

# Superb fairy-wren males aggregate into hidden leks to solicit extragroup fertilizations before dawn

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Female superb fairy-wrens *Malurus cyaneus* initiate extragroup fertilizations by forays to the territory of preferred males, just before sunrise, 2–4 days before egg laying. Over a prolonged breeding season, males advertise their availability to foraging females by singing during the dawn chorus. Here, we show that 1) males commence dawn advertisement at the same time of the year regardless of their quality or status; 2) subordinate males advertise by singing in close proximity to the dominant, or by using the dominant's song perch, despite inevitable punishment; 3) low-quality dominants and their helpers sing from the boundary of their own territory, which increases their proximity to attractive neighboring dominants; 4) each spatial cluster of males use a common dialect of a song that is implicated in extragroup choice, despite the ability of individual males to sing several dialects; and 5) there is leakage of paternity to lower-quality helpers and neighbors as a result of their "satellite" behavior. Collectively, these data suggest that Wagner's hidden lek hypothesis (Wagner RA, 1998. Hidden leks: sexual selection and the clustering of avian territories. In: Parker PG, Burley NT, editors. Avian reproductive tactics: female and male perspectives. Ornithological Monographs No. 49. Allen Press. p. 123–145) can be extended to birds that defend year-round all-purpose territories and that mating induced by parasitic behavior of low-quality satellites can be one explanation for polyandry in birds. *Key words*: cooperative breeding, dawn chorus, extrapair copulation, hidden lek, *Malurus*, polyandry, song dialect. [*Behav Ecol* 20:501–510 (2009)]

Despite considerable effort, there remains little consensus on the ecological determinants of the extreme differences between bird species in the importance of extrapair fertilizations (Griffith et al. 2002; Westneat and Stewart 2003). High breeding density has been suggested to facilitate access to extrapair mating, but support for this hypothesis remains equivocal (Westneat and Sherman 1997). Wagner (1998, 1993) has offered the alternative perspective that rather than determining the possibility of extrapair fertilization, density may instead be determined by male aggregation that facilitates access to extrapair mates (the hidden lek hypothesis). He proposes that the desirability of obtaining extrapair matings from neighbors could cause breeding birds to aggregate into colonies and that territorial migratory birds could occupy just a small proportion of suitable habitat in order to increase proximity to conspecifics. Wagner (1998) describes two paths by which this could occur. In the first case, females may settle near high-quality males, because even if not paired to those males, they can procure their sperm through extrapair mating. In the second, which is analogous to the hotshot model of lek formation (Beehler and Foster 1988), males aggregate because physical proximity to high-quality males gives them the opportunity to parasitize the attractiveness of nearby

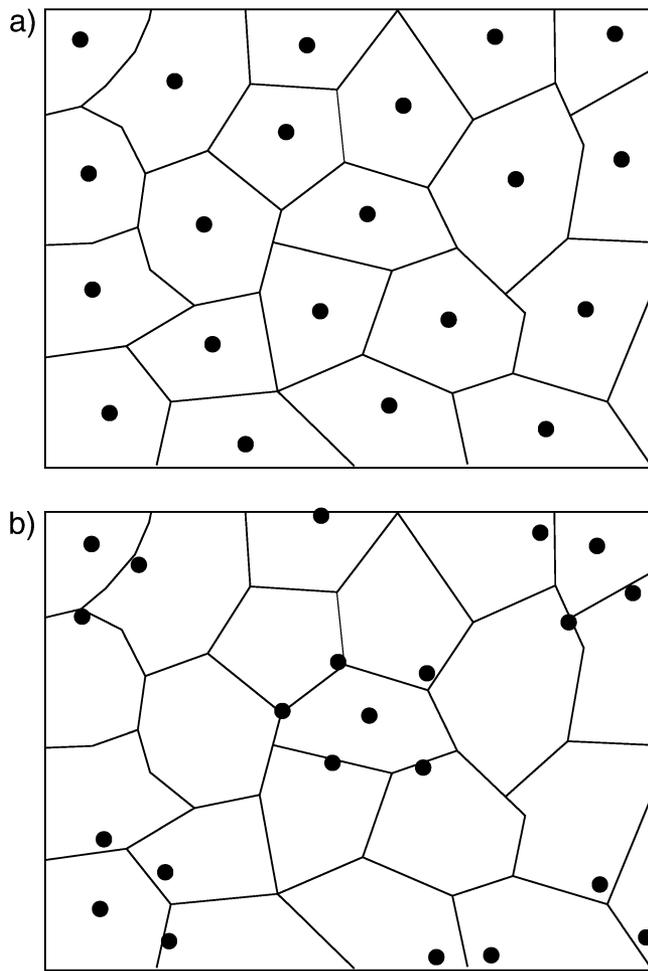
males that visit those males in order to procure extrapair matings. Although there is growing evidence that migratory birds use the presence of conspecifics in choosing where to breed (Safran 2004; Fletcher 2007), there are currently few explicit tests of all aspects of the hidden lek hypothesis, though criteria for detection of the hypothesis have been refined (Tarof et al. 2005; Fletcher and Miller 2006), and both supportive (Hoi and Hoi-Leitner 1997; Ramsay et al. 1999; Formica et al. 2004), and negative (Safran 2004, 2007) results are starting to emerge.

The hidden lek hypothesis initially seems ill suited to explain the spatial distribution of breeding birds that defend year-round, all-purpose territories that collectively occupy much of the landscape, as settlement options are constrained to a far greater extent and are completely different from the case of species settling on return from migration or winter flocks, or to colonies that are only occupied to rear young (Møller 1992). Here, we propose an extension of the hidden lek hypothesis that is applicable to year-round, all-purpose territories. Our extension is based on the logic of the hotshot hypothesis and depends on females visiting male territories to obtain extrapair fertilizations. According to this view, if only a few males are likely to be sufficiently attractive to provoke female visits, lower-quality males should attempt to gain benefits through satellite behavior and advertise as close to those males as is allowed by the constraints of territory, generating conspecific aggregation (Figure 1).

We illustrate this model with our own observations of the superb fairy-wren *Malurus cyaneus*, in which extrapair

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**Figure 1**  
The formation of hidden leks via spatial aggregation of males in year-round all-purpose territories (a) advertisement from the center of territories, (b) advertisement in close proximity to attractive neighbors.

fertilization is unusually prevalent (Mulder et al. 1994). In this cooperatively breeding species, females initiate extragroup fertilization during predawn forays to the territory of the preferred male (Double and Cockburn 2000). Females will travel as far as six territories from their own to encounter attractive males. Here, we use a number of observational data sets to demonstrate that males aggregate spatially to court females during the dawn chorus. We report behavioral and parentage data that suggest that these aggregations are competitive rather than cooperative, and interpret these data against the classification by Höglund and Alatalo (1995) of hypotheses proposed to explain aggregations of displaying males in lekking species.

## METHODS

### Study species and area

We have studied a color-ringed population of *M. cyaneus* at the Australian National Botanic Gardens continuously since 1988, monitoring social organization (Cockburn et al. 2003; Cockburn, Osmond, et al. 2008), reproductive attempts (Cockburn, Sims, et al. 2008), and resolving parentage through microsatellite-based parentage analysis (Double, Cockburn, et al. 1997; Double, Dawson, et al. 1997). The

breeding season lasts on average from the construction of the first nests in late August until the last young are fledged in February. Females lay a succession of clutches that usually comprise two to four eggs, and although they are only capable of rearing three successful broods per season, they can initiate as many as eight clutches in response to frequent nest predation. Fairy-wrens are facultative cooperative breeders, and although just one female breeds on the territory, there may be as many as five adult males resident on each territory during the breeding season (Cockburn, Osmond, et al. 2008), all of which contribute to the rearing of young (Dunn and Cockburn 1996). The oldest male is socially dominant, displacing subordinate males from access to food and the breeding female (Cockburn, Osmond, et al. 2008).

Despite the presence of many males on the territory of the female, males from outside the social group dominate paternity (Mulder et al. 1994; Dunn and Cockburn 1999). Extragroup fertilizations are initiated by the female on extraterritorial forays that take place in the half hour before sunrise, 2–4 days before the first egg of the clutch is laid (Double and Cockburn 2000). Males respond to the opportunity for extragroup fertilization by courtship displays during daytime on the territory of the female (Mulder 1997) and singing on their own territory in the dawn chorus (Dalziell and Cockburn 2008). Females prefer to mate with the small proportion of males that acquire nuptial plumage months before the start of the breeding season (Dunn and Cockburn 1999; Green et al. 2000; Double and Cockburn 2003; Cockburn, Osmond, and Double 2008), perhaps because males begin courtship displays as soon as they have full nuptial plumage (Peters et al. 2001), and only old, high-quality males can sustain such display (Peters 2000; Peters et al. 2000, 2001; Cockburn, Osmond, and Double 2008).

Fairy-wrens produce two sorts of songs (Langmore and Mulder 1992; Dalziell and Cockburn 2008). The most common, a variable chatter song, is sung by both males and females and is implicated in territory defense (Cooney and Cockburn 1995). The alternative trill song is sung only by males and comprises a long low frequency trill component that ultimately degenerates into a higher frequency conclusion that resembles the chatter song. During the day, trill songs are prompted by the calls and wing beats of large predatory birds (Langmore and Mulder 1992). Males also incorporate unprompted trill songs in their dawn recital (Dalziell and Cockburn 2008). Regardless of time of day, older males sing longer trill components, implicating this aspect of singing in extragroup mate choice (Dalziell and Cockburn 2008).

### Focused observations

Here, we synthesize data from several data sets of the behavior of males during the dawn chorus. As each study was designed to focus on different aspects of behavior, each employs different methods and sampling criteria. The studies are described below:

- a) *Breeding season behavior.* Between 1999 and 2004, we undertook regular surveys of the behavior of males singing in the dawn chorus during the breeding season. We conducted observations from 1 h before sunrise, initially monitoring the bush in which the group had roosted overnight. We maintained a continuous narrative of the behavior of males after they moved to the song perches from which they sang in the dawn chorus. In territories with more than one male, a separate observer monitored the song post of each male. Because an additional focus of these surveys was to observe the interactions between males and their own fertile mate

after the chorus concluded, we selected males whose mate was initiating a new nest. Hence, our sample of predawn behavior is biased toward males whose mate was fertile.

- b) *Winter song.* In 1999, we studied singing behavior of males during the winter. We chose 18 focal males according to the criteria that they lived on territories that afforded easy visibility and that a sample of them ( $N = 8$ ) had molted early (before 2 July) according to the criteria of Cockburn, Osmond, and Double (2008). Seven had retained nuptial plumage in the postbreeding molt, and one acquired nuptial plumage before 2 July. The remaining 10 late molters either fell into the prebreeding ( $N = 7$ ) or intermediate ( $N = 3$ ) classes of Cockburn, Osmond, and Double (2008), but all were in brown eclipse plumage for a considerable proportion of the sampling period. We sampled the birds at approximately 14-day intervals from early June until late September, by which time some females were starting to initiate their first nest. We arrived on the territory an hour before sunrise and measured the intensity of dawn singing by counting the number of songs males sang during their dawn recital, from the moment they moved to their song perch until they abandoned singing, usually just before sunrise.
- c) *Trill song during the day.* Between August and December 2000, we conducted surveys of the variation in the trill component of trill songs sung by males during the day, using predator calls to prompt singing. We played taped calls of a pied currawong *Strepera graculina* to targeted males using a Sony Walkman WM-FX195 and a Sony SRS-A60 speaker. Responses were recorded with a Sennheiser MZW60 directional microphone and a Sony TCD-D10 ProII Digital Audio Tape Recorder. We attempted to obtain a minimum of 10 trill songs from each male. Variants (dialects) of the trill component were distinguished according to the type of elements and their organization into one of more distinctive phrases (Figure 5). For example, songs were considered to belong to the same dialect if they shared the same element/s, though varied in the extent of repetition of the element/s. For example, six males classified as using Dialect G show variation only in the repetition of the single element (Figure 5a–f). By contrast, their neighbors singing Dialect H can be distinguished as singing a distinctive dialect, this time comprising three elements arranged in a characteristic order (Figure 5g–h).
- d) *Trill song during the dawn chorus.* During the 2004/2005 breeding season, we recorded the full dawn recital of most of the males in the study area. Our methods were described in detail in Dalziell and Cockburn (2008). We used the recordings to determine the dialect/s of the trill component sung.
- e) *Spatial distribution of males during the dawn chorus.* As part of our measurement of dawn recitals in 2004/2005, we mapped the distribution of song posts used by males during the dawn chorus. Because males sometimes used several posts, we divided the study area into 15-m  $\times$  15-m cells. Each cell was also assigned as belonging to one of the territories in the study area or as unoccupied space (an area of open lawn and a plantation of rainforest). We then assigned the song posts of each male to a particular cell. Although this meant that males could have theoretically assigned their time equally between two cells, in practice, all males in our date spent at least 90% of the dawn chorus in a single cell, so there were no problems in assignment.

In order to model whether the resulting distribution of males was random, we first calculated the number of 15-m units

from the cell of each male and the cell of the male that sang in closest proximity to him. We then conducted a randomization test in “Matlab” that involved assigning each male randomly to one of the cells within its territory, allowing us to calculate the average nearest male distances for this randomized distribution. This randomization was repeated 10 000 times, and the resulting set of simulated values for the mean distance, under a null hypothesis of random male location, was compared with the observed distribution.

### Paternity analysis

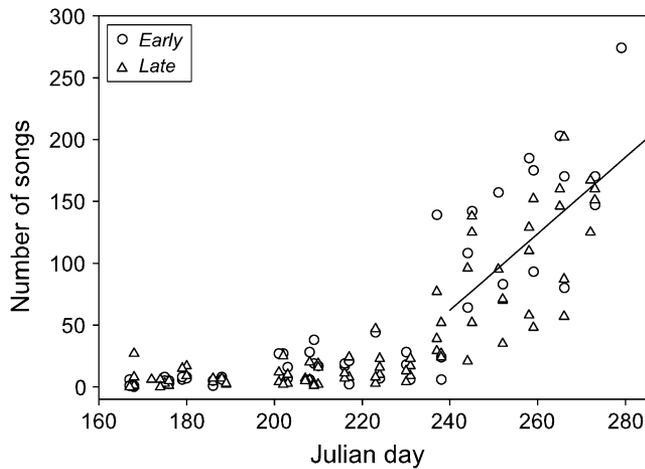
Exploratory analysis revealed that because the clutch size of fairy-wrens is small (2–4), and some paternity can be allocated to members of the female’s social group, individual broods provided a poor sample of the males with which the female may have copulated. However, repeated nesting allowed a greater sample to be obtained for individual females. Because the extragroup males available to females changes each year, we analyzed female choice on an annual basis. We confined our analysis to females that had produced at least six extragroup young during the course of the breeding season, as exploratory analysis suggested that we would underestimate the range of possible sires until that many young had been sampled. We discuss possible biases resulting from this criterion below.

For each female, we asked: 1) whether there was an a priori attractive male, defined by early molting, that sired offspring in all or most (>75%) of the broods the female produced that season. We called this the preferred male. It is important to make this distinction on a priori criteria in order to estimate the paternity preferred males lose to subordinates and other satellites. We then classified any additional extragroup sires as: 2) a subordinate of the preferred male; 3) a dominant from an immediately neighboring territory of the preferred male; 4) a subordinate from an immediately neighboring territory of the preferred male; or 5) a more distant male. Some females have offspring that could not be sired by any male in the population. This is most likely near the edge of our study area, indicating that the female has mated with a male from outside the study area. Because the status of these males could not be determined and it is impossible to be certain which sire was preferred, we excluded females from consideration unless we knew the sires of all their young.

In 2004/2005, when we knew the song post of each male, we estimated seasonal variation in the opportunity for extrapair mating by assigning a female as fertile when she was 2–3 days before laying the first egg in each clutch, because although females occasionally undertake forays 4 days before egg laying, they are only common on day –2 and day –3 (Double and Cockburn 2000), and within-pair matings are also confined to this period (Cockburn A, unpublished data). Because, our analyses indicated that males aggregated into clusters, and that females only visited one cluster of males, we also estimated the number of visits each cluster was likely to receive, and whether the absolute and per capita visitation rates were predicted by the number of males in the cluster.

### Statistical analysis

All statistical tests were carried out in “Genstat for Windows v. 9.” For simple models based on least squares or goodness-of-fit, we report the test used in the Results. Where repeated sampling of individuals occurred, we used the REML procedure to fit mixed models with the identity of the male as a random term. We discarded nonsignificant terms ( $P > 0.05$ ) in a stepwise way to obtain parsimonious models.



**Figure 2**

The intensity of dawn singing measured as the number of songs produced by advertising males from their song perches during the dawn chorus. Males are distinguished by whether they gained nuptial plumage early (before 2 July; circles) or after that date (triangles). The line depicts the best fit of separate REML models for the data collected before and after day 235 (22 August).

## RESULTS

### Winter song

During winter, males sang very little in the dawn chorus until late August (Figure 2, approximately day 235). Thereafter, all males increased singing until late September (day 270), when most females were commencing their first nests, and males were producing a continuous recital. We explored a variety of methods of statistical modeling, but the only technique that produced a Normal distribution of residuals was to analyze data from before and after day 235 separately. Before day 235, the number of songs increased gradually, but there was no difference between birds that were in full nuptial plumage (early) or had not yet molted (late) (REML test with identity of the male as a random term: interaction: Wald  $\chi^2 = 3.1$ ,  $df = 1$ ;  $P = 0.08$ ; early versus late;  $\chi^2 = 1.2$ ,  $df = 1$ ;  $P = 0.3$ ; Julian day  $\chi^2 = 32.7$ ,  $df = 1$ ;  $P \ll 0.001$ ). The same was found once singing started to accelerate after day 235. All males increased at a similar rate, though some of the late class were molting into nuptial plumage (interaction:  $\chi^2 = 0.0$ ,  $df = 1$ ;  $P = 0.98$ ; early vs. late;  $\chi^2 = 2.8$ ,  $df = 1$ ;  $P = 0.09$ ; Julian day  $\chi^2 = 41.6$ ,  $df = 1$ ;  $P \ll 0.001$ ).

During the breeding season, males generally contributed to the dawn chorus every morning, regardless of social status (183/187 mornings; 98%; sample derived from 37 males). The four exceptions involved three dominant males that did not sing when their own female had departed on a foray that morning, though they always sang when their mate had not departed. This is a small proportion of males whose female had departed on a foray (3/37; 8%), though the males that did sing when their mate was fertile often delayed the onset of singing. The actual incidence of singing by males during the season will be even higher than 98%, as our sampling was biased toward males whose own mates were fertile.

### Singing males are spatially aggregated and adopt a distinctive dialect

Males either sang exclusively from one song post or moved between two or three adjacent song posts during the dawn chorus and used the same sites on each morning they were observed. Most dominant males sang from a prominent, exposed branch

of a tall shrub, generally between 1 and 4 m in height, though subordinates sometimes sang from more concealed locations.

Although some males sang from central locations in their territory, many did not, and sang instead on the boundary of their territory, allowing them to sing in very close proximity to their neighbors (Figure 3). As a consequence, distances between nearest song posts were considerably shorter (observed mean =  $2.83 \pm 0.20$  SE;  $N = 67$ ; units = 15 m cells) than predicted by the simulations (mean = 3.42; Figure 4; observed mean lower than 9980/10 000 of the simulated outcomes;  $P = 0.002$ ).

Clustering of males becomes even more obvious when the form of predawn song is considered. Following predator playback during daytime, most males sang more than one trill dialect (95/136 [70%] sang more than one dialect; mean =  $2.1 \pm 1.0$  SD dialects). However, all but one male sang just one dialect in the dawn chorus, and the males in physical clusters adopted the same distinctive dialect (Figure 5). The exception was a subordinate that sang both the dialect adopted by the other males on his territory and the dialect used by the neighbors with a territory boundary in close proximity to his song post.

### Dominant males attack subordinates

Although males devoted most of the dawn chorus to continuous singing, we also detected direct physical interactions between males in two contexts.

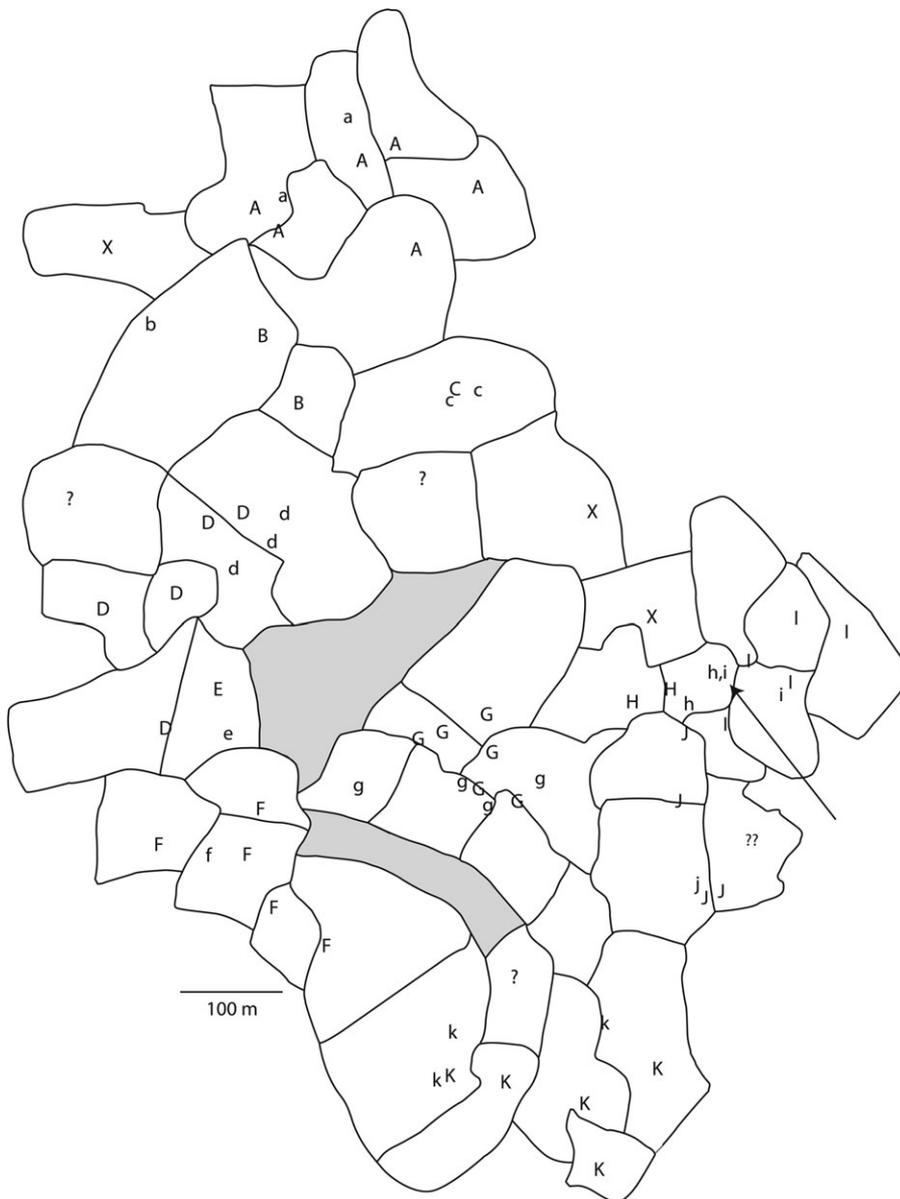
First, dominant males flew to the song post of their subordinate/s at least once during the dawn chorus and attacked them ( $N = 50/52$  mornings [96%] when viewing conditions were adequate; sample involves 13 different social groups). In the 47 cases where the timing was recorded, the dominant initiated the attack  $14 \text{ min} \pm 6$  SD before sunrise. Attacks by the dominant led the subordinate to stop singing briefly, but subordinates inevitably recommenced shortly thereafter ( $N = 50$ ). The two cases where no attacks took place coincided with the only two instances where a dominant with a helper refrained from singing in response to the departure of his mate on an extragroup foray.

Second, occasionally dominants left their song post for other reasons, most often in response to movements by their own mate. When these departures occurred, the subordinate left his own perch and commenced singing from the song perch of the dominant ( $N = 6$ ). In all but one case, when the dominant returned, the helper was physically attacked ( $N = 3$ ) or fled and was chased ( $N = 2$ ). The exception occurred on one of the cases where the dominant failed to sing in the dawn chorus at all, because he was waiting on the territory boundary for the return of his mate from her extragroup foray. In this case, the subordinate commenced singing from the song perch of the dominant and did so for the entire dawn chorus.

### Preferred males lose substantial paternity to parasitic satellites

We obtained data for 105 breeding seasons of 85 females that had produced more than six or more young from extragroup sires, but were forced to discard 39 of these because a male from outside the study population had sired at least one of the young they reared. Hence, the sample we report here involves 66 breeding seasons from 54 females, who produced 447 extragroup young (range from 6 to 11 per season). There is some bias in our sampling, as females rarely reach the threshold of six young in their first year of breeding and in drought years. We previously reported the impact of drought on female choice of sires (Cockburn, Osmond, and Double 2008) and will report an analysis of choice by first-year females elsewhere.

There was multiple extragroup parentage in 48 of the 66 samples (73%). Multiple extragroup paternity was almost inevitably shared between birds living on the same territory or



**Figure 3**

The location of the main song post used by males in the dawn chorus in relation to the boundaries of their territories. The lines represent territory boundaries. Upper case letters denote dominants, and lower case letters denote subordinates. Each letter represents a distinct dialect characterized by variation in the trill component of the trill song used in the dawn chorus. One subordinate (indicated by an arrow) sang two dialects—that of his dominant and the neighbor nearest his song post. The two shaded areas represent habitat not part of the territory of breeding fairy-wrens (a rainforest gully and an open lawn), though it can be traversed by foraging females.

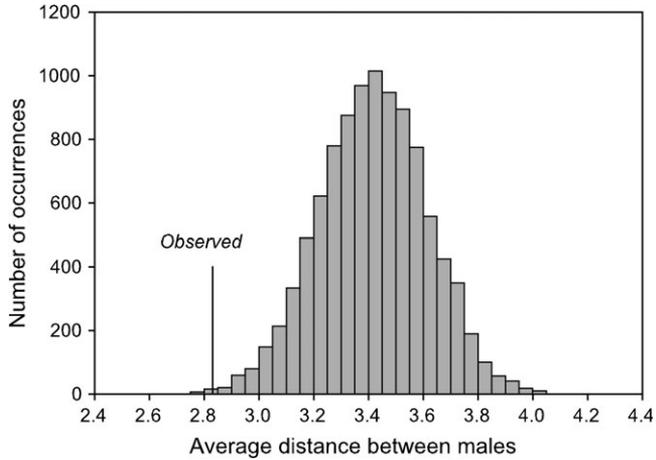
immediate neighbors, all of which are likely to be members of the same song cluster (443/447 young; 99%). The four young that did not come from neighboring territories were from three cases where females also sampled a male at 180 degrees from the main cluster. We have discussed these exceptions elsewhere (Double and Cockburn 2000). Despite these very rare exceptions, our data overwhelmingly suggest that females establish an area from which they will seek extragroup fertilizations by the first brood of the season, and continue to visit the same area throughout the season (66/66 seasons).

In 52/66 seasons (79%), the female apparently targeted an early-molting sire, on three occasions producing young from two sires that both molted early. In these latter cases, the two early-molting males were immediate neighbors. Attractive male/s gained 100% of extragroup parentage in just 17/52 seasons (33%). In 32 cases, the attractive dominant had one or more subordinates, which also gained parentage in 12 seasons (38%). However, the attractive dominants also lost paternity to immediate neighbors in 25 cases (48%). Collectively, the early-molting male obtained 262/391 (67%) of extragroup young produced by the female.

The failure of some females to choose an early-molting extragroup sire in the remaining 14 cases occurred in a number of contexts. In 7/14 cases, the high-quality male visited by the female in the previous breeding season had once again acquired nuptial plumage early and displayed to the female throughout the winter, but was no longer present on the territory when she was ready to mate, because he died close to the start or during the breeding season ( $N = 6$  males, as two females were apparently affected by the same death). In the remaining cases involving five females in seven seasons, we could not contrast preference between seasons, because the female had not produced extragroup young in the previous year. However, all five females initially chose a poor male in circumstances that we have demonstrated are unfavorable to mate assessment (Cockburn, Osmond, and Double 2008), either because few males acquired early blue plumage ( $n = 3$ ), because there was heavy mortality of the early-molting males just prior to the season (1), or because the female was mating for the first time ( $n = 1$ ). Nonetheless, two of these females subsequently mated with the same male in the following year, suggestive of consistent preference, so occasional choice of low-quality males apparently occurs.

### Visits by females are rare

The number of females we knew to be fertile, and hence we estimated to be undertaking forays on any particular morning, never exceeded eight (from a sample of 66 breeding on the study area) and was well described by a quadratic function



**Figure 4**  
The average nearest distance between song posts of males observed in our study contrasted with the results of 10 000 simulations where the position of males was allocated randomly within their territory.

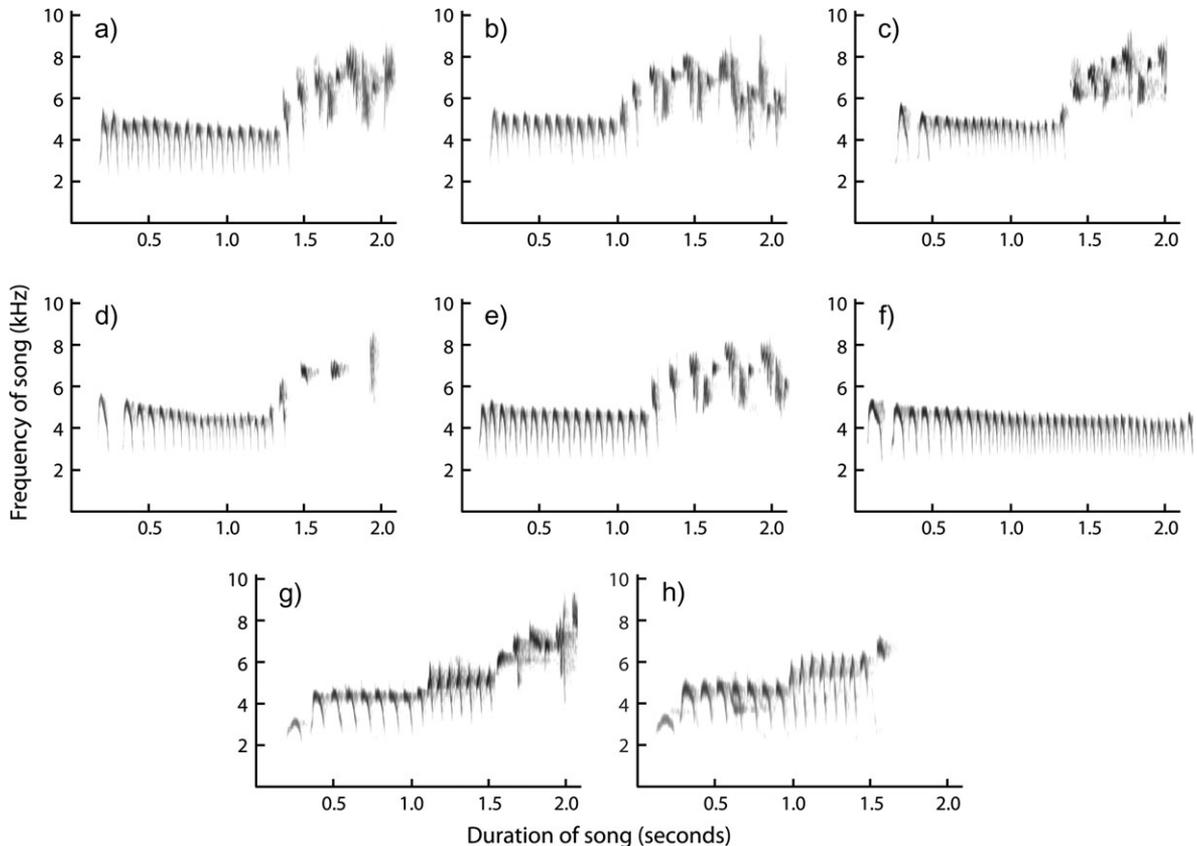
(Figure 6; estimate for quadratic term in multiple regression:  $F_{1,122}=41.2$ ;  $P \ll 0.001$ ).

Our data for such visits to particular clusters were less complete, as from the 66 females, two produced only a single brood of legitimate young, three failed to rear any young to the age when we sample young for DNA to establish parentage (day 6 of nestling life), and eight apparently preferred males whose dawn song we had not recorded. In addition, females from outside the study area also visit some of our clusters. Our analysis is therefore based on 53 females visiting the 12 main clusters as determined by the males that sired their young (Figure 3). The probability that any cluster group receives a visit on any morning is low (14.5% of mornings;  $N = 1488$ ). Although as many as three females may visit a cluster on a morning, visits by multiple females are rare (1.5% of mornings), and such multiple visits are close to that predicted by a random Poisson process (Figure 7), suggesting that females act independently in seeking male clusters.

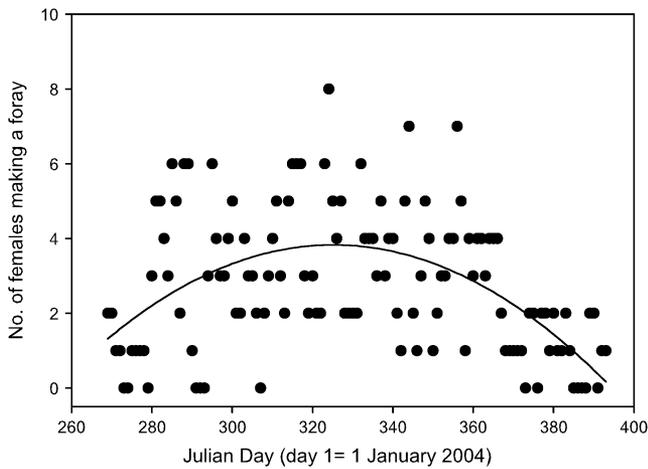
Larger clusters attract more visits (Figure 8a; linear regression;  $F_{1,10} = 5.9$ ,  $P = 0.04$ ,  $R^2 = 37\%$ ), but this does not translate into an increased visiting rate per male in the cluster (Figure 8b; linear regression;  $F_{1,10} = 1.0$ ,  $P = 0.70$ ,  $R^2 = 2\%$ ; the significance in this case is for a negative estimate of the relationship between size of cluster and per capita visit rate).

### Copulations are initiated by the female

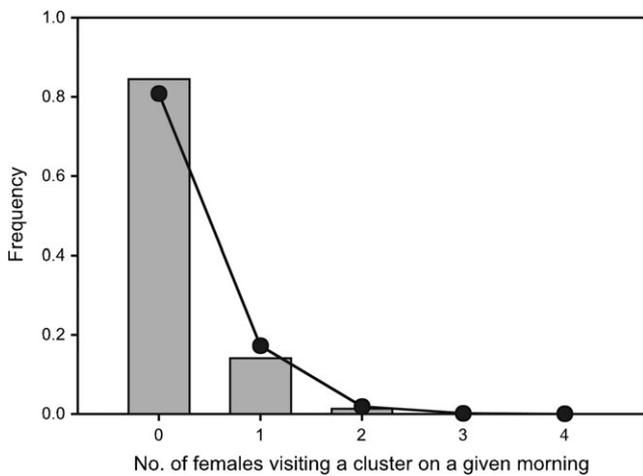
Although we have previously characterized female forays using radiotelemetry (Double and Cockburn 2000), it has been



**Figure 5**  
Variation in the trill component between males singing the G dialect, which is defined by repetition of a single element in the introductory component (a-f), together with the trill components of two of their neighbors that sang the H dialect, which is defined by a single low-frequency introductory element, followed by two phrases defined by repetition of distinctive elements (g-h). The songs are truncated at 2 s, removing all or part of the concluding chatter.

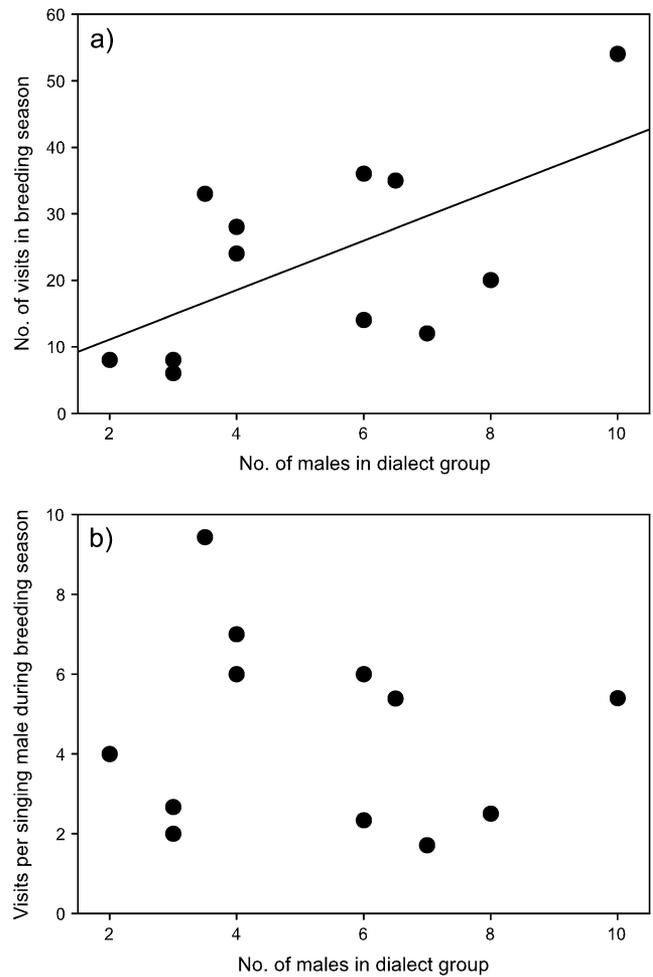


**Figure 6**  
The number of female fairy-wrens (from a sample of 66 females) estimated to be making an extragroup mating foray on each morning of the 2004/2005 breeding season. The line represents the prediction of a quadratic regression function.



**Figure 7**  
The probability that a given number of females will visit a dialect cluster of males singing during the dawn chorus on any morning. The bars represent the observed probability. The line represents the expectations from a Poisson distribution given the observed mean of 0.21 visits per cluster per morning.

pointed out that we have not previously described the actual process of extrapair copulation (Westneat and Stewart 2003). During the collection of our dawn recital data in the 2004/2005 breeding season, we witnessed the arrival of four foraging females in 47 mornings of recording (8.5%), which is close to our overall estimate of a 14.5% visitation rate, particularly as some of the males in each cluster would not be visited by females. In each case, the female flew to a perch on or near the branch from which the male was displaying. The male then started the characteristic blue-black display used in day-time courtship. The female moved slowly toward the male, and in at least one case approached him to the point their bills touched. This precipitated immediate copulation, or the birds dropped into denser shrubbery, where copulation presumably took place. Three of the copulations were with a dominant (two early molters, one not) and one with a subordinate.



**Figure 8**  
The effect of the size of a dialect cluster on visits by foraging females to each cluster during the 2004/2005 breeding season: (a) total visits received, with a significant regression depicted by the line; (b) per-capita visits received. One male sang two dialects, and both he and the visits he attracted have been assigned 50:50 to the two dialect clusters involved. The estimates are conservative as the choice of some females could not be assessed.

**DISCUSSION**

Despite being confined to year-round territories, male superb fairy-wrens aggregate physically during the dawn chorus, which is when female fairy-wrens seek the extragroup fertilizations that dominate paternity. Each cluster shares a distinctive dialect of a song used in intersexual advertisement, although at an individual level, males know more than one dialect. Therefore, several males singing similar recitals in close proximity confront females visiting their preferred male. The clusters she encounters appear to be competitive rather than cooperative, as dominant males impose physical punishment on their subordinates. Despite this resistance from dominants, both subordinates and neighbors appear able to parasitize the attractiveness of high-quality birds in the cluster, and gain one-third of the fertilizations from females whose preferred sire can be identified. This supports the proposition that aggregation represents satellite behavior on the part of lower-quality males and that year-round territoriality provides no impediment to the applicability of Wagner’s (1998) hypothesis of the hidden lek.

Participation in the dawn chorus by males is independent of social status or male quality. Although males differ by many

months in the time that they acquire nuptial plumage, and such differences are a primary criterion of mate choice (Dunn and Cockburn 1999; Green et al. 2000; Double and Cockburn 2003; Cockburn, Osmond, and Double 2008), all fairy-wrens increase dawn singing at about the same time, which is also close to the time when they are developing cloacal swelling in readiness for the breeding season (Mulder and Cockburn 1993). The only context we found where dawn singing was reduced was the tendency for a small proportion of dominant males to refrain from singing when their own mate had left on an extragroup foray, and for those males that sang to start the chorus later when their mate was fertile. These observations reject the hypothesis that males should sing more vigorously when their own mate is fertile as a form of guarding (Møller 1991).

Despite living on year-round all-purpose territories, male fairy-wrens aggregated to sing, with some males singing as close as physically possible to the boundary of their territory. This creates a number of male clusters within the study site, the distinctiveness of which was reinforced by the use of a common trill dialect by all members of the cluster. Here, we evaluate these observations in the context of the framework proposed by Höglund and Alatalo (1995) for the formation of conventional leks, because a primary aim of their synthesis was to explain why breeding males should aggregate.

Two of the main hypotheses for formation of leks are inapplicable in the current case. The hotspot hypothesis proposes that males aggregate where female home ranges or foraging routes coincide (Bradbury 1981; Bradbury et al. 1986) and is supported in some lekking frugivorous birds (Westcott 1994). In contrast, female fairy-wrens have nonoverlapping territories and do not make extraterritorial forays except to seek extragroup fertilizations. Alternatively, the black hole hypothesis suggests that in species where sexually receptive females are subject to considerable harassment, females gain an advantage in visiting exclusive male territories, and males are advantaged because they quickly regain any mates they have lost due to disruption (Clutton-Brock et al. 1992; Stillman et al. 1993). To the contrary, in fairy-wrens, females initiate copulation, visit male territories only briefly and exclusively for the purpose of copulation, and make those visits so rarely that the appropriate dynamics are unlikely to emerge in any case.

Males could also be forced to aggregate because suitable display sites are limited (Parker 1978). In the case of our study site, there is no shortage of song posts. Territories in both the natural and plantation vegetation in our study site usually contain large numbers of shrubs of the appropriate growth form and size, and this is particularly true for the plantation areas, where gardening practices increase the suitability of song posts. Aggregating males could also enjoy protection from predators, through heightened corporate vigilance, dilution of risk, or selfish herd effects (Oring 1982). Several studies have suggested that choice of song post by birds is sensitive to the risk of predation (Krams 2001; Duncan and Bednekoff 2006; Møller et al. 2006; Parker and Tillin 2006). Clustering of birds that sing loudly from exposed locations may expose the group collectively to greater risk of predation, but may allow individuals both better monitoring and dilution of their own predation risk. We doubt the general relevance of predation for clustering in fairy-wrens for two reasons. First, the degree of clustering is probably insufficient to provide a reliable source of information or dilution. Second, neither of the preceding hypotheses helps explain why each cluster adopts a distinctive dialect.

By contrast, a suite of hypotheses concerning the attraction of females predicts that members of clusters should share a dialect. The idea that aggregation into conventional leks occurs

because more males provide a unified stimulus has been discredited on theoretical grounds (Bradbury 1981; Höglund and Alatalo 1995). However, it is possible that females may prefer to mate in aggregations of males in order to facilitate comparison between them (Alexander 1975; Bradbury 1981). Males may advertise the size of the aggregation by joint display. For these ideas to promote male aggregation, we would expect per capita success to be higher on larger clusters, as is true for some lekking species. Although larger clusters attract more female fairy-wrens, males enjoy no per capita advantage (Figure 8), undermining the applicability of this hypothesis.

Our data strongly suggest that males aggregate and converge vocally to parasitize the attractiveness of high-quality males. Dominant males respond to participation of their subordinates in the dawn chorus by physical attack, and by increasing the performance rate of their song (Dalziell and Cockburn 2008), suggesting that their interaction is competitive rather than cooperative. Despite the interference from dominants, low-quality individuals gain two advantages from clustering. First, because attractive early-molting males are vulnerable to mortality just before and at the start of the breeding season (Cockburn, Osmond, and Double 2008), males can "inherit" their attractiveness, and be the beneficiary of forays by females unaware that their preferred male has died. Such "temporal spillover" has been previously noted in lekking species such as sage grouse (Gibson et al. 1991; Gibson 1992).

Second, low-quality males gain parasitic success by mimicking the behavior of attractive males. The deceptive mimicry hypothesis of dialect formation suggests that low-quality males gain advantages by singing songs similar to their neighbors in order to minimize aggression from high-quality birds, or to obtain access to mates (Payne 1981; Podos and Warren 2007). Microgeographic structuring and rapid temporal change of dialects has been reported for two groups that display in leks: hummingbirds (Snow 1968; Wiley 1971; Gonzalez and Ornelas 2005) and cotingas (Kroodsma 2005; Saranathan et al. 2007), but data on parentage are not available to dissect the significance of variation in these species. Our data from fairy-wrens support the mate access version of the deceptive mimicry hypothesis. We have shown that the best predictor of extragroup mating in subordinate males was the attractiveness of their own dominant (Double and Cockburn 2003). Here we present new data that support the hypothesis that early-molting males also lose parentage to neighbors. Indeed, though all our evidence suggests that females are seeking early-molting males in the dawn chorus, and that early molt enjoys strong selection as a consequence (Dunn and Cockburn 1999; Green et al. 2000; Double and Cockburn 2003; Cockburn, Osmond, and Double 2008), parasitic satellite males appear to garner on average 33% of extragroup fertilizations. Dominant males do obtain two-thirds of paternity from a cluster that on average contains 5.25 males ( $\pm 2.4$  SD,  $N = 12$ ), which represents substantial mating skew, and unlike conventional lekking species, this skew is unlikely to be distorted by processes like mate-choice copying (Gibson and Höglund 1992; Westneat et al. 2000), as the probability that females will be in a position to observe the behavior of other females is extremely low. Despite this advantage obtained by attractive males, success through spatial and temporal spillover represents an important alternative mating strategy, and is consistent with the predictions of the hotspot hypothesis (Beehler and Foster 1988).

Collectively, these observations lead us to conclude that despite year-round territoriality, fairy-wrens conform to the hidden lek concept espoused by Wagner (1998) and suggest that comparable effects should be examined in other birds.

Finally, our data raise the possibility that at least some cases of polyandry arise when females fail to mate with their

preferred sire and that such failure is a source of selection on male behavior. Although lekking systems in birds provide the most extreme example of pure female preference for male phenotypes (Bradbury et al. 1985; Wiley 1991), in some cases multiple parentage is common (Lank et al. 2002). Recent attempts to explain reproductive success among low-quality males have contrasted the ability of males to force copulations or fertilizations with advantages females obtain from mating with diverse or compatible mates (Lank et al. 2002; Reichard et al. 2007). However, there is growing evidence for strong selection on reproductive parasitism by deception in lekking birds (Jukema and Piersma 2006). Deceptive strategies in turn make female choice more difficult, increasing the likelihood of error. The role of perceptual error has not attracted attention in recent discussions of variability in female mating behavior (Jennions and Petrie 2000; Simmons 2005; Kokko et al. 2006), though Johnstone and Earn (1999) modeled the effect of perceptual error and suggested that it would be most potent in affecting skew when lek size was large. Our data suggest a more general effect.

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