CLASSES OF FREE-LIVING MALE RED-BACKED FAIRY-WRENS FROM QUEENSLAND, AUSTRALIA

Male type	Plumage	Soft part	Morphology/Physiology			
	Back ^a	Tail ^a	Bill ^a	Body Condition	Cloacal Protuberance ^{a,b}	Circulating androgens
Red/black breeder	Red ^{c,d,e}	Black & short ^{f,g}	Black ^h	High ⁱ	Large ^{c,e,i}	High ⁱ
Brown breeder	Brown w/ some red ^{c,d}	Brown & long ^{f,g}	Dark ^{h,j}	Intermediate ⁱ	Moderate ^{c,e,i}	Moderate ^{i,j}
Auxiliary	Brown ^d	Brown & long ^{f,g}	Light ^{h,j}	Low ⁱ	Small ^{e,i}	Low ^{f,j}

Table modified from Karubian et al. (submitted for publication).

^aDevelopment of this trait is positively associated with levels of circulating androgens during trait development.

^bDifferences between male types in cloacal protuberance volume are mirrored by differences in total sperm number and ejaculate volume.

^cKarubian (2002).

^dKarubian et al. (2008).

^eRowe et al. (2010).

^fKarubian et al. (2009).

^gSwaddle et al. (2000).

^hKarubian (2008).

ⁱLindsay et al. (2009).

^jKarubian et al. (submitted for publication).

breeding behavior of red-backed fairy-wrens for every breeding season during the years 1998–2000 and 2003–2010 (breeding seasons are designated by the year that breeding ended; that is, the 1998 season began in October 1997 and extended to February 1998). The second site is located at Kalinvale Farm, approximately 10 km from Moomin, where we have monitored breeding every year since 2005.

During each breeding season, we captured most adults and marked them with individually specific combinations of colored leg bands and an Australian Bird and Bat Banding Scheme (ABBBS) numbered aluminum band. At the time of capture, we measured several morphological traits, including tarsus length, wing length, bill measures, and weight, and also collected a small (~20–50 μ l) blood sample from the wing, tarsus, or jugular vein for genetic and hormonal analyses. All blood samples were centrifuged

to separate plasma from red blood cells; the former were frozen in liquid nitrogen and the latter were stored in lysis buffer (White & Densmore, 1992) at 4 °C.

At the time of capture, we scored adult plumage coloration using the system described in Karubian (2002). Briefly, each bird's body was divided visually into five parts (head, back, belly, chest, tail) and each area was scored on a scale of 1–10 for the proportion of that area that was in bright (jet black or crimson red) or dull (brown) plumage. These scores were then summed and multiplied by two to produce an overall brightness score ranging from zero (completely dull) to 100 (completely bright). Plumage scores were highly consistent across scorers (Webster et al., 2008). For some analyses, we placed each male into a plumage class based on plumage color score: dull males had plumage scores less than 33, intermediate males had plumage scores between 33 and 66, and bright males had plumage scores greater than 67. Although this categorization is somewhat arbitrary, it is unambiguous and our results were not affected by using somewhat different cutoffs between categories because few males had intermediate plumages.

For groups with more than one male, we defined the dominant breeding male as that male who spent the most time with and sang with the group's breeding female; other males in the group were defined as auxiliary helpers. In all cases, these designations were unambiguous and were consistent with known pedigree information (i.e., the auxiliary was typically a male offspring from a previous season). We monitored the breeding activity of each group through daily observations of nesting behavior and by searching appropriate areas for nests. Nests were monitored by brief visits once every three days. When nestlings were approximately 6 days old, we banded and measured them (weight, tarsus), and collected blood samples.

Blood samples collected from captured adults and nestlings were used for two different types of analysis. First, plasma samples were used for radio-immunoassays to determine levels of androgens, as detailed in Lindsay et al. (2009). Second, we extracted DNA from red blood cells and used a panel of microsatellite loci to examine parentage and relatedness within and across groups. Methods are detailed elsewhere (Webster et al., 2008). In brief, we PCR-amplified several microsatellite loci from the DNA extracted from each individual sample, and then determined the size of amplified fragments (alleles) by electrophoresis through a gel matrix. Allele sizes were scored for each individual at each locus, and these were compared across individuals to determine parentage of nestlings using CERVUS 3.0 (Kalinowski et al., 2007). Because we used a

large number (> 10) of microsatellite loci that were highly polymorphic, we were able to unambiguously assign nestlings to adult parents (Webster et al., 2008).

We also conducted a series of aviary- and field-based experiments at our study sites. Aviary-based mate choice and social dominance experiments were conducted using socially naïve, locally captured birds in breeding condition (Karubian, 2002; Karubian et al., 2008). Presentation experiments of caged stimulus birds were conducted on free-flying groups exhibiting equivalent nesting stages and group composition (see Karubian et al., 2008). Removal experiments were aimed to change the status of 1-year-old males from auxiliary helpers to breeders via removal of established breeding males from groups consisting of a breeding pair with an auxiliary (Karubian et al., submitted for publication). Treatment males (i.e., auxiliary males) were processed as described above, while the breeding male was released in suitable habitat > 10 km from the capture site (no removed males returned). We also plucked back and tail feathers of the treatment male to induce feather growth at a time when the birds normally do not molt, and ensured that all treatment groups began the experiment at an equivalent nesting stage. Treatment males were recaptured approximately 1 month after the removal of the breeder male and processed following methods above. To serve as controls for this experiment, we used 1-year-old auxiliary males captured at approximately 1 month interval that had not undergone a switch in breeding status between captures.

IV. ECOLOGICAL INSTABILITY AND BREEDING

A major difference between temperate and tropical habitats is not so much in the degree of seasonality—habitats in both regions often show pronounced seasonality across the annual cycle—but rather in the type of seasonality. Temperate-zone habitats at high latitudes show marked seasonal changes in average daily temperature, and to deal with harsh conditions in the colder months most organisms do not breed, focusing instead on survival and self-maintenance, sometimes by going into torpor or hibernation and/or migration to lower latitudes (Dingle, 1980; Geiser, 1994; Wang, 1989; Wikelski et al., 2003). In contrast, most tropical habitats show relatively less seasonal change in daily temperatures, but often do show seasonality (often pronounced) in the amount of precipitation (e.g., Shine and Brown, 2008). This seasonality in precipitation may lead to marked changes across the year in primary productivity and insect availability, thus affecting the food resources available for many tropical vertebrates. The seasonality of precipitation in tropical habitats may also be unpredictable, as these

habitats typically show pronounced year-to-year variation in the timing of the onset of the annual rainy season as well as the amount of precipitation (Shine and Brown, 2008).

Red-backed fairy-wrens adjust their breeding effort to coincide with the period of moderately heavy rains, which at our study site in northern Queensland typically starts sometime in October (Fig. 1A). However, the exact timing of breeding—that is when females begin to form and lay eggs—is variable across time and space in a way that clearly illustrates the importance of rainfall. Within any given year, the initiation of nesting is strongly tied to the onset of the annual rains, but the onset of the rainy period varies unpredictably from one year to another. For example, in 2007 the rains started relatively early, with cumulative rainfall (from September 1) reaching 80 mm by October 15, and in that year six females had constructed nests and begun egg laying by October 10 (Fig. 1B). In contrast, the wet season was relatively late in 2010 (Fig. 1C), with cumulative rainfall not reaching 80 mm until early December, and the population did not reach the six nest mark until the end of November, nearly two months later than in 2007. Thus, the breeding of red-backed fairy-wrens is tied to an ecological variable that is both variable and unpredictable across years.

The high temporal and spatial variability in rainfall experienced by red-backed fairy-wrens may be a common ecological factor facing many tropical organisms (Hau, 2001; Hau et al., 2008), particularly those in highly seasonal wet-dry habitats. For example, across most of tropical Australia precipitation is highly seasonal, and also shows pronounced year-to-year variation in both the amount of rainfall and the onset of the wet season (Shine and Brown, 2008), and similar patterns are seen in other tropical habitats (Colwell, 1974). Accordingly, many tropical organisms require a flexible physiological mechanism to regulate the timing of breeding and synchronize it with the rains that affect food availability (Hau, 2001; Wingfield et al., 1992). The effects of rainfall on breeding can be particularly strong for relatively sedentary species living in highly seasonal tropical habitats, as many of these will skip breeding altogether, or allocate relatively little energy to breeding, in years when rainfall is minimal (see discussion in Shine and Brown, 2008). In years with low-to-moderate levels of rainfall, individuals in relatively good condition may breed while those in poor condition may not (Rubenstein, 2007), and accordingly, high year-to-year variation in rainfall may promote cooperative breeding (Rubenstein and Lovette, 2007). At the other extreme, more mobile species, particularly those in arid regions of both the tropics and temperate zones, have evolved a nomadic lifestyle and move to regions where conditions are more favorable for breeding (Allen and Saunders, 2002; Davies, 1984).

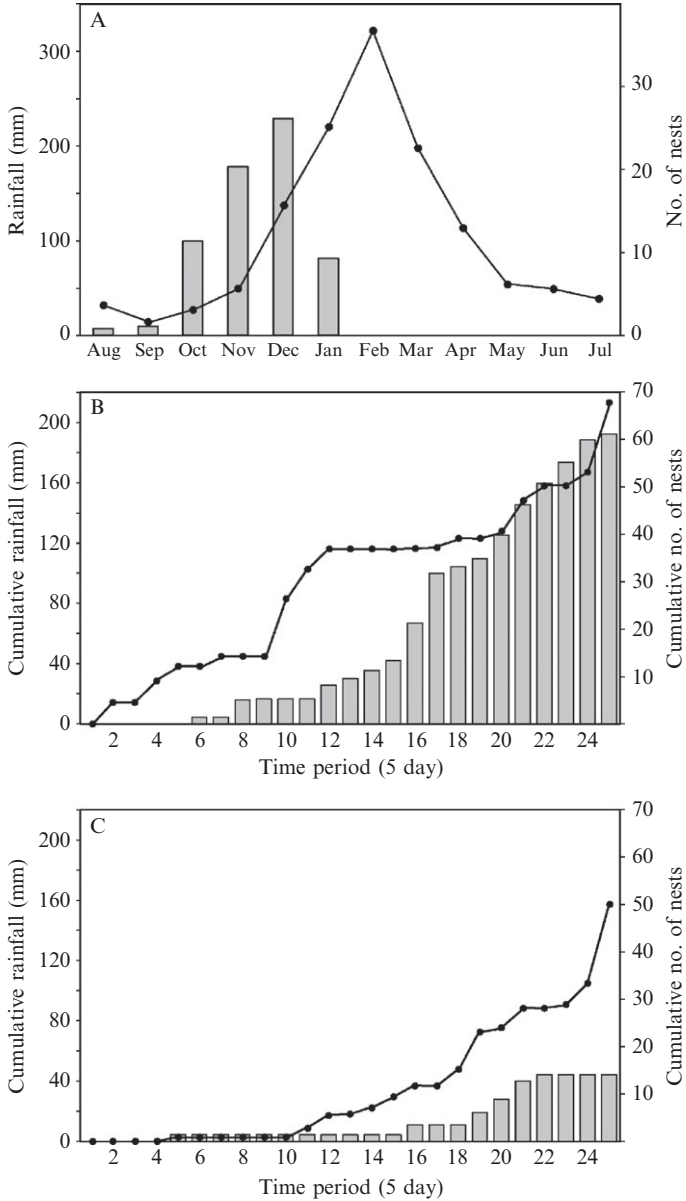


FIG. 1. Rainfall and breeding in red-backed fairy-wrens. (A) Average rainfall (lines) and number of nests receiving eggs (gray bars) versus month. Monthly rainfall data are averages for the years 2001–2009 from the nearby Wondecla weather station (Station #31029, Australian Bureau of Meteorology). Nesting data are based on the first egg date for nests constructed each

Fire is another ecological factor that can have pronounced effects on habitat quality in tropical biomes, particularly in highly seasonal tropical woodlands and savannahs (Bowman et al., 2009). In these areas naturally occurring “bushfires” are a common phenomenon during the dry season, as are intentional fires used for management and agricultural purposes (Bradstock et al., 2002). In general terms, the effect of such fires is to substantially reduce dense grass and shrubs near the ground for some years following the fire, with a slow return to prefire (or somewhat altered) conditions over time. The more specific effects of fires on local habitat suitability and wildlife are poorly understood, particularly for high-intensity fires (Williams et al., 2003), but likely depend on the seasonal timing, intensity, and size of the fire. It is clear that the short-term effects of fire can be strongly negative for some species, but positive for others (e.g., species such as some granivorous and/or cavity-nesting birds that depend on fire to enhance foraging or nesting opportunities)(Kotliar et al., 2002; Legge et al., 2008; Woinarski et al., 1999). Indeed, some bird species are “fire-followers” that specialize in recently burned areas in some areas of the tropics (e.g., Parker and Willis., 1997).

Red-backed fairy-wrens often show sharp population declines after a bushfire (Crawford, 1978; Legge et al., 2008; Valentine et al., 2007; Woinarski, 1990) and generally are not found in areas that burn frequently (Woinarski et al., 1999). Recently, Murphy et al. (2010) examined the mechanisms underlying these population patterns by examining the short-term effects of dry season fires on the survival, physiology, and behavior of red-backed fairy-wrens. Somewhat surprisingly, they found that fire had little effect on adult mortality, as birds were often able to survive a fire by relocating to unburned areas. However, the physiological condition of wrens was low in areas that burned early in the dry season, relative to wrens in unburned areas, and birds in areas that burned late in the dry season had relatively high nestling mortality, shorter breeding seasons, and were unlikely to attempt multiple broods (Murphy et al., 2010). These effects

month during the 2004–2009 breeding seasons at the Moomin study site. (B) Cumulative rainfall (lines) and cumulative number of nests receiving eggs (i.e., first egg date, gray bars) versus date (in five-day time blocks) during a year with a relatively early wet season (2007) at the Moomin study site. In that year, cumulative rainfall (from September 1) reached 80 mm by October 15, by which time the population had six active nests. (C) Cumulative rainfall (lines) and cumulative number of nests receiving eggs (gray bars) versus time during a relatively late wet season (2010) at the Moomin study site. In this late-rain year, the cumulative rainfall did not reach 80 mm until early December, and the population did not reach the six-nest mark until the end of November, fully seven weeks later than in 2007. The axes scales are the same for (B) and (C), with the first date time block being September 1–5 in each year.

were likely due to reduced food availability and high predation rates in burned areas, which had reduced foraging and nesting substrate. Thus, bushfires appear to have a negative effect on fairy-wren reproduction, and the primary behavioral responses of these birds appear to be to move out of or curtail reproductive effort in areas that are heavily burned. Similar responses may be exhibited by other insectivorous birds that rely on the understory for foraging and/or breeding (e.g., [Brooker and Rowley, 1991](#)).

Despite these negative effects of fires on red-backed fairy-wrens, habitat suitability for these birds may actually depend on fires over the long term, particularly in wetter regions where prolonged fire suppression can lead to a more rainforest-like habitat that is unsuitable for these birds ([Woinarski et al., 2002](#)). Indeed, at the edges of our own study site, which sits along a pronounced ecotone between wet rainforest and drier sclerophyll habitat, areas that were once suitable for fairy-wrens appear to have reduced population densities in recent years (unpubl. data). Accordingly, fires in some tropical areas may help maintain a mosaic of habitat types that promote higher levels of biodiversity (see discussion in [Parr and Andersen, 2006](#)).

The effects of unpredictable rainfall and fire patterns on the breeding of red-backed fairy-wrens are well illustrated by the breeding season of 2009–2010. During that year, the onset of rains was severely delayed, and this was correlated with an extreme delay in the onset of breeding by red-backed fairy-wrens at our Moomin study site ([Fig. 1B](#)). By mid-December—several weeks after the typical onset of breeding—only a few females had begun nesting. On 15 December, a fast-moving wildfire swept across the study site. Many of the adult fairy-wrens at Moomin survived the fire and were observed foraging in the intact forest canopy after the fire (unpubl. data). However, most of the understory was destroyed, including the few nests that had been built and virtually all of the suitable nesting substrate. Consequently, the few birds that had been breeding stopped doing so, and the breeding season effectively ended at Moomin (though birds continued to breed at the Kalinvale site, which did not burn).

V. SOCIAL INSTABILITY AND REPRODUCTION

One of the most basic life history “decisions” that an animal faces is whether (or when) to reproduce, and this decision can be affected by the ecological environment (above). However, nonecological factors also likely play a role, because often within any given year and any given habitat, some individuals breed but others do not. In the red-backed fairy-wren, approximately one-quarter of young (1-year-old) males remain on their natal

territory and forgo breeding (Karubian, 2002). As discussed in this section, the decision of whether or not to breed likely depends, in large part, on opportunities provided in a dynamic and ever-changing social environment.

Auxiliary male red-backed fairy-wrens are nonbreeding in the sense that they do not have a social mate and therefore do not produce any social young. However, auxiliary males are reproductively capable, and our genetic analyses have revealed that some do sire offspring (Fig. 2), usually by siring extra-pair young produced by a female on a neighboring territory. Auxiliary males can also produce young on their own territories, though they rarely do so and typically only when the breeding female is not the

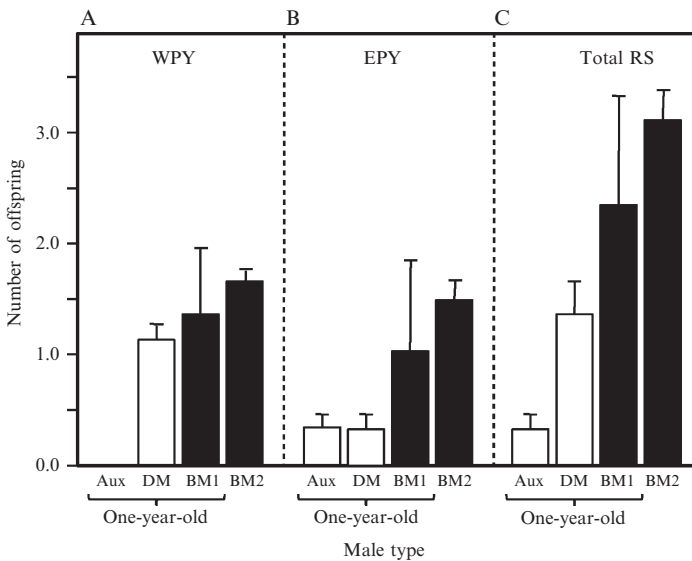


FIG. 2. Male phenotype and reproductive success. Figure shows number of young sired by auxiliary males (Aux, $n = 28$), brown breeding males (DM, $n = 50$), 1-year-old red-black breeding males (BM1, $n = 12$), and older red-black breeding males (BM2, $n = 124$). (A) The number of within-pair young (WPY) sired was only weakly associated with male type (breeding males only, Kruskal–Wallis $H = 5.6$, $DF = 2$, $P = 0.0602$). However, (B) the number of extra-pair young (EPY) sired was strongly associated with male type ($H = 23.6$, $DF = 3$, $P < 0.0001$), even after auxiliary males were excluded ($H = 19.4$, $DF = 2$, $P < 0.0001$). As a consequence, (C) the total number of young sired (WPY + EPY) was strongly related to male phenotype ($H = 37.2$, $DF = 3$, $P < 0.0001$), with older red-black breeding males siring the most offspring and auxiliary males siring the fewest, and this result remained strongly significant even after excluding auxiliary males (breeding males only, $H = 15.4$, $DF = 2$, $P = 0.0005$) and also when analyses were restricted to 1-year-old males ($H = 7.86$, $DF = 2$, $P = 0.020$). Shading of columns indicates plumage color (white = brown coloration, black = red-black coloration; males with intermediate coloration excluded). All males except BM2 are 1 year olds. Figure modified from Webster et al. (2008).

auxiliary male's mother, for example after the breeding female dies and is replaced by a new breeding female (see Webster et al., 2004). In these cases there is likely a strong reproductive conflict of interest between the group's dominant breeding male and the auxiliary, as both should be capable of siring offspring with the group female (Emlen, 1995, 1997). Nonetheless, overall auxiliary males produce very few offspring relative to breeding males (Fig. 2), and therefore have very low direct fitness.

Somewhat surprisingly, auxiliary males also appear to have little, if any, effect on the reproductive output of the breeding pair, indicating that the indirect fitness benefits of being an auxiliary are weak. Auxiliary helpers do assist the breeding pair by feeding nestlings (unpubl. data), but our analyses to date have not detected any difference in the number, condition, or survival of fledglings produced by females with auxiliaries versus females without (Varian-Ramos et al., 2010). Moreover, females with auxiliaries do not appear to have higher survival than females without auxiliaries (Varian-Ramos et al., 2010), suggesting that there are likely not any subtle effects of auxiliaries on parental fitness (see Russell et al., 2007, 2008). Finally, our demographic data do not show any difference in survival between auxiliary and breeding males (Karubian et al., 2008), indicating that auxiliaries likely do not enhance their own survival by forgoing breeding.

Taken together, our data suggest that the direct and indirect fitness benefits of being an auxiliary are weak at best, and very unlikely to outweigh the substantial direct fitness cost of not breeding (Fig. 2). This begs the question of why auxiliary males do not disperse to breed independently. Work with other cooperatively breeding birds indicates that auxiliaries often remain on the natal territory due to a lack of breeding opportunities (Emlen, 1991; Hatchwell and Komdeur, 2000)—specifically a lack of available breeding habitat and/or mates—and our observations suggest that this may also be the case for red-backed fairy-wrens. First, we typically do not see any unpaired females during the breeding season and pairing is socially monogamous. Accordingly, and because the adult sex ratio is biased toward males (~ 1.25 males per female in our study population), some males necessarily remain unpaired each season. Second, anecdotal observations indicate that an auxiliary male will sometimes disperse from its natal territory to pair with a young unpaired female that immigrates into the study population, which sometimes occurs early in the season but after breeding has commenced. Finally, whenever a breeding male disappears during the course of the breeding season, the breeding vacancy is quickly filled, often within a day and typically by an auxiliary male who disperses from a neighboring territory (see below). In contrast, widowed males often remain unpaired for weeks, and sometimes for the entire breeding season, supporting the idea that there are few, if any, unpaired females available.

We directly tested the hypothesis that limited breeding opportunities constrain some young males to remain as auxiliaries on their natal territory (Karubian et al., submitted for publication). Specifically, we created breeding opportunities for auxiliary males by removing the breeding male from a neighboring territory (see Section III for details); this experimental manipulation mimics the situation in which a female is widowed by the death of her mate during the course of the breeding season. We conducted 16 such removals: in nine cases the focal auxiliary male quickly (in less than one day) filled the newly created breeding vacancy, and in an additional four cases the auxiliary dispersed to fill a different vacancy that was created when a nonfocal breeding male filled the experimentally created breeding vacancy (i.e., a breeding male left his mate to pair with the widowed female). Thus, in 13 of 16 cases (81%) the breeding auxiliary filled a breeding vacancy immediately after it became available, and in only three cases did the focal auxiliary male remain in the area as an unpaired 'floater' male before disappearing (in these cases the breeding vacancy was filled by a different auxiliary male, thereby excluding the focal male from filling it). These results parallel those from a similar experiment conducted on a congener (Pruett-Jones and Lewis, 1990), and strongly support the hypothesis that mate and/or habitat limitation constrain some young males to remain as nonbreeding auxiliaries on the natal territory.

These results also give insight into the dynamic nature of the fairy-wren social environment. As the breeding season begins, most old and some young (1-year-old) males obtain mates to become breeding males, but other young males do not and instead remain as nonbreeding auxiliaries on their natal territory. As the breeding season progresses, some breeding males die, or (more rarely) unpaired females disperse into the population, to create new breeding opportunities. When this occurs, auxiliary males quickly fill the vacancies because breeding yields much higher fitness pay-offs than does nonbreeding (above). Because auxiliary males are virtually always cryptic brown in coloration (Webster et al., 2008; see also below), and because these breeding vacancies arise midway through the season after the prenuptial molt, these former-auxiliaries become cryptic brown breeders. Thus, the ever-changing social landscape leads to a number of auxiliary males becoming breeders, and a steady increase in the number of brown breeding males, as the breeding season progresses (Fig. 3).

VI. SEXUAL SIGNALS IN THE RED-BACKED FAIRY-WREN

Once the behavioral decision to breed has been made, males are faced with finer-grained reproductive decisions regarding relative investment in development of sexual ornaments versus other reproductive behaviors

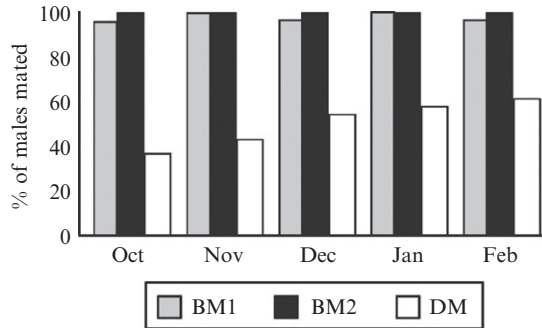


FIG. 3. Proportion of males of each plumage phenotype that are breeding across the season. From the start of the season most or all red/black males are socially paired breeders, whether they are 1-year-old males (BM1) or older (BM2). In contrast, only about one-third of brown colored males (DM) are paired with females and the remainder is auxiliaries on their natal territory. As the season progresses, breeding vacancies arise and auxiliary males (all in brown plumage) move to fill them to become breeders, leading to a progressive increase in the proportion of brown males that are breeding. Figure modified from [Karubian \(2002\)](#).

(e.g., parental care) or self-maintenance. As with many other birds, male red-backed fairy-wrens exhibit multiple sexual ornaments. The primary visual ornaments appear to be nuptial plumage, bill coloration, and tail length. As is often the case with multiple ornaments, it can be challenging to identify the intended receivers and the signal content for individual signals in this context ([Bro-Jørgensen, 2010](#); [Møller and Pomiankowski, 1993](#)). Therefore, before relating these signals to the social environment, we first provide a brief summary of our current understanding of the signaling function of these traits based on field observations and experiments.

A. NUPTIAL PLUMAGE

Several lines of evidence suggest that nuptial plumage is positively associated with female mate choice. First, relative to brown males, red-black males invest relatively little in parental care and mate guarding and spend a greater proportion of their time intruding on neighboring territories and displaying to the fertile females there ([Karubian, 2002](#)). This “philandering” behavior is generally consistent with seeking extra-pair copulations with females from neighboring groups, and is a common reproductive strategy among other *Malurus* that exhibit high rates of sexual promiscuity ([Rowley and Russell, 1997](#)). In contrast, brown males invest more heavily in parental care, remain in close proximity to their females throughout the

reproductive cycle, and rarely depart from their territories, behaviors consistent with mate guarding and seeking to improve fitness by means other than direct female choice (Karubian, 2002).

Aviary mate choice trials and molecular analyses of paternity both indicate that these behavioral differences between breeding male types are associated with reproductive benefits for red-black males. In aviary mate choice trials, sexually receptive females associated significantly more with red-black than with brown breeding males (Karubian, 2002). Molecular analyses revealed that across several years, red-black males enjoyed higher overall reproductive success, measured as the number of young sired within a season, than did brown breeding males (Fig. 2). Partitioning components of reproductive success into numbers of within-pair versus extra-pair offspring sired, we find no difference in the rate at which red-black and brown males are cuckolded or the number of within-pair offspring sired, but we do find a dramatic advantage in the number of extra-pair young sired by red-black males (Webster et al., 2008). Thus, the reproductive advantages associated with red-black plumage appear to be due in large part to female preference for red-black males as extra-pair reproductive partners.

Nuptial plumage color also appears to be associated with intra-sexual social dominance. In aviary-based dominance trials, red-black males were socially dominant to brown males (Karubian, 2002) and, in presentation experiments to free-flying pairs, red-black stimulus males attracted significantly higher levels of aggression from free-flying males than did brown stimulus males (Karubian et al., 2008). Based on these results, we conclude that nuptial plumage is likely to be positively associated with female mate choice and that it may also be associated with male dominance, though the relative importance of nuptial plumage color *per se*, versus tail length, for dominance interactions remains unclear (below).

B. TAIL LENGTH

Red-black males have shorter tails than do females or brown males (Swaddle et al., 2000), and this reduction in tail length appears to function mainly in male–male dominance interactions. Aviary-based social dominance trials, in which red-black males with similar body size and coloration but relatively large differences in tail length were paired and forced to compete for limited food resources, demonstrated that shorter-tailed males were socially dominant (Karubian et al., 2009). In the field, shorter tails are correlated with components of reproductive success that may be related to social dominance, such as clutch size, and (nonsignificantly) the number of surviving young. There was no relationship between tail length and female mate choice in aviary-based mate choice trials, and molecular

analyses of parentage demonstrated that males with longer, rather than shorter tails, tended to sire more young via extra-pair copulations, the opposite pattern predicted if short tail males were selected by females (Karubian et al., 2009). Thus, while results are somewhat ambiguous for the role of tail length in female mate choice, there appears to be clear evidence that shorter tails are associated with social dominance in this species. It is worth noting, however, that our study population is based in a hybrid zone between two subspecies of the red-backed fairy-wren that differ in tail length and that the signaling roles of this trait may differ geographically across the species' range.

C. BILL COLORATION

The bill is nearly always black in red-black males but can vary from horn-colored to black among brown males (the bill is horn-colored in females). While experimental evidence (below) suggests that it is likely to play a role in social signaling, the relative importance of this signal for mate choice versus social dominance is at present unknown.

VII. SOCIAL INSTABILITY AND SEXUAL SIGNALS

Red-backed fairy-wrens potentially experience social instability at various times throughout the annual cycle that may influence the expression and adaptive costs and benefits of sexual signals. Here, we break the year into the nonbreeding and breeding seasons, which occupy approximately two-thirds and one-third of the year at our study site, respectively. Below, we characterize how red-backed fairy-wrens respond to the uncertainty characteristic of each time period, and relate these findings to broader trends among tropical and temperate species.

A. UNCERTAINTY AND SIGNAL DEVELOPMENT DURING THE NONBREEDING SEASON

Adult red-backed-fairy-wrens undergo two extensive body molts per year, during which all feathers except the primaries and secondaries are molted (Rowley and Russell, 1997; Schodde, 1982). One molt—the post-breeding or prebasic molt—occurs after breeding is complete (February–April) and is homologous to the single prebasic molt exhibited by birds with only a single molt each year (Palmer et al, 1972). In this molt, most males develop dull brown plumage although a small number of males may molt directly into nuptial plumage (Schodde, 1982). The other molt—the prenuptial or

prealternate molt—occurs prior to and somewhat into the early breeding season (peaking September–November; [Lindsay et al., 2009](#)). The latter molt is critical to male sexual signals because it is during this molt that males develop their nuptial plumage, be it red-black or cryptic brown (few males develop intermediate plumage types, [Fig. 4](#)). Therefore, conditions during the nonbreeding period that lead up to this molt are likely to have an important influence on the type of plumage signals that a male develops. In fact, the nonbreeding period is a time of intense social activity during which red-backed fairy-wrens form large flocks of 15 or more individuals. It is also a time of considerable social instability, as young birds disperse from their natal territories and older individuals die. In this section, we consider the effects of this social instability during the nonbreeding season and in particular during the prenuptial molt on development of male plumage signals used during the breeding season.

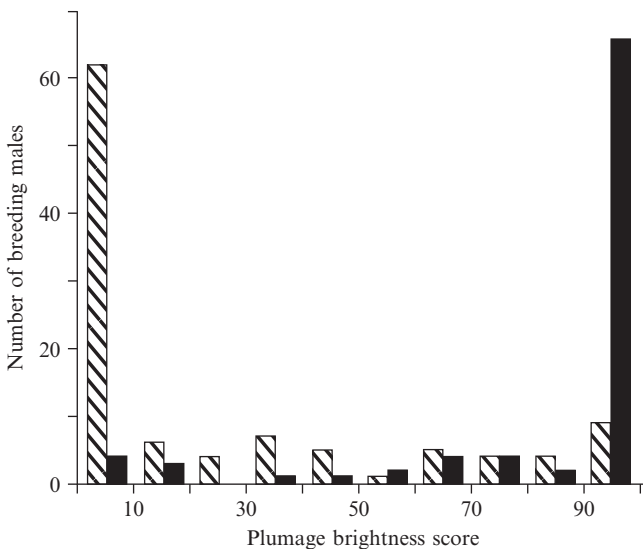


FIG. 4. The distribution of plumage brightness scores (0 = brown and unornamented, to 100 = entirely ornamented with red and black feathers) for 1-year-old (hatched bars) and older (solid black bars) breeding males (auxiliaries not included). Plumage brightness score is the percentage of the body covered in red/black (rather than brown) feathers. Note that whereas most 1-year-old breeding males were brown in coloration, several had some red-black plumage and some had plumage scores of 100. Figure modified from [Webster et al. \(2008\)](#).

Male nuptial plumage color is partially age-dependent in red-backed fairy-wrens, in that most 1-year-old males develop cryptic brown plumage in the prenuptial molt whereas most older males develop red-black plumage (Fig. 4). Thus, most (but not all) reproductively capable males delay acquisition of the bright (red-black) nuptial plumage until after the first potential breeding season, which is a widespread phenomenon in birds referred to as “delayed plumage maturation” (DPM). DPM has evolved independently several times, has been recorded in at least 33 avian families, and is common among both tropical and temperate species (Chu, 1994; Lawton and Lawton, 1986; Stutchbury, 1991; Thompson and Leu, 1995).

The type of plumage developed by male red-backed fairy-wrens during the prenuptial molt, however, is not wholly a function of age: among 1-year-old males, approximately 75% develop brown phenotypes, and 25% develop red-black or intermediate phenotypes (Fig. 4). Thus, age alone does not explain variation in plumage type developed during the prenuptial molt of 1-year-old males. This may be a common phenomenon: although age-related patterns of plumage acquisition appear invariant in some species (e.g., some seabirds and manakins; Chu, 1994; DuVal, 2005; Doucet et al., 2007), in many cases DPM appears to be a flexible strategy only loosely associated with age (e.g., Greene et al., 2000). The widespread taxonomic and geographic distribution of flexible acquisition of nuptial plumage suggests that it may be a “conditional” strategy (Gross, 1996) used by male birds to deal with a variable social and ecological environment.

To understand the extent to which males tailor expression of sexual signals to fit the social environment (i.e., a conditional strategy), it is necessary to understand the mechanisms that underlie signal development and expression. At a proximate level, the response of a given male to social environment and condition is often mediated by circulating levels of testosterone and other androgens (e.g., Mougeot et al., 2009). It is unclear whether this holds true for bright nuptial plumage in male passerine birds, however, as most evidence to date indicates that testosterone is not involved in acquisition of bright nuptial plumage, and indeed may even suppress molt in male passerine birds (but not some other bird groups; Kimball, 2006). However, the vast majority of these studies have been conducted on temperate-zone species that undergo just a single post-nuptial molt each year; in seasonal breeding birds androgen levels usually decrease at the end of reproduction, and therefore it is not surprising that they may not play a role in acquisition of plumage signals at that time. In contrast, a number of bird species, many of which live in the tropics, acquire their plumage signals during a prenuptial molt when their testes can be expected to become active and androgen levels increase (but see Stutchbury and Morton 2008). Thus, androgens could potentially

affect expression of nuptial plumage signals in species that undergo a prenuptial molt, yet relatively few studies have examined the role of androgens in regulating male plumage signals in these species.

Our results for the red-backed fairy-wren clearly show that androgens (i.e. testosterone) play a critical role in acquisition of bright (red-black) plumage coloration during the prenuptial molt. First, during the prenuptial molt, males developing the red-black phenotype have higher levels of circulating androgens than do males developing the brown phenotype (Fig. 5A). Moreover, molting males developing into the red-black phenotype are in better body condition than those developing into the cryptic brown phenotype (Fig. 5B). Thus, testosterone and/or other androgens appear to provide a physiological link between male plumage signals and body condition during the prebreeding period (Lindsay et al., 2009). To explicitly test whether these androgens trigger the molt into red/black plumage, we conducted a testosterone implant experiment in the field (Lindsay et al., in preparation). The results were unequivocal: 1-year-old males implanted with biologically relevant levels of testosterone immediately entered into a heavy molt and acquired red/black plumage, whereas control males implanted with an empty silastic tube showed limited and normal progression of molt, and acquired cryptic brown plumage. Testosterone has also been found to trigger molt to bright nuptial plumage in the closely related superb fairy-wren (*M. cyaneus*; Peters et al., 2000), although in this species males do not vary in nuptial plumage color. Thus, in fairy-wrens, testosterone appears to regulate acquisition of elaborate nuptial plumage in males, and this may be true of other tropical and temperate species that undergo a prenuptial molt during which plumage signals are acquired.

If testosterone regulates acquisition of bright plumage signals in fairy-wrens (and possibly some other tropical species), then what factors regulate testosterone levels themselves? This question has received considerable attention from researchers falling into two different camps, each of which tends to approach the question from a different set of starting assumptions (Kempnaers et al., 2008): many behavioral ecologists tend to view testosterone levels and the traits that they control as being influenced by intrinsic factors (e.g., individual condition), such that the signals are “honest indicators” of individual quality, whereas many behavioral endocrinologists view testosterone-mediated traits as being influenced by exogenous factors (e.g., ecological and social cues), such that testosterone helps synchronize an individual's behavior and signals with its environment. In reality, a combination of the two approaches is more likely, where hormones such as testosterone integrate both endogenous cues of individual quality and exogenous environmental cues, thereby leading to appropriate behavior and levels of signaling (Kempnaers et al., 2008).

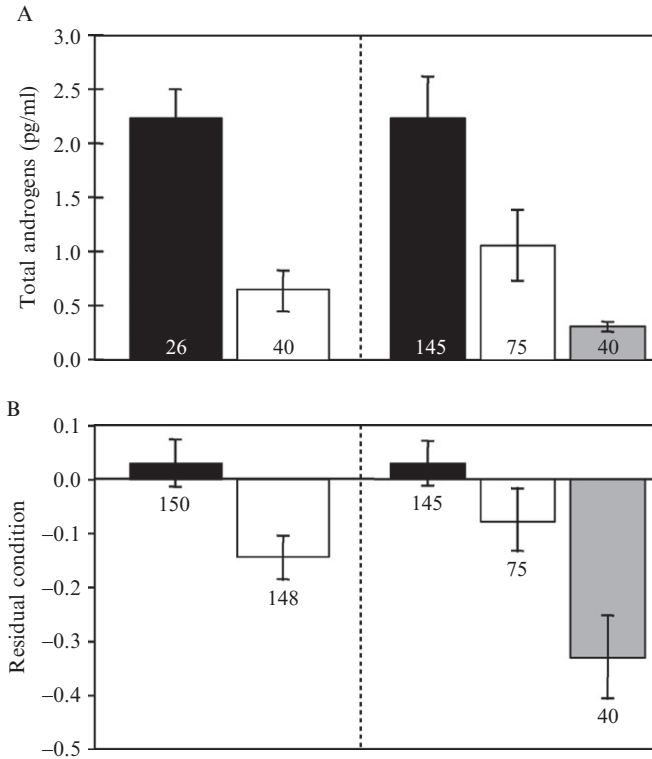


FIG. 5. (A) Total plasma androgen concentration, and (B) male body condition (measured as residuals of regression of male body mass on tarsus length), of male red-backed fairy-wrens during the prenuptial molt. In each figure, the left panel shows males categorized by the plumage color that they acquired during the molt (black = red/black plumage and white = brown plumage), and the right panel shows the males categorized by the behavioral phenotype exhibited during the subsequent breeding period (black = red/black breeder, white = brown breeder, and gray = auxiliary). For (A), males molting into red/black plumage had higher androgen levels than males molting into brown plumage (ANOVA: $F_{1,57} = 43.22$, $P < 0.0001$, $R^2 = 0.392$), and androgen levels also differed significantly between molting males according to the phenotype assumed during the subsequent breeding season (ANOVA: controlling for nesting stage: $F_{2,68} = 30.26$, $P < 0.0001$, $R^2 = 0.562$). For (B), males molting into red/black plumage were in significantly better condition than males molting into brown plumage (ANOVA: $F_{1,285} = 8.758$, $P = 0.003$, $R^2 = 0.03$), and condition during molt also was correlated with subsequent breeding phenotype (ANOVA: $F_{2,256} = 6.179$, $P = 0.002$, $R^2 = 0.056$). Error bars show one standard error, and numbers below each column give the sample size for each category. Figure modified from Lindsay et al. (2009).

Our previous work has shown that male condition is associated with both plumage type acquired during the molt (Fig. 5B) and testosterone levels (Lindsay et al., 2009), and future experimental work will further examine

the possible role of intrinsic cues of individual quality. It is also highly likely that testosterone levels and plumage signals are modulated by social interactions prior to and during the prenuptial molt, as the social environment during this period should provide cues to males about the probability of obtaining a breeding position in the upcoming breeding season. For example, adult sex ratio and/or dominance interactions in prebreeding season flocks could provide information about the relative availability of unpaired females, and indeed adult sex ratios appear to affect the likelihood that a female will produce sons versus daughters (Varian-Ramos et al., 2010). By integrating intrinsic and extrinsic cues, males can assess their own competitive ability and likelihood of obtaining a social mate. When this probability is high, testosterone levels should rise and males should molt into red-black plumage. When it is low, testosterone levels should be lower and the males will molt into the cryptic brown plumage typical of auxiliaries. In this way, social instability during the prebreeding molt is likely to be a primary factor in the development (or suppression) of sexual signals in this species.

B. UNCERTAINTY AND SIGNAL DEVELOPMENT DURING THE BREEDING SEASON

For auxiliary males who remain on the natal territory, the breeding season is an inherently unstable period, because at any moment there is potential for a breeding vacancy to be created by the death of a breeding male or immigration of a young female into the area. As discussed above, auxiliary males quickly fill these available breeding vacancies, and thereby undergo a change in “status”, which we use in a broad sense to mean both breeding status and social status, because in these cases a male is switching from socially subordinate auxiliary to socially dominant breeder. Because plumage coloration is likely fixed for the duration of the breeding season once the prenuptial molt is completed, males that make the switch from auxiliary to breeder face a signaling challenge shared by group-living temperate and tropical organisms alike: how can a rapid temporal response to an unpredictable change in status be achieved when the primary signal (in this case, plumage) is relatively static?

One potential solution to this challenge is for auxiliary males to delay molt so that, if a change in status occurs relatively early in the breeding season, males will still have sufficient time to respond to this change and produce nuptial plumage. However, there appear to be reproductive benefits associated with early onset and completion of molt among *Malurus* fairy-wrens. In the superb fairy-wren *Malurus cyaneus*, for example, males who initiate and complete molt earlier sire more young (Dunn and Cockburn, 1999). Among red-backed fairy-wrens, those males molting earlier were more likely to develop red-black nuptial plumage (Lindsay et al., 2009), which is in turn

associated with increased reproductive success (Webster et al., 2008). In this sense, early molt might be an honest signal of male quality (Dunn and Cockburn, 1999), and delayed molt may therefore reflect relatively poor physiological condition. Nonetheless, delayed molt also may be a “bet hedging” strategy that allows males of relatively low quality to gather information from their social or ecological environment, thereby gauging their probability of being an independent breeder, before committing to a plumage phenotype. This possibility requires further investigation.

An alternative solution is that males that change status may turn to more flexible secondary signaling mechanisms. In birds, vascularized soft parts (e.g., exposed skin, bill, or eye) may provide a relatively flexible alternative signaling mechanism compared to plumage (e.g., Faivre et al., 2003; Velando et al., 2006). Indeed, experiments on captive birds have demonstrated two instances in which soft parts—comb size (but not color) in fowl *Gallus gallus* (Zuk and Johnsen, 2000) and bill color in zebra finch *Taeniopygia guttata* (Gautier et al., 2008)—responded rapidly to changes in social environment, probably via increased levels of testosterone (McGraw et al., 2006; Zuk and Johnsen, 2000). Yet few field studies have directly linked social environment and/or status to expression of a plumage-based or soft-part visual signal in any wild bird population.

Consistent with the idea that birds may use soft parts as dynamic signals, observations of un-manipulated male red-backed fairy-wrens suggest that change in status from auxiliary to breeder is associated with development of darker bills. Among auxiliary males that switched status in response to the sudden opening of a breeding opportunity, bills became significantly darker within two weeks (Karubian, 2008), whereas there was little or no change in the bill color of males that remained as auxiliaries for a similar time period. Plumage coloration, in contrast, did not change for either type of male (as they normally do not molt at that time). While the results of this correlative study are consistent with the idea that social environment may affect bill coloration, the direction of causality between changes in phenotype and status was unclear and a proximate mechanism for observed phenotypic changes was not identified.

To better understand the effects of social environment on sexual signals, we turned to a field-based removal experiment designed to manipulate social status of free-living male red-backed fairy-wrens by inducing a switch from auxiliary to breeder (Karubian et al., submitted for publication). Following the experimentally induced shift in status from auxiliary to breeder (see General Methods for details), males exhibited rapid increases in circulating androgens (as measured in fecal samples) and sperm storage capacity (as measured by cloacal protuberance volume). Treatment males did not exhibit any overall change in nuptial plumage color, but plucked feathers

grew in as black/red for several of these males. This indicates that these males have the capacity and mechanisms to develop bright plumage but are constrained from doing so by the molt schedule. In contrast to the lack of change in plumage color, experimental males did show a rapid darkening of their bills, reflecting their newly acquired breeding status and elevated androgen levels. Thus, results from the removal experiment suggest that plumage signals are constrained by the molt schedule, but that males may use bill color as a secondary signal of status that is more flexible than plumage color.

VIII. CONCLUSIONS

We have integrated the results summarized above to develop a working model for the regulation of reproductive signals and related behaviors in the red-backed fairy-wren (Fig. 6); this working model should be applicable

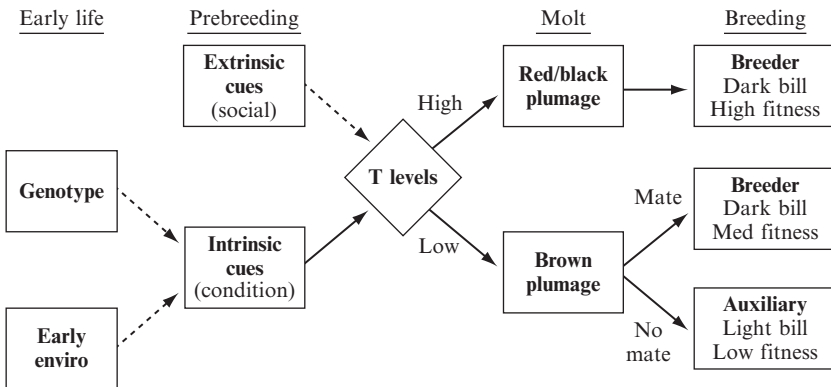


FIG. 6. A working model for the development of discrete male sexual phenotypes in male red-backed fairy-wrens during their first year of life. Under this model, extrinsic cues (particularly social interactions, but potentially also ecological cues) interact with individual intrinsic cues (particularly cues of condition/quality) to affect testosterone (T) levels. Intrinsic cues of condition/quality might themselves be affected by the male's genotype (e.g., "good genes"), and also by environmental effects during early development and prereproductive life. (e.g., food delivery while in the nest). Testosterone levels at the time of the prenuptial molt determine the plumage phenotype that male acquires. Independent of age, most or all males who acquire red/black plumage go on to become breeders during the breeding season. In contrast, most brown males start the breeding season as auxiliaries, but can become breeders if a breeding opportunity arises such that the male is able to acquire a mate mid-season. In this case, the male's androgen levels increase and his bill darkens to reflect the change in social status. This model can also accommodate the fact that most males older than 1 year become bright breeders. Solid arrows depict connections supported by our research, whereas dashed arrows depict hypothesized connections.

to other tropical and temperate species faced with an uncertain ecological and social environment. Under this model, hormone levels (e.g., testosterone) during signal development in the prebreeding period are affected by both intrinsic cues of individual quality and extrinsic cues from the ecological and social environment. By integrating both types of cues, males are able to assess their own relative competitive ability and likelihood of breeding, and tailor reproductive decisions and traits accordingly (Kempnaers et al., 2008). Hormone levels will thus reflect the probability that an individual will be able to breed, and will prevent breeding behavior and signals when conditions are not favorable.

Accordingly, hormonal mechanisms would lead to suppression of reproductive behaviors under some ecological conditions, for example low rainfall (see discussion in Hau, 2001; Hau et al., 2004; Small et al., 2007). These effects of ecological factors might vary across individuals according to relative body condition, for example by altering the relative costs and benefits of independent breeding for individuals in poor condition (Creel and Creel, 1991; Rubenstein 2007). Thus, highly variable rainfall might be a factor that promotes cooperative breeding in general (Rubenstein and Lovette, 2007).

Breeding behavior and investment in sexual signals would also be modified by unfavorable social conditions, for example when there are few available females or a male is in relatively poor condition relative to rivals. Under these conditions, hormone levels would be low and males would “make the best of a bad job” by remaining on the natal territory as non-breeders. Suppressed expression of ornamental coloration may be adaptive for auxiliary red-backed fairy-wrens because it reduces aggression from dominant breeders (see Lyon and Montgomerie, 1986), and presumably risk of expulsion from the natal territory (Karubian et al., 2008). This scenario is consistent with the idea that high social costs of cheating may enforce honesty in signals that are physiologically inexpensive to produce, such as melanin-based coloration of bills (Rohwer, 1977).

However, the social environment is dynamic, and breeding vacancies may arise well after the onset of the breeding season. Suppression of sexual traits may become maladaptive for an auxiliary filling a breeding vacancy during the breeding season, because auxiliary males have lower reproductive success than breeders (Webster et al., 2008). Accordingly, auxiliary males who obtain breeding positions dynamically up-regulate hormone levels that affect a labile visual ornament (bill coloration) as well as sperm production. Accurately signaling status is thought to be most important in species that live in social groups (e.g., Rohwer, 1975), and our findings suggest that soft parts may allow group-living birds to fine-tune status-signaling in response to changing social environment at

fine temporal scales (see Bro-Jørgensen, 2010). Because group living is common among both tropical and temperate species, it is likely that individuals in many species fine-tune signals to match changing social conditions. In mandrills (*Mandrillus sphinx*), for example, males experiencing a rise in social status exhibit rapid reddening of skin areas surrounding genitalia (Setchell and Dixson, 2001). In birds, soft parts are known to respond quickly to a wide range of exogenous and endogenous cues beyond social environment (e.g., Mougeot et al., 2010; Perez-Rodriguez, 2008; Perez-Rodriguez and Vinuela, 2008; Rosen and Tarvin 2006), suggesting that fine-scale temporal variation in these traits may also function as an honest signal in mate choice (e.g., Faivre et al., 2003; Velando et al., 2006) and/or social dominance interactions (e.g., Murphy et al., 2009) more broadly than is currently appreciated regardless of latitude.

This working model reflects our current understanding of how red-backed fairy-wren males maximize flexibility in development and expression of sexual signals in the face of unpredictable ecological and social conditions. A complex interplay of endogenous and exogenous factors likely affects hormone levels, which in turn shape timing and extent of signal production and reproductive traits, some of which are relatively static (e.g., plumage) whereas others are relatively labile (e.g., bill coloration and gamete production). This multi-tiered understanding of the mechanistic, ecological, and social causes underlying phenotypic differences among male red-backed fairy-wrens highlights the complex factors regulating flexible reproductive strategies in animals. It also illustrates the broader and often underappreciated point that reproductive and life history strategies of tropical as well as temperate animals, especially those living in groups, are likely to be shaped by uncertain environmental conditions.

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