ORIGINAL ARTICLE

How do Southern House Wrens *Troglodytes aedon musculus* achieve polygyny? An experimental approach

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Abstract I designed two experiments to evaluate how polygyny is achieved in Southern House Wrens (*Troglodytes aedon musculus*) breeding in a south-temperate population. In the first experiment, I manipulated territory attractiveness by adding high quality nesting sites (nest-boxes) to 50% of monogamous territories ($n = 24$) and evaluated if males can attract a second female when defending high quality resources. In the second experiment, I simulated high male mortality early in the breeding season by removing 30 territorial males in plots where wrens had been breeding in nest-boxes ($n = 47$ territories). The first experiment did not induce polygyny: although females switched from breeding in tree cavities to nest-boxes when boxes were erected on their territory, none of the neighbouring females who did not receive a box moved to breed as a secondary female. The male removal experiment did induce polygyny: of 21 experimentally widowed females, 38% bred as secondary females of neighboring males—who expanded their territories in the absence of a defending male—and accepted polygyny even in the presence of neighbouring territories held by bachelor males. Secondary females mated to polygynous males were rarely helped by the male while feeding nestlings, but

primary and secondary females overlapped very little in the use of space. Hence, females mated to polygynous males may share parental care disproportionally but not territorial resources. Female attachment to territories and exclusive use of space together with male's expansion of territories to achieve polygyny suggests that Southern House Wrens engage in sublease polygyny.

Keywords Female use of space · Southern House Wren · Social mating systems · Polygyny · Monogamy

Zusammenfassung

Wie bewerkstelligen die Südliche Hauszaunkönige *Troglodytes aedon musculus* ihre Vielweiberei? Ein experimenteller Ansatz.

Ich unternahm zwei unterschiedlich angesetzte Versuche, um herauszufinden, wie Südliche Hauszaunkönige (*Troglodytes aedon musculus*) einer Population der südlich-gemäßigten Klimazone es anstellt, Vielweiberei zu etablieren. Im ersten Experiment manipulierte ich die Attraktivität des Brutgebiets, indem ich in 50% der „monogamen"Reviere ($n = 24$) hochkomfortable Brutplätze (Nistkästen) anbrachte und untersuchte, ob Männchen mit solchen besonders attraktiven Ressourcen ein zusätzliches Weibchen anziehen konnten. Im zweiten Experiment simulierte ich früh in der Brutzeit eine hohe Männchen-Sterblichkeit, indem ich 30 territoriale Männchen an andere Plätze verbrachte, in denen Zaunkönige schon einmal in Nistkästen gebrütet hatten ($n = 47$ Reviere). Im ersten Experiment trat keine Vielweiberei auf: obwohl die Weibchen vom Brüten in Baumhöhlen zu den Nistkästen übergingen, wenn diese in ihrem Revier angebracht worden waren, tat sich keines der benachbarten Weibchen ohne Nistkasten mit einem Nistkasten-Besitzer zusammen, um als

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zusätzliches Weibchen für ihn zu brüten. Im Experiment mit den herausgenommenen Männchen trat jedoch Polygynie auf. Von den 21 künstlich zu Witwen gemachten Weibchen taten sich 38% mit Männchen angrenzender Reviere, die diese wegen des Fehlens eines verteidigenden Männchens vergrößern konnten, als „Nebenweibchen" zusammen und akzeptierten dessen Vielweiberei sogar auch dann, wenn es in angrenzenden Revieren unverpaarte Männchen gab. Die mit polygamen Männchen verpaarten „Zweitweibchen" wurden von ihren Männchen nur selten beim Füttern unterstützt; in der Ausnutzung des vorhandenen Platzes überlappten Erst- und Zweitweibchen nur sehr wenig. Es scheint also, daß sich mit polygamen Männchen verpaarte Weibchen die elterliche Betreuung, nicht aber die Nutzung territorialer Ressourcen unverhältnismäßig teilen. Die weibliche Bindung an Reviere und exklusive Platz-Nutzung zusammen mit der Revier-Ausweitung von Männchen zur Erlangung von Polygynie legen nahe, dass die Südliche Hauszaunkönige eine Art von „Gelegenheits-Vielweiberei" betreiben.

Introduction

The term mating system describes the pattern of mating between individuals of a given population. The assumption that social mating reflects the genetic mating system has been challenged by the discovery of the widespread occurrence of extra-pair fertilisations in otherwise monogamous birds (Gowaty 1985, 1996; Hasselquist and Sherman 2001). This led to the conclusion that the social mating system can differ from the genetic mating system. Territorial polygyny is a social mating system where a male forms a breeding association with more than one female whose nests are located within his territory (Searcy and Yasukawa 1989). Females mated to social polygynous males will pay different costs depending on how they share male parental care and territorial resources. While in some species females receive no help in feeding the young (Dickcissel *Spiza americana*, Zimmerman 1966; Zitting Cisticola *Cisticola juncidis*, Ueda 1984; Red Bishop *Euplectes orix*, Friedl and Klump 2000), in other cases male parental care is shared unevenly between females (Northern House Wren *Troglodytes aedon aedo*, Johnson et al. 1993; Red-winged Blackbird *Agelaius phoeniceus*, Searcy and Yasukawa 1995; Pied Flycatcher *Ficedula hypoleuca*, Alatalo et al. 1982; Yellow-headed Blackbird *Xanthocephalus xanthocephalus*, Willson 1966). Similarly, variation in how females share territorial resources has also been recorded in several species. Competition for food should be reduced when females forage outside the territory (Dickcissel *Spiza americana*, Zimmerman 1966; Corn Bunting *Miliaria calandra*, Hartley et al. 1995), and competition for both food and nesting sites should be reduced

when females' use of space does not overlap, either because males are polyterritorial (Wood Warbler *Phylloscopus sibilatrix*, Temrin et al. 1984; Pied Flycatcher, Lundberg and Alatalo 1992) or because females reside within subterritories (Yellow-headed Blackbirds, Willson 1966; Red-winged Blackbird, Hurly and Robertson 1984; but see Searcy 1986). Variation in how resources (parental and territorial) are shared between females will result in variation in ecological constraints to social polygyny. While biparental care cannot be essential for breeding success for social polygyny to be maintained, in some species males may also need to be able to defend larger or extra territories, increasing the cost of social polygyny to males. Hence, understanding both how females share male parental care and territory resources is essential for understanding how social polygyny can be maintained across different species and populations.

Territorial polygyny is more frequent in Northern House Wren (5–40%; e.g. Johnson et al. 1993; Soukup and Thompson 1998; Poirier et al. 2004; Dubois et al. 2006), than in the Southern House Wren (*Troglodytes aedon musculus* 1–5%; e.g. Freed 1986; Llambías and Fernández 2009). Additionally, populations seem to differ in how social polygyny is achieved. In the Northern House Wren, most cases of polygyny are the consequence of a male attracting more than one female to his territory (Johnson 1998), while in the tropical Southern House Wren, observations suggest that polygyny occurs when a male takes over the territory and female of a neighbouring male, either by evicting or replacing him after its death (Freed 1986). I designed two experiments to evaluate how social polygyny is achieved in temperate Southern House Wrens and how resources are shared between females paired to polygynous males. In the first experiment, I evaluated whether males can attract a second female when defending high quality nesting sites by manipulating territory attractiveness: I erected two nest-boxes in 50% of the territories in plots where monogamously-paired wrens were breeding in tree cavities. In the second experiment, I evaluate whether males can achieve polygyny by monopolising neighbouring females: I simulated high male mortality early in the breeding season by removal of monogamous territorial males in plots with nest-boxes. Understanding how polygyny is achieved (by female attraction or territory takeover), and how females mated to polygynous males share resources in the Southern House Wren, may shed new light into our understanding of geographic variation in mating systems.

Methods

Study species

The House Wren (*Troglodytes aedon*) is a sexually monomorphic, small (10–14 g) territorial passerine that

breeds in tree cavities or holes excavated by other bird species (Johnson 1998). Though its distribution ranges from Tierra del Fuego to Canada (Brewer 2001), it is considered a single species (Remsen et al. 2011; but see Brumfield and Capparella 1996 for suggestions on splitting the taxon into three species).

The present study was carried out in a temperate population of Southern House Wrens (*T. a. musculus*) breeding in nest-boxes and tree cavities in Buenos Aires Province, Argentina. Southern House Wrens are sedentary and remain in their territories year round (Brewer 2001). The dominant social mating system at my study site is monogamy, with polygyny representing approximately 1% of the breeding attempts (Llambías and Fernández 2009), although 33% of the broods contain extra-pair young (LaBarbera et al. 2010). House Wrens have distinct parental roles: females incubate and brood the nestlings, and both sexes cooperate in building the nest and feeding the young (Freed 1987; Johnson 1998). At my study site, breeding success in nest-boxes is greater than in natural cavities, and females preferentially pair with males that defend box-containing territories (Llambías and Fernández 2009).

Field procedures

During October–January, 2003–2007, I studied Southern House Wrens breeding in nest-boxes and tree cavities on a cattle ranch (Los Zorzales), near the town of General Lavalle, Buenos Aires Province (36°26′S, 56°25′W), Argentina. Wrens have been breeding in nest-boxes in the study plot Z1 (total area 4.1 ha, box density = 23 boxes/ha) since 2003, when I erected two boxes per male territory (n = 47 territories) in three forest fragments. The forest fragments are mainly composed of *Celtis tala* trees (4–7 m high) surrounded by pasture. I studied wrens breeding in natural cavities in Z2 plots where boxes were added during 2004 (see below). I visited territories every other day to monitor the presence of colour-banded individuals and check the nesting stage and breeding success. I captured unbanded adults with mist nets or inside nest-boxes and assigned each individual a unique colour-band combination. For detailed field procedures and study site description, see Llambías and Fernández (2009). Nests were filmed with a camouflaged camera for 4 hours beginning 1 h after sunrise when nestlings were 2–3, 7–8 and 11–12 days old. Later video analysis allowed me to assess male participation during feeding. To evaluate male parental care and breeding success, I used data from 2003 to 2007, including natural and induced polygynous nests.

Addition of nest boxes to increase polygyny rate

If, as is true of Northern House Wren males, Southern males can achieve polygyny by attracting a second female

to a high quality nesting site, the addition of nest-boxes should induce polygyny. During 2004, I increased the attractiveness of 50% of monogamous territories by the addition of nest-boxes to randomly chosen territories, creating heterogeneity in territory quality. In five wood patches (Z2 plot, total area = 5 ha) where pairs had been breeding in tree cavities, I added two nest-boxes in each of 12 territories, 16 days before the first egg was observed in the population. Each patch was separated by at least 100 m of pasture from the next closest patch, and together the five patches contained 34 male territories, 24 occupied by pairs and 10 defended by bachelor males. Nests in tree cavities and boxes were checked every other day and breeding success was recorded. By the end of the 2005 breeding season, two nest-boxes had been added to the remaining territories and breeding was monitored until 2007. Note that the manipulation of territory quality started in September 2004 and was finished by the end of December 2005, and included two early breeding seasons, two breeding seasons, and one non-breeding season. The purpose of the addition of two nest-boxes to all territories was to replicate Johnson and Kermott's (1991) experiment in which 2–3 boxes were erected in Northern House Wren territories during 2 years with the subsequent increase of polygyny when compared to a year where no boxes were erected. I started the experiment by the end of December 2005 and breeding was monitored until the end of December 2007, including two non-breeding seasons, two early non-breeding seasons and two breeding seasons. This broad temporal range guarantees that the experiments have included periods where both resident and floater females may be prospecting for mates and places to breed.

Removal of males to increase polygyny rate

If, as in tropical wrens, polygyny in Southern House Wrens is achieved by taking over the territory and female of a neighbour, mortality early in the breeding season should induce polygyny, since no territorial male will be present to defend the territory and resident female. Between 6–8 days before the onset of egg laying in 2004–2005, I captured 30 territorial males (9 bachelors, 21 monogamously mated) from randomly chosen territories in Z1 plot and released them 50 km away in the botanical gardens of San Clemente del Tuyú. If a floater occupied a vacant territory in the next 24 h, I also captured and translocated the floater. I assumed that a male was a floater if it was unbanded (most territorial males were colour-banded) and a territory held by an unbanded male was not observed vacant during the same day. Immediately after the translocation, a proportion of females whose mates were removed (widowed females) were left unpaired in their territories, a proportion of bachelors' territories were vacant, and several monogamous

Table 1 Changes in territory availability after male removal experiments

Territory type	Number of territories 2004		Number of territories 2005	
	Before manipulation	After manipulation	Before manipulation	After manipulation
Widowed territories	0	28% (13)	0	25% (8)
Vacated bachelor territories	0	9% (4)	0	16% (5)
Monogamous territories	85% (40)	57% (27)	69% (22)	44% (14)
Bachelor territories	15% (7)	6% (3)	31% (10)	16% (5)

Changes in the proportion of territorial categories (*n*) of Southern House Wrens after male translocations during 2004–2005

Widowed territories territories where a paired male was removed and a female was present in the territory the day of removal, *Vacated bachelor territories* territories defended by an unpaired male that was removed, *Monogamous territories* territories where paired male and female were present, *Bachelor territories* territories defended by an unpaired male

pairs and bachelor males were left in their territories (Table 1). Since all territories contained two nest-boxes, each experimental "widowed" female had the choice of abandoning her territory and settling somewhere else (either as secondary or monogamous female; Table 1). Breeding activities were monitored in all plots until the end of December 2007. Male translocation experiments and procedures were approved by the Institutional Animal Care and Use Committee (protocol number: 20576-EM), Cornell University, and are in line with national laws.

Territory size measurements

To compare territory sizes of experimentally-induced polygynous and monogamous males and of females mated to these males, I used data gathered during 2004–2007 and included two polygynous males who achieved polygyny by replacing a neighbour after his death. All territories measured were from different adults to avoid pseudoreplication.

I use the minimum convex polygon (MCP; Mohr 1947; Odum and Kuenzler 1955; Barg et al. 2005) procedure to map territories of 21 females mated to monogamous males, 16 females mated to polygynous males (8 primary and 8 secondary), 20 bachelor males, 68 monogamous males and 9 polygynous males. Due to early nest failure or insufficient points to complete the polygon, I was unable to measure territory size in seven males and nine females. I defined the core of the territory as the area surrounding the nest-box where the female bred and defined its boundaries by observing the male and female for 20 min while foraging when nestlings were 2–3, 7–8, and 11–12 days old. Additionally, I used song playback to map male territories. I observed the male's movements during two sessions of 15 min after stimulating aggressive behaviour for 2–5 min. This was essential for mapping male territories because polygynous males only on rare occasions fed the nestlings of the secondary female (see below), but they did defend the territory surrounding the nest of this female. To complete the polygon, I recorded the location of the adults

during each nest check. All birds were followed between dawn and 1230 hours EDT. To calculate the territory area, I later connected the outermost locations (stored on GPS Garmin eTrex and Vista HCx) using the program Map Source v.4.00 (Garmin 2006) or the track function on a GPS (Garmin Vista HCx). The outermost polygon was measured using the data collected from nest building until the day the nestlings fledged, so it represents a maximum area of use during the entire nesting cycle. This area does not necessarily represent the maximum size at a given time, since territorial boundaries might change throughout the season.

Statistical analysis

Since I was not able to measure territory size, parental care or breeding success in all polygynous and monogamous nests, sample sizes differ between analyses. I compared territory size of monogamous and polygynous males and of females mated to monogamous or polygynous males with a general linear model (GLM) using social status and year as fixed factors. I compared breeding success (nestlings fledged/eggs laid) and fledging success (number of nestling fledged) of primary versus secondary females and of primary and secondary females versus monogamous females with a Mann–Whitney *U* test. Statistical analyses were carried out in SPSS v.14 (SPSS Institute 2005).

Results

Nest-boxes did increase the quality of the nesting site: the probability of monogamous pairs producing at least one fledgling from nest-boxes was significantly higher than for pairs breeding in tree cavities (0.56, $n = 141$ vs. 0.35, $n = 54$, $X^2 = 14.22$, $P = 0.009$). Although the probability of producing fledglings for a secondary female was 0.60 ($n = 10$ nests), there was no significant difference between this and the probability of producing fledglings from nests

in tree cavities ($X^2 = 2.18$, $P = 0.14$), probably due to the small sample size.

Nest-boxes increase breeding success relative to tree cavities and females seem to prefer to pair with males with nest-boxes on their territory (Llambías and Fernández 2009). Addition of nest-boxes, however, did not induce polygyny. During 2004–2005, 83% (10/12) of the pairs who received two nest-boxes in their territories switched from breeding in tree cavities to breeding in nest-boxes, indicating a strong preference for nest-boxes. By the end of 2007, all pairs were breeding in nest-boxes. None of the males attracted more than one female to their territories during the 2004–2005 breeding season, and I observed no cases of polygyny during 2006–2007 after each of the territories in Z2 plot received two boxes by the end of the 2005 breeding season.

The male removal experiments induced polygyny in the Z1 plot. Of the 21 experimentally widowed females, 18 (86%) remained in their territories. Of these 18, 8 (44%) bred as secondary females with neighbouring, previously-monogamous males who expanded their territories, and 10 (56%) bred as monogamous females with territorial males or floaters who moved into their territories. The other 3 widowed females were not seen again at the study site. No secondary females were observed in control territories where the male was captured for banding early in the breeding season but not translocated.

Males either shifted or expanded their territories to overlap with the widowed females. During 2004–2005, eight males expanded their territories to breed polygynously and seven bachelor males (four from the study plot and three from nearby areas) abandoned their territories to move into an experimentally widowed female territory. Three vacancies were occupied by unbanded males presumed to be floaters, while 89% ($n = 8/9$) of vacated bachelor territories remained empty for more than 7 days; only one of these territories was claimed by a floater.

During 2003–2007, I observed five cases of natural polygyny ($n = 222$ breeding attempts) where I could determined how polygyny was achieved. In four cases, I was able to confirm that a male expanded his territory to overlap with a female whose mate had disappeared. In one case, I observed a male actively seizing the mate and territory of a neighbour. Similarly, Freed (1986) studied a population of Southern House Wrens breeding in nest-boxes in Panama and reported six cases of polygyny ($n = 471$ breeding attempts); three cases were achieved by territorial takeover and three cases were achieved by replacement of a male who had previously disappeared. No cases of secondary females settling on the territory of a monogamous male have been observed in Panama (Freed 1986) or at my study site, although in both populations all territories had extra nest-boxes.

I did not find significant differences in the territory sizes of females mated to polygynous versus monogamous males (637.06 ± 41.40 m², $n = 16$ vs. 695.30 ± 54.21 m², $n = 21$, respectively; GLM, $F_{33} = 0.04$ $P = 0.82$). Similarly, I did not find significant differences in the territory sizes of bachelor and monogamous males (576.92 ± 45.18 m², $n = 20$ vs. 727.05 ± 47.03 m², $n = 68$, respectively; GLM, $F_{83} = 3.34$, $P = 0.071$). Territories of polygynous males were significantly larger (1,511.36 ± 176.13 m², $n = 9$; GLM, $F_{71} = 27.90$, $P \leq 0.001$) than territories of monogamous males. Primary and secondary females were restricted to their territories with very little overlap (range 0–0.3%, $n = 8$ pairs). During 2003–2007, I observed seven females (one secondary and six paired to monogamous males) visiting and inspecting the nest-box content of a neighbouring female, but these intrusions were not observed during feeding bouts. On four occasions, the resident female attacked and chased the intruder away.

Males fed nestlings preferentially at the primary females' nests and less often at the secondary females' nests when nestling were 2–3 days (100%, $n = 6$ vs. 0% $n = 7$ nests), 7–8 days (71%, $n = 7$ nests vs. 0% $n = 6$ nests) and 11–12 days old (100%, $n = 5$ vs. 40% $n = 5$ nests). Although sample size is small, these data suggest that males may bring food to the secondary females' nests late in the nestling stage, when primary females' nestlings have already fledged. Primary and secondary females did not significantly differ in fledgling success (nestlings fledged/eggs laid, 0.76 ± 0.14, $n = 7$ vs. 0.50 ± 0.14, $n = 10$, respectively, Mann–Whitney U test, $Z = -1.28$, $P = 0.20$) nor in the number of nestlings fledged (3.43 ± 0.65 $n = 7$ vs. 2.40 ± 0.70 $n = 10$, respectively, Mann–Whitney U test, $Z = -0.91$, $P = 0.39$). Similarly, females mated to polygynous males did not significantly differ in fledgling success from females mated to monogamous males (0.61 ± 0.10 $n = 17$ vs. 0.53 ± 0.04 $n = 115$, respectively, Mann–Whitney U test, $Z = -0.67$, $P = 0.50$) nor in the number of nestlings fledged (2.88 ± 0.49 $n = 17$ vs. 2.61 ± 0.19 $n = 119$, respectively, Mann–Whitney U test, $Z = -0.357$, $P = 0.72$).

Discussion

Manipulation of territory attractiveness and removal of territorial males suggest that in the Southern House Wren polygyny is achieved mainly by taking over the territory of a neighbour and its resident female, and not by attraction and subsequent settlement of additional females to a surplus high-quality nesting site. Empirical data from the southern temperate (Llambías and Fernández 2009) and from a tropical site (Freed 1986) support this conclusion. In the Northern House Wren, addition of extra nest-boxes increases both polygyny rate (Johnson and Kermott 1991)

and male attractiveness to females (Dubois et al. 2006; Eckerle and Thompson 2006; Demory et al. 2010). Similarly, in the Southern House Wren, females seem to prefer males with nest-boxes in their territories, as the proportion of bachelor males is lower in plots provided with nest-boxes than in plots where wrens breed in natural cavities (Llambías and Fernández 2009). Southern House Wren females clearly prefer nest-boxes to natural cavities as all the wrens eventually switched from breeding in natural cavities to nest-boxes when boxes were added to their territories. Still, addition of nest-boxes did not enhance polygyny of Southern House Wrens. Hence, Northern and Southern House Wrens not only differ in polygyny rate but in the way polygyny is achieved. In the Northern House Wren, secondary females are able to fledge some nestlings although they receive less help in raising the brood when compared to primary females (Johnson et al. 1993; Johnson and Kermott 1993). In the Southern House Wren, I observed a similar pattern, with secondary females receiving less help but able to fledge at least some nestlings. However, these results should be treated with caution since the sample size on breeding success of secondary females was small.

The fact that social polygyny and extra pair fertilisations seem to be less frequent in Southern than Northern House Wrens (Llambías and Fernández 2009; LaBarbera et al. 2010) together with the predominant way social polygyny is achieved (territory takeover in the south vs. territory advertising in the north) suggests that inter-sexual competition should be dominant in the north while intra-sexual competition should be dominant in the south. Hence, males' physical and behavioural attributes may also differ between populations. Territorial takeover does occur in the Northern House Wren (Johnson and Kermott 1990; Kermott et al. 1991), but it seems that territory advertising is the prevalent way to achieve polygyny. Why do Northern and Southern House Wrens differ in the way polygyny is achieved? A possible explanation for this pattern is that the sedentary life-style imposes constraints to mate attraction. In the migratory Northern House Wren, males arrive at the breeding grounds before females and settle in breeding territories from where they advertise a nesting site, with females arriving later and choosing between territories and/or males (Johnson 1998). In contrast, Southern House Wrens are sedentary and females remain in the territories year round (Freed 1987; Llambías and Fernández 2009). To attract a secondary female, a male should attract a floater female or a female who has recently divorced or whose mate has died. Hence, it may be easier to achieve polygyny by territorial takeover than by female attraction. It is tempting to conclude that takeover polygyny is a consequence of a sedentary life-style, but this interpretation should be treated with caution. After the nestlings of the first brood have fledged, Northern House Wren females

often switch territories and mates (Drilling and Thompson 1991; Poirier et al. 2003). Although females might have initially settled on a territory to breed, high divorce rates and territorial infidelity may still occur, providing monogamous males with new opportunities to attract a secondary female. Hence, takeover polygyny may be a consequence of high territorial fidelity rather than a sedentary life-style per se. Alternatively, Davies (1992) proposed that, in migratory birds, males may predict the territories where females will settle and monopolise nesting sites before their arrival, suggesting that, rather than female choice, male–male competition determines the mating system. Under this scheme, polygyny in both Northern and Southern House Wrens is achieved by monopolisation of females' resources, the main difference being in the timing when those resources are monopolised (before or after females have settled). Finally, if unpaired females are scarcer in the south than in the north, males may only be able to achieve polygyny by territorial takeover in the south (Freed 1986; Kermott et al. 1991).

Although Southern House Wren females paired to polygynous males may share the male's parental care, they did not seem to share space. Since female's use of space showed very little overlap, aggression from resident females may prevent the settlement of secondary females as has been proposed for other bird species (Wittenberger and Tilson 1980; Sandell and Smith 1997; Cézilly et al. 2000), precluding males from attracting a secondary female when provided with two nest-boxes. Territory size of polygynous males was significantly greater than that of monogamous males while the area used by females mated to monogamous or polygynous males did not differ significantly. As a consequence, a Southern House Wren polygynous male defended a territory twice as big as that of a monogamous male. Additionally, females did not abandon their territories even when their mates were removed and bachelor males with nest-box territories were present in the area. Males, on the other hand, abandoned their territories or expanded them only if a female was present; territories where bachelor males were removed remained empty for more than a week while male-removed territories where a female was present were occupied in less than 12 h. Similarly, removal experiments in migratory Black-throated Blue Warblers (*Dendroica caerulescens*; Marra and Holmes 1997) and in the resident Superb Fairy-wren (*Malurus cyaneus*; Pruett-Jones and Lewis 1990) show that new or neighbouring males move to territories that are occupied by females but not to territories without females.

The Southern House Wren social mating system may be seen as a consequence of: (1) female distribution; since females' use of space overlap very little, a polygynous male needs to defend a territory twice as big as a monogamous male; and (2) female territorial fidelity; even in the

presence of what may be better breeding options, resident females remained on their territories although the resident male was removed and replaced. This general pattern is likely leading to male–male competition for monopolising female's territories. Hence, the low polygyny rate of the Southern House Wren may be attributed to the high costs of defending such big territories. Indeed, none of the males bred polygynously for more than one breeding event, and all polygynous males eventually lost part of their territory to a floater or neighbouring male.

The kind of mating system where the male monopolises more than one female's territory has been termed "sublease territorial polygyny" by Gould and Gould (1989) and is a specific case of resource-defence polygyny (Cézilly and Danchin 2008). Sublease territorial polygyny is not well documented in birds, perhaps because much more effort has gone into describing male than female territoriality. It has been shown in the Song Sparrow (*Melospiza melodia*; Arcese 1989) and Dunnocks (*Prunella modularis*; Davies 1992) that the two females mated to polygynous males overlap little in the areas used. Additionally, in several species, it has been observed that males become polygynous by expanding their territories and incorporating a second female (Seaside Sparrows, *Ammodramus maritimus*, Greenlaw and Post 1985; Song Sparrows, Smith et al. 1982; Blue Tits, *Cyanistes caeruleus*, Kempenaers 1995). This kind of mating system has been termed usurpatory bigamy by Freed (1986) and replacement polygyny by Kempenaers (1995), and in the case of the Southern House Wren may be synonymous with sublease polygyny.

Future research with an experimental design involving the separate manipulation of territory and male quality will do much to further illuminate our understanding of social mating systems. Evaluation of the determinants of female breeding success will help to assess whether female distribution is affected by male or territory quality, and whether a particular social system is the consequence of female choice or intra-sexual competition.

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