

Male quality influences male provisioning in house wrens independent of attractiveness

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Female reproductive investment can vary according to their mate's attractiveness, and males may differentially invest according to their own attractiveness. Thus, when studying female parental investment, male investment must also be considered. We tested the hypothesis that the attractiveness of male house wrens (*Troglodytes aedon*) influences their investment independent of their own intrinsic quality by manipulating the number of nest sites (one = control; 4 = attractive) in each male's territory. Treatments (attractive or control) were applied prior to (natural state) or after (imposed state) male settlement, and male investment was determined twice during the nestling stage by the number of trips males made to the nest to provision their nestlings. Males that settled in the attractive territories were significantly older than those that settled in control territories in the natural state. There was a significant interaction effect between state and treatment on male provisioning. Provisioning rates of attractive and control males in the imposed state did not differ, but attractive males in the natural state provisioned at a lower rate than control males late in the nestling stage. Thus, provisioning by males is influenced more by their intrinsic quality than their attractiveness. *Key words*: attractiveness, house wren, mate choice, provisioning, reproductive allocation, *Troglodytes aedon*. [*Behav Ecol* 21:1156–1164 (2010)]

Males in biparental bird species vary in both the indirect genetic benefits they confer on their offspring as well as the amount of the material resources they contribute to their offspring (Trivers 1972; Burley 1981; Iwasa et al. 1991). Because of this variation, females in iteroparous species are often paired with males of varying quality and attractiveness over the course of their reproductive lifetime. By quality, we mean aspects of a male's phenotype that are positively correlated with fitness (Wilson and Nussey 2010), whereas attractiveness refers to the extent that a male is preferred by females. Typically, quality and attractiveness covary so that a male's attractiveness is a good indicator of his intrinsic quality, that is, his physical condition and genetic constitution (Hill 1991; Veiga 1993; Keyser and Hill 2000), although this may not always be the case (Viljugrein 1997). Previous studies on birds have shown that females vary their investment in offspring in relation to the attractiveness of their mate, doing so even when male quality and attractiveness have been experimentally decoupled (Sheldon 2000; Saino et al. 2002; Rutstein et al. 2005).

Offspring quality is not, however, solely a product of female reproductive investment in biparental bird species (Cockburn 2006) because males can potentially invest at any or all the 3 stages of the breeding cycle, the egg production, incubation, and nestling/fledgling stages. Depending on the species, males can engage in "courtship feeding" of the female during egg production and incubation, share incubation duties with the female, and assist in provisioning the offspring during the nestling/fledgling stage (Clutton-Brock 1991). Therefore, when studying differences among females in their investment in reproduction when paired with males of different attractiveness, it is necessary to take into account paternal investment and the possibility that males may vary their investment in relation to their own quality and attractiveness. One way to

control for such differences in male investment is to randomly assign male attractiveness, thereby decoupling the usual covariation between attractiveness and quality (e.g., Alatalo et al. 1986) and equalizing male investment across treatments. Any resultant differences in offspring quality should, therefore, be attributable solely to differential female investment (Sheldon 2000; Limbourg et al. 2004). However, this will be true only if males do not change their reproductive investment when their attractiveness has been experimentally altered (Smith 1995; Sanz 2001).

We tested the hypothesis that paternal investment in house wrens (*Troglodytes aedon*) is influenced by male attractiveness independent of male quality. Paternal investment in house wrens is confined almost exclusively to provisioning of nestlings and fledglings as males rarely courtship feed and never incubate the eggs or brood nestlings (Johnson 1998). To manipulate male attractiveness, we altered the number of nest sites that males could make available to potential mates (Dubois et al. 2006; Eckerle and Thompson 2006) in 2 contexts. In the natural attractiveness state, male attractiveness and quality covaried because males were allowed to sort themselves out among territories of differing attractiveness. In the imposed attractiveness state, any correlation between male attractiveness and quality was decoupled because attractiveness was randomly assigned. We predicted that if male investment through nestling provisioning is influenced primarily by male attractiveness independent of quality, differences in provisioning by attractive or control males would be the same in the 2 states. Alternatively, if male provisioning is influenced primarily by male quality, there should be a significant interaction between attractiveness and the manner in which attractiveness was assigned (natural or imposed) in their effect on male provisioning.

MATERIALS AND METHODS

Study species and study site

House wrens are small (10–12 g), woodland passerines that feed primarily on invertebrates (Johnson 1998). They are

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sexually monomorphic in size and plumage and are mainly socially monogamous; however, social polygyny does occur and extrapair fertilizations are common (Soukup and Thompson 1997; Forsman et al. 2008). Males of the study population return to the breeding grounds in late April and compete for territories before females arrive. After establishing territories around a nest cavity, males add sticks to the cavity and sing nearby to attract a female. Females are typically the choosy sex and examine the available nesting cavities before choosing a mate. They then complete the nest by constructing a cup of fine plant material over the rough stick platform that the male erects in the cavity (Kendeigh 1941; Johnson 1998).

House wrens in the study population typically produce 2 broods each breeding season, with each clutch consisting of 6–8 eggs, and frequently switch mates between broods (Drilling and Thompson 1988). Incubation lasts 12–13 days and nestlings fledge 16–18 days after the first egg in the clutch hatches (brood day 0). Typically, both the male and female provision the nestlings, bringing only one food item to the nest at each visit. After fledging, one or both adults continue to provision their young for another 2 weeks. Paternal investment occurs mainly as nestling/fledgling provisioning (Johnson 1998). If male provisioning is experimentally eliminated, there is an increase in nestling mortality and a decrease in nestling growth rates compared with nestlings in control nests (Johnson et al. 1992).

Because house wrens are secondary cavity nesters (i.e., they do not excavate cavities and are dependent on the presence of preformed cavities for nest sites), the availability of suitable high-quality nesting cavities is often limited making them a valuable resource for which males and females compete (Johnson and Kermott 1991; Poysa H and Poysa S 2002). Three independent studies of house wrens have shown that when males are provided with extra nest cavities (i.e., nest-boxes) before females settle, males with multiple nest-boxes acquire mates sooner than those with fewer nest-boxes (Dubois et al. 2006; Eckerle and Thompson 2006; Grana 2009). Thus, it is possible to manipulate male attractiveness independent of male and territory characteristics.

The experiment was conducted during the 2009 breeding season on the Mackinaw study site (Figure 1) in McLean County, IL (lat 40°40'N, long 88°53'W), an area of upland and bottomland second-growth deciduous forest bordering the Mackinaw River (see Eckerle and Thompson 2006). Nest-boxes were mounted above 48.3-cm-diameter aluminum disks on 1.5-m steel poles to discourage predators.

Experimental design

We manipulated male attractiveness by varying the number of nest-boxes on each territory (one or 4 nest-boxes) under 2 states: 1) when the number of nest-boxes was established prior to male arrival so that males were free to choose between one and 4 nest-box sites (natural attractiveness) or 2) when the number of nest-boxes was established after a male had settled at one nest-box but before a female had arrived (imposed attractiveness). These 2 factors were replicated in 2 habitats (upland and floodplain forest). Thus, we employed a split-plot experimental design in which treatment (attractive and control) was the subplot factor and was applied within the main-plot factor of state (natural and imposed) (Figure 1).

Nest-boxes on the Mackinaw study site are situated 30 m apart on north–south lines 60 m apart resulting in a density of 5.4 boxes/ha, but for this experiment, we closed every other nest-box on each line on the study plots so that the central nest-boxes used in the experiment were 60 m apart (Figure 1). For the natural attractiveness state, treatments were established prior to male arrival, with approximately

one-half the territories attractive and containing 4 nest-boxes (3 nest-boxes 10 m north, south, and west of the central box) and the other half control with just a single nest-box. In a few cases, barriers, such as tilled fields, forced the additional boxes in the attractive treatments to be set up east, west, and south, or north, east, and west of the central box. The entrance to all nest-boxes faced east. The 4 and one box territories were established in alternating order starting at the northeast corner of the site. A coin was flipped to determine the first treatment (attractive or control) and subsequent treatments alternated along the south edge of the site as well as along the individual north–south lines. In the natural attractiveness state, there were 27 attractive treatments (13 upland and 14 floodplain) and 26 control treatments (14 upland and 12 floodplain).

In the imposed attractiveness state, single nest-boxes 60 m apart were established before male arrival and attractiveness was manipulated after male settlement but before female arrival. Nest-boxes were monitored daily for evidence that males had settled, that is, presence of a male actively singing and 50% of the floor of the nest-box covered with sticks (see Eckerle and Thompson 2006). After the first male settled, a coin was flipped to assign the first treatment (attractive or control); treatments were alternated thereafter as males settled. Treatments (4 or one nest-boxes as described above) in the upland and floodplain habitats were assigned independently to maintain a similar number of attractive and control treatments in each habitat. Fifty-six single nest-boxes (27 upland and 29 floodplain) were available for males to occupy on their arrival on the breeding grounds. At the end of the male settlement period (01 May to 01 June), 10 attractive and 9 control treatments had been assigned in the upland and 12 attractive and 12 control treatments in the floodplain. It is conceivable, of course, that given the extended period between male settlement and capture (see below), males in the imposed attractiveness state competed for attractive territories after initial settlement, resulting in higher quality males occupying the attractive territories. As a check on this possibility, one of us (C.F.T.) periodically conducted visual sightings of settled males that were either color banded (having bred on the study area previously) or aluminum banded (having hatched on the study area in a previous year); in no instance was any of these males replaced by a male without a band or a male with a different color band combination. In addition, in our daily censuses of males, there was never any period in which a male disappeared and the territory resettled at a later date. These observations leave us confident that most, if not all, of the males that initially settled territories retained them through the period of mate attraction and subsequent nesting.

Field methods

A male's time-to-pairing was measured in 2 ways: 1) the interval between the date of male settlement and the date the first egg of the clutch was laid (i.e., egg-1 day) (see Eckerle and Thompson 2006) and 2) the interval between the date of male settlement and the first evidence that a female had begun to complete the nest (see Dubois et al. 2006). Two measures were used because, although the former is easily determined, the interval includes not only the time required for the male to attract a female but also the time required for her to complete the nest and to produce her first egg. In contrast, although the latter measures only the time required to attract a female, the determination of the start of nest building is somewhat subjective.

Adults were captured during the incubation or nestling stages either in the nest-box by closing a trapdoor permanently mounted over the entrance or in a mist net in

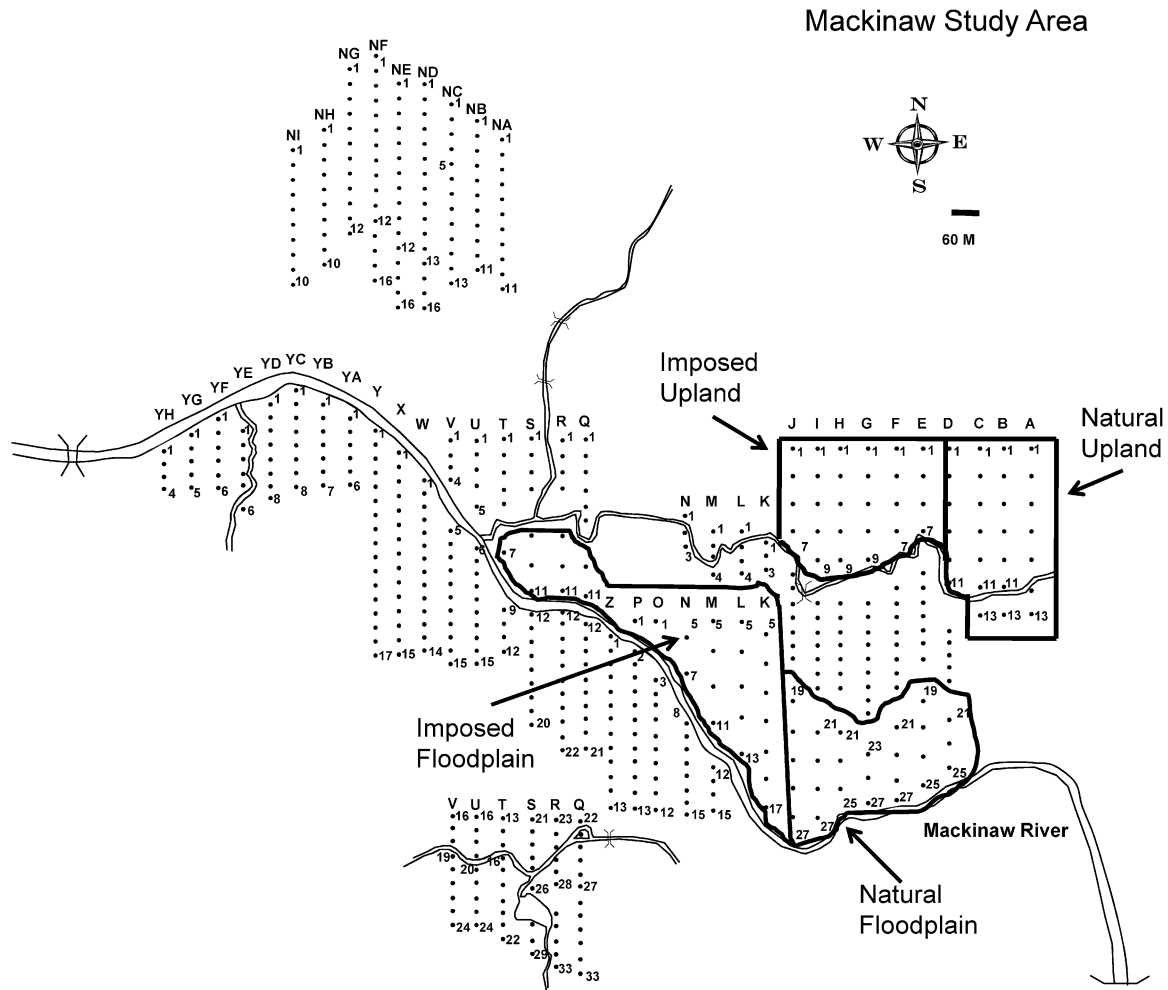


Figure 1

Map of Mackinaw study site. Each dot represents a nest-box. A split-plot design was used such that the main plot factor was state (imposed or natural attractiveness), and the subplot factor was treatment (attractive and control). There were 2 replicates in this experiment (upland and floodplain).

conjunction with playback of a recording of songs of male house wrens. Females were identified by the presence of a brood patch and males by the absence of a brood patch and presence of a cloacal protuberance. Adults were weighed to the nearest 0.1 g on a digital scale (Acculab Pocket Pro 250-B or PP-201), and tarsus length was measured to the nearest 0.1 mm using dial calipers. Adults and nestlings were banded with a numbered US Fish and Wildlife Service aluminum band, and adult males were given 3 additional colored bands (total of 2 bands per leg) so they could be identified without being recaptured. Approximately 50 μ l of blood was collected from adults in a heparinized capillary tube after puncturing the brachial vein. The blood was stored on ice in a cooler until later the same day in the laboratory, the plasma was separated from the whole blood and preserved by freezing at -20°C for later analysis of the plasma proteins (see below).

Male quality was characterized based on a variety of morphological and physiological measures (body mass, tarsus length, body condition index, age, hematocrit, and plasma protein level). Tarsus length was used as a measure of structural size (Senar and Pascual 1997), and a body condition index was produced using the residuals of a multiple regression of mass on tarsus length and time-of-day of weighing. Hematocrit percentage and plasma protein levels were used as measures of health state (Ots et al. 1998; Forsman et al. 2008).

Provisioning rates

Male and female provisioning rates were recorded during 2 observation periods, brood days 2–4 (nest watch 1) and brood days 9–10 (nest watch 2). On brood days 2–4, females spend most of their time brooding the ectothermic nestlings, whereas males provision at a high rate. On brood days 9–10, the rate of nestling mass gain is greatest (Zach 1982), and provisioning rates are at their highest. Provisioning rates during 45- to 60-min intervals were determined either by an observer stationed 20–30 m away from the nest-box using a spotting scope or by recording with a digital camera. When using spotting scopes, the observation period began when there was no evidence the birds were aware of, or distracted by, human presence. For digitally recorded nest watches, a dummy camera was placed 10 m from the nest-box 24 h prior to filming. The first 2 min of each recording were discarded to allow the birds to resume normal activity after the observer had replaced the dummy with the camera and departed. Only the first 60 min of recordings were included in the analyses. The sex of provisioning adults was determined by the differences in their bands or by their behavior. All behaviors by males and females were recorded during the nest watches, including the frequency and duration of any singing by males. Nest watches during which the adults' provisioning behavior was interrupted for any reason were discarded.

Laboratory methods

Whole blood samples were centrifuged at 6000 rpm for 60 s to separate the plasma and red blood cells (Hematostat II; Separation Technology, Sanford, FL), and the hematocrit (percent of whole blood volume occupied by packed red blood cells) was recorded. Hematocrit is a good indicator of an individual's ability to distribute oxygen to the entire body (Ots et al. 1998). Specific blood plasma proteins were identified using gel electrophoresis following instructions by the manufacturer (Quick-Gel System, cat. no. 3550; Helena Laboratories, Beaumont, TX). Each sample was run at 400 V for 8.5 min on a pre-prepared agarose gel, after which the gel was dried and stained using protein-specific acid blue stain (QuickGel System; Helena Laboratories). Destain was used to remove excess blue stain from the gel. A densitometer was used to scan the stained gels and quantify the relative amounts of protein present in electrophoretic bands (QuickScan 2000 WIN version 2). The 2 major proteins of interest were albumin and gammaglobulins, the ratio of which (A/G) is a good indicator of health state (Ots et al. 1998).

Statistical analyses

Statistical analyses were performed using Statistical Analysis Software (SAS) Version 9.1 (SAS Institute 2004). A significance level of $P \leq 0.05$ was used in all analyses. Failure-time analysis was used to examine the effects of treatment and habitat on time of male settlement, using separate Cox regressions (PHREG procedure) for each state (imposed and natural). Male time-to-pairing was analyzed using the same PHREG procedure in which the dependent variable was time-to-pairing (lining) or time-to-pairing (egg). The independent variables included in the analysis were treatment (attractive or control), state (imposed or natural), habitat (upland or floodplain), and male settlement date.

Measures of male size (mass and tarsus) and quality (body condition index, hematocrit, and plasma protein level) were analyzed using a split-plot analysis of variance (ANOVA) (PROC GLM), in which state and treatment were the fixed effects. The random effect was habitat within state, which quantified variation attributable to the plot or other random effects. Tarsus measurements could not be normalized because of several outliers, so the best transformation (squared) was used. For male mass and body condition index, hour of weighing had to be taken into account by including it in a regression of mass on hour to produce residuals for the dependent variable. For hematocrit and plasma protein analyses, brood day was included by using the residuals of a linear regression of health measure on brood day. For protein level analyses, albumin and the albumin/gammaglobulin ratio were examined in separate analyses. The natural log transformation was used for albumin/gammaglobulin ratios.

To analyze the effects of age, separate 2-way contingency tables (PROC FREQ) were employed for the imposed attractiveness state and the natural attractiveness state with treatment (attractive or control) as the independent variable. Age had 2 categories in which the "new" category contained males of unknown age that have never been captured before, as well as birds that were banded as nestlings on the study area in 2008 and were known yearlings. The "old" category contained birds that had been caught at least once before as a breeding adult and thus were at least 2 years old.

Male and female provisioning rates were analyzed separately using a repeated-measures split-plot ANOVA (PROC GLM). Provisioning rates were quantified by the number of trips per hour per nestling. The within-subjects effect was nest

watch in which the same individuals were compared in nest watch 1 and 2. The fixed, or between-subjects, effects were state (imposed or natural) and treatment (attractive or control), and the random effect was habitat (state). Tukey-Kramer pairwise comparisons of least squares means were used as follow-up tests. Male and female provisioning rates were also pooled to obtain the total number of feeds per nestling per hour and analyzed using the same repeated measures split-plot ANOVA.

RESULTS

Settlement pattern

In the natural attractiveness state, 100% (13 of 13) of the attractive territories and 93% (13 of 14) of the control territories were settled in the upland habitat. In the floodplain, 93% (13 of 14) of the attractive territories and 75% (9 of 12) of the control territories were settled. The proportions of the total number of attractive territories and control territories that were settled were not significantly different ($\chi^2_1 = 2.12$, $P = 0.146$). In the imposed state, 18 territories in the upland habitat (9 attractive and 9 control) and 23 territories in the floodplain (12 attractive and 11 control) were settled. Any territory that had a failed first nest and was resettled was omitted from the analyses. In 4 cases (3 natural and one imposed) in which more than one male settled on a single attractive territory, only the first male was included in the analyses. Second males in these situations did not contribute anything to the first male's breeding attempt but instead attracted their own mates and helped rear their own nestlings.

In the imposed attractiveness state, there was a significant effect of habitat on time of male settlement, with males settling earlier in the floodplain than in the upland (Wald $\chi^2_{1,40} = 5.739$, $P = 0.017$) (Figure 2). However, as would be expected by the random assignment of attractiveness, there was no effect of treatment on time of male settlement (Wald $\chi^2_{1,40} = 0.063$, $P = 0.802$) (Figure 3). In the natural attractiveness state, time of male settlement was not affected by habitat (Wald $\chi^2_{1,46} = 0.120$, $P = 0.730$) (Figure 2), but treatment did have an effect, with attractive territories settled earlier than control territories (Wald $\chi^2_{1,46} = 6.659$, $P = 0.010$) (Figure 3).

Male time-to-pairing (lining) was not significantly affected by treatment (Wald $\chi^2_{1,87} = 0.259$, $P = 0.611$), state (Wald $\chi^2_{1,87} = 0.553$, $P = 0.457$), habitat (Wald $\chi^2_{1,87} = 0.024$, $P = 0.876$), or date of male settlement (Wald $\chi^2_{1,87} = 1.283$, $P = 0.257$). Male time-to-pairing (egg) was also not affected by state (Wald $\chi^2_{1,87} = 0.327$, $P = 0.567$), habitat (Wald $\chi^2_{1,87} = 0.964$, $P = 0.326$), treatment (Wald $\chi^2_{1,87} = 3.361$, $P = 0.067$), or date of male settlement (Wald $\chi^2_{1,87} = 3.463$, $P = 0.063$). Two males, both attractive, succeeded in attracting a secondary female. In both cases, we included data from the nest of the primary female but omitted data from the nest of the secondary female in subsequent analyses.

Male quality

There were no significant effects of state or treatment on male mass, tarsus, or body condition (Table 1), or on any measures of health state (Table 1). However, in the natural attractiveness state, attractive males were significantly older than control males ($\chi^2_1 = 6.908$, $P = 0.009$) (Figure 4). As expected, this difference disappeared when attractiveness was randomly imposed ($\chi^2_1 = 1.619$, $P = 0.202$). Unlike males, there was no association between treatment and female age for either the imposed attractiveness state ($\chi^2_1 = 1.51$, $P = 0.22$) or natural attractiveness state ($\chi^2_1 = 0.25$, $P = 0.62$).

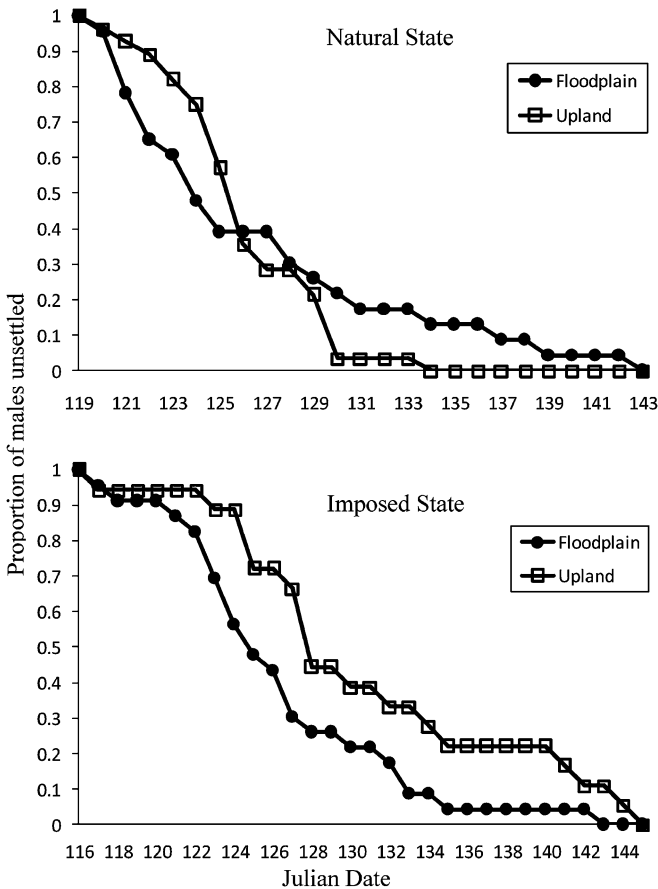


Figure 2
Effect of habitat on male settlement in the natural and imposed states.

Provisioning rates

Males provisioned at a significantly higher rate during nest watch 1 than during nest watch 2 (Pillai's Trace, $F_{1,62} = 8.46$, $P = 0.005$) (Figure 5). There were no other significant within-subject effects. There was a significant between-subjects interaction between state and treatment ($F_{1,62} = 5.64$, $P = 0.021$). Follow-up tests using Tukey–Kramer pairwise comparisons failed to identify the source of the interaction, but attractive males provisioned at a lower rate than control males in the natural attractiveness state during nest watch 2 ($P = 0.067$) (Figure 5). There were no other significant between-subject effects (Table 2).

During nest watch 1, only 4 males (2 control and 2 attractive) failed to provision, whereas 27 of the 68 experimental males failed to provision during nest watch 2. In the natural attractiveness state, the proportion of attractive males that failed to provision (12/21) was significantly larger than the proportion of control males (2/16) ($\chi^2_1 = 8.343$, $P = 0.004$), whereas in the imposed attractiveness state, the proportions of attractive and control males that failed to provision were not significantly different (attractive: 6/15; control 7/16; $\chi^2_1 = 0.447$, $P = 0.833$). Males that failed to provision were not simply absent from their territories during the nest watch, as ~70% of all those that failed to provision were observed singing regularly during the nest watch.

Females provisioned at a significantly higher rate during nest watch 2 than during nest watch 1, the opposite pattern to that documented for males (Pillai's Trace, $F_{1,62} = 79.22$, $P < 0.0001$) (Figure 5). There were no other significant within-

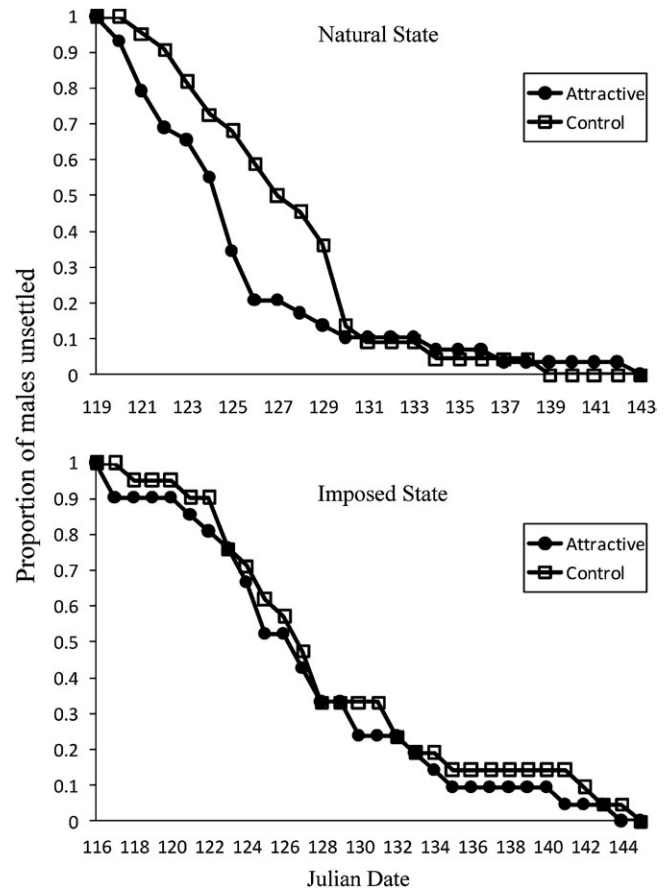


Figure 3
Effect of treatment on male settlement in the natural and imposed states.

subject effects (Table 3). There was a significant interaction between state and treatment ($F_{1,62} = 7.58$, $P = 0.008$). Follow-up tests using Tukey–Kramer pairwise comparisons showed that females paired with attractive males provisioned at a significantly higher rate than those paired with control males during nest watch 1 in the natural attractiveness state ($P = 0.042$) (Figure 5). There were no other significant between-subject effects. Male and female provisioning rates, pooled across all replicates, were negatively correlated during both nest watch 1 ($N = 68$, $r = -0.26$, $P = 0.029$) and nest watch 2 ($N = 68$, $r = -0.54$, $P < 0.0001$).

There was a significant difference in total (male and female pooled) provisioning rates between nest watch 1 and 2 ($F_{1,62} = 44.97$, $P < 0.0001$) (Figure 5), with a higher rate of provisioning during nest watch 2. There were no other significant within-subject effects or between-subject effects on the total number of provisioning trips per nestling per hour.

DISCUSSION

Manipulation of territory attractiveness

In the imposed attractiveness state, in which treatments were applied after male settlement, males settled the floodplain earlier than the upland habitat, suggesting that the floodplain is preferred when the number of available nest cavities does not differ among territories. Preference for floodplain over upland forest is likely associated with a greater food supply on the floodplain (Thompson CF, unpublished data) and a more open understory, particularly around the nest cavity, which

Table 1
Health and condition measures of male house wrens

Variable	Imposed attractiveness						Natural attractiveness					
	Control			Attractive			Control			Attractive		
	N	Mean ± SE	Minimum–maximum	N	Mean ± SE	Minimum–maximum	N	Mean ± SE	Minimum–maximum	N	Mean ± SE	Min-Max
Mass (g)	18	10.9 ± 0.1	9.9 to 11.7	18	11.0 ± 0.1	9.9 to 12.0	19	10.9 ± 0.1	9.9 to 12.2	25	10.8 ± 0.1	9.7 to 11.9
Tarsus (mm)	18	19.3 ± 0.1	18.1 to 20.0	18	19.2 ± 0.1	17.9 to 19.8	19	19.2 ± 0.1	17.7 to 19.9	25	19.2 ± 0.1	18.3 to 20.1
Condition Index (g)	17	-0.06 ± 0.1	-0.87 to 0.70	18	0.14 ± 0.1	-0.70 to 0.97	19	0.04 ± 0.1	-0.96 to 1.64	22	-0.10 ± 0.1	-1.14 to 0.98
Hematocrit (%)	16	46.2 ± 0.9	42.0 to 52.3	17	46.7 ± 0.4	44.5 to 50.6	18	46.0 ± 1.2	32.7 to 54.3	24	46.2 ± 0.7	38.9 to 52.0
A/G	14	3.35 ± 0.5	1.71 to 9.37	17	3.54 ± 0.8	1.17 to 15.84	18	3.05 ± 0.3	0.84 to 6.17	23	3.51 ± 0.5	0.94 to 10.67

Health and condition measures of male quality were analyzed using a split-plot ANOVA (PROC GLM), in which state and treatment were the fixed factors. The random factor was habitat (state), which quantified variation attributable to the plot or other random effects. Neither fixed factor nor the random factor had a significant effect on any measure of male health or condition (all $P > 0.05$); SE, standard error.

probably makes it easier to defend the nest against predators (Belles-Isles and Picman 1986). In the natural attractiveness state, males settled earlier in the attractive territories than in the control territories, regardless of habitat. Thus, nest-box number trumped preference for floodplain habitat, indicating that benefits gained from settling on a territory with multiple nest sites outweigh any costs associated with lower food abundance or an increased risk of nest depredation, or both.

Manipulation of male attractiveness

There was no effect of state, treatment, or time of male settlement on male time-to-pairing based on appearance of lining material or the day the first egg was laid. This is contrary to the results of Dubois et al. (2006), who studied a house wren population in Michigan, and used the criterion of the appearance of nest-lining material to identify pairing date, as well as Eckerle and Thompson (2006) and Grana (2009), who studied our Illinois population, and used the date the first egg of the clutch was laid to identify the date of pairing.

Nest-box number and male quality

In the natural attractiveness state, male quality and attractiveness were allowed to covary, and we anticipated, therefore, that larger or more experienced males, or those in especially good condition, would outcompete smaller or less experienced

males, or those in poor condition, for the attractive 4 nest-box territories (Price 1984; Kokko 1999). In the imposed attractiveness state, in contrast, the treatments were designed to decouple male quality and attractiveness. Thus, we expected a statistically significant interaction between state (imposed or natural attractiveness) and treatment (attractive or control) in their effects on male quality. Although there was no significant interaction between state and treatment in their effect on male condition or health, a larger proportion of attractive territories were settled by older males than by new males when males were free to select their territories but not when attractiveness was imposed. Many studies have reported that age/experience covary with various measures of male quality in birds, including the ability to obtain and to defend a territory (e.g., Lanyon and Thompson 1986; Hyman et al. 2004). In addition, there is evidence that older males arrive on the breeding grounds before younger males in house wrens (Kendeigh 1941) and other bird species (e.g., Lozano et al. 1996; Dittmann and Becker 2002), thus giving them a better chance to acquire an attractive territory. In general, males arriving first on the breeding grounds are likely to be those best able to endure the hardships of early migration and arrival (Møller 1993; Kokko 1999; Eckerle and Thompson 2006). Because age/experience differed significantly across treatments when males were allowed to determine their own attractiveness (i.e., in the natural state), this trait is probably a good indicator of male quality. In many bird species, age/experience, not surprisingly, is positively correlated with reproductive success (Rowley 1983).

Male attractiveness and provisioning

We tested the hypothesis that male attractiveness influences provisioning behavior independent of male quality, predicting that attractive and control males in both the natural and imposed states would differ in provisioning rates. In contradiction of this prediction, the difference in provisioning by attractive and control males was significantly influenced by whether attractiveness was imposed or natural. Attractive and control males in the imposed attractiveness state provisioned at similar rates during both nest watches. In contrast, control males in the natural state provisioned at a higher rate than attractive males at both nest watches. In addition, in the natural attractiveness state, a higher proportion of attractive males than control males did not provision at all. This pattern was not observed in the imposed attractiveness state. Thus,

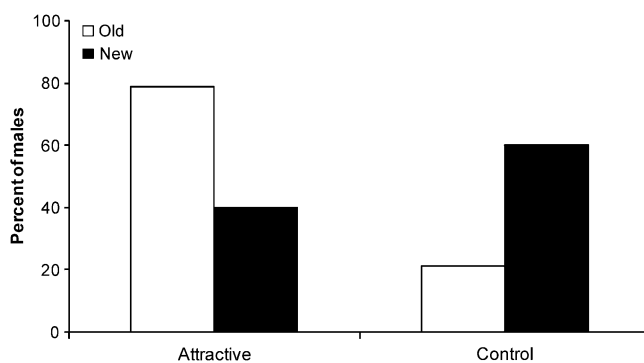


Figure 4
 Percent of males classified as “old” or “new” when males were free to choose between one (control, $N = 20$) and 4 nest-box (attractive, $N = 25$) sites.

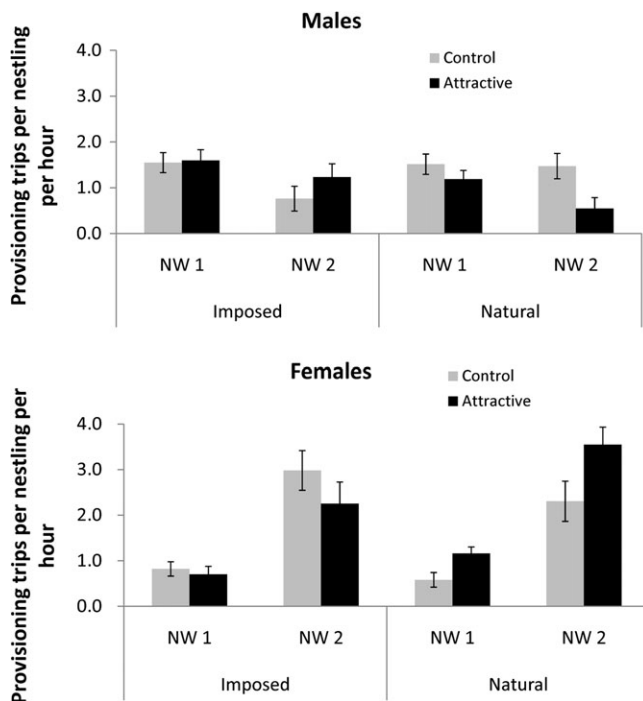


Figure 5
Average provisioning rates across treatments for males (top) and females (bottom) during 2 nest watches. Bars represent least squares means \pm standard error of provisioning rates (provisioning trips per nestling per hour).

male provisioning rates were dependent on male quality and not influenced by attractiveness independent of male quality. These results correspond to those reported in blue tits (*Cyanistes caeruleus*; Limbourg et al. 2004).

Why would male quality affect provisioning rates? First, it may be more advantageous for older males to invest in the attraction of additional mates than in provisioning their current broods after the female is freed from brooding the nestlings (Houston et al. 2005). Second, females mated to older males may increase their level of parental care because offspring sired by these males are more valuable (Burley 1988; Sheldon 2000). This in turn would allow males to devote more effort to mate attraction without harming the brood. Compared with younger males, older males may have acquired skills, such as producing an attractive song that makes it more likely that they can attract an additional female (Emlen and Oring 1977; Smith 1995; Komdeur et al. 2002). Indeed, the majority of the males that failed to provision sang regularly on their

Table 2
Repeated-measures ANOVAs summary statistics for between-subjects effects on male provisioning rates

Source	df	Mean square	<i>F</i>	<i>P</i>
State ^a	1	0.366	0.126	0.757
Habitat (state)	2	2.909	2.58	0.084
Treatment	1	1.078	0.95	0.332
State \times treatment	1	6.362	5.64	0.021
Error	62	1.129	—	—

^a The denominator for the *F* ratio for the state effect is mean square (habitat (state)). The denominator for the *F* ratio for the remaining effects is mean square (error); df, degrees of freedom.

Table 3
Repeated-measures ANOVAs summary statistics for between-subjects effects on female provisioning rates

Source	df	Mean square	<i>F</i>	<i>P</i>
State ^a	1	1.421	6.65	0.123
Habitat (state)	2	0.214	0.11	0.892
Treatment	1	1.905	1.02	0.317
State \times treatment	1	14.191	7.58	0.008
Error	62	1.872	—	—

^a The denominator for the *F* ratio for the state effect is mean square (habitat (state)). The denominator for the *F* ratio for the remaining effects is mean square (error); df, degrees of freedom.

territories during nest watches. Older males should invest in mate attraction rather than provisioning if at least some of the current brood will survive and unmated females are available (Maynard Smith 1977). This is likely to have been the situation in the study population. Provisioning by attractive males was less than that of controls during nest watch 2 but not during nest watch 1 in the natural attractiveness state. During nest watch 1, nestlings are dependent on male provisioning because females must remain on the nest for long periods to brood the nestlings. At this time, early in the breeding season, most of the nests are at the same stage of the nestling cycle (Drilling and Thompson 1991) and there are likely few unpaired females available (Neill 1990). Thus, all males should provision when females are brooding. Later, when nestlings require little or no brooding, females can provision at a high rate and high-quality males can reduce their provisioning and invest in attracting new mates. In contrast, low-quality males maximize their reproductive success by continuing to provision rather than switching to attempting to attract additional mates.

Why would females prefer attractive high-quality males if they provision nestlings less than low-quality males? One possibility is that females secure indirect genetic benefits for their offspring by pairing with high-quality males (Fisher 1930; Jennions and Petrie 2000). Both high- and low-quality males provision at a similar rate when it is most important to females, and only when females are able to provision successfully do high-quality males stop provisioning. Another explanation is that having a highly attractive territory is more important to a female than obtaining maximum paternal care for her offspring. Because predation accounts for most nest failures in house wrens (Evans and Burn 1995), finding a territory in good habitat with multiple nest-boxes from which to choose would greatly benefit females. There is abundant evidence that female house wrens use nest-site quality, at least partially, when choosing a mate (Kendeigh 1941; Drilling and Thompson 1988; Johnson and Kermott 1991; Johnson and Searcy 1993; Dubois et al. 2006; Eckerle and Thompson 2006). It is possible that nest-site quality is a better indicator of female reproductive success than any other male characteristic (Alatalo et al. 1986). Johnson and Searcy (1993) argued that this is why some female house wrens choose to pair with already paired males with surplus nest-boxes rather than with nonpaired males with a single nest-box, even at the cost of reduced paternal investment.

Female provisioning and negotiation

Females in both treatments provisioned at low rates during nest watch 1 and more than doubled their rate during nest watch 2, whereas males across both treatments and states

decreased their provisioning rate during nest watch 2. This pattern was expected as females need to spend most of their time brooding their ectothermic young during nest watch 1, whereas males do most of the provisioning. The general patterns in male and female provisioning rates are consistent with past studies on this study population (Morton 1984).

The pattern of adult provisioning rates suggests that females adjust their rates based on those of their mate. Because male provisioning and quality were correlated, females may be responding to their mate's quality by increasing or decreasing their provisioning. Females paired with attractive and control males in the imposed attractiveness state provisioned at similar rates during nest watch 1, but at different rates in the natural state. Furthermore, even though provisioning rates differed between attractive and control males and females in the natural state, there was no significant effect of state or treatment on total provisioning rates. Thus, a decrease in provisioning by the male was compensated for by an increase in provisioning by the female.

Although the results indicate that male and female house wrens adjust their provisioning rates, the process leading to this adjustment remains unclear. There are 2 main hypotheses for how adults respond to each other's provisioning rates. The sealed-bid model proposes that parents make independent decisions and that negotiations over levels of provisioning are resolved across evolutionary time (Houston and Davies 1985). The negotiation model proposes that provisioning rates are negotiated in real time during a given breeding event as each parent responds to the other's level of effort (McNamara et al. 1999; Johnstone and Hinde 2006). Both models accommodate potential adjustments in parental care with respect to mate, season, prey availability, and other factors. Schwagmeyer and Mock (2003) and Nakagawa et al. (2007) investigated these models in the house sparrow (*Passer domesticus*) and found that repeatability in provisioning rates was high in males but low in females, suggesting that males set the pace following the sealed-bid model and females adjust their provisioning rates depending on the situation. However, in applying repeatability to the negotiation model, Johnstone and Hinde (2006) observed that a high repeatability in provisioning rates might simply suggest that variation in parental ability is much greater than variation in brood need. Our results suggest that rates of paternal provisioning are influenced by variation in male quality and that females adjust their level of provisioning based on that of their mates'.

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