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# Behavioral plasticity in response to perceived predation risk in breeding house wrens

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## Abstract

Predation is a significant cause of nest failure in passerine birds, and, thus, natural selection is expected to favor behavioral plasticity to allow birds to respond to perceived changes in predation risk. However, behavioral plasticity in response to perceived predation risk, and its potential fitness-related costs, are understudied. In a wild population of breeding house wrens (*Troglodytes aedon*), we tested the hypotheses that (1) birds show behavioral plasticity in response to perceived nest-predation risk to reduce self-risk or risk to offspring, but (2) this plasticity incurs fitness-related costs. We experimentally increased the perceived risk of nest predation by enlarging the diameter of the nestbox entrance from the standard 3.2 cm to 5.0 cm once incubation began. Unexpectedly, large-hole females spent significantly less time being vigilant than small-hole (control) females during late incubation. Both males and females also exhibited plasticity in their provisioning behavior. Large-hole males increased and large-hole females decreased provisioning visits with increasing brood size, whereas small-hole males and females behaved similarly and were unaffected by brood size. Females did not show plasticity in their incubation or brooding behavior. Notwithstanding this behavioral plasticity in response to increased perceived predation risk, treatment had no effect on hatching success or early hatchling survival, nor did it affect nestling body condition or fledging success. We conclude, therefore, that house wrens show behavioral plasticity in response to perceived nest-predation risk, but that any short-term fitness-related costs associated with this flexibility appear negligible.

### Keywords

behavioral plasticity; incubation; nonlethal effects; parental care; predation risk; nestling provisioning

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**Compliance with Ethical Standards**

**Conflict of Interest** The authors declare that they have no conflict of interest.

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## Introduction

Predation is one of the main causes of nest failure in passerine birds (Thompson 2007; Remeš et al. 2012) and, consequently, imposes strong selection on avian breeding behaviors (Martin 1993; Conway and Martin 2000; Lima 2009; Ibáñez-Álamo et al. 2015; Martin et al. 2015). The risk of nest predation varies across both space and time (Lima and Bednekoff 1999), which should favor the evolution of behavioral plasticity (the ability of a genotype to produce multiple behavioral phenotypes; West-Eberhard 1989) that would allow birds to respond adaptively to changes in perceived predation risk by reducing the immediate risk to themselves or to their offspring. Such plasticity, however, may come at a cost in the form of trade-offs, with more time allocated to antipredator behavior leading to less time allocated to self-maintenance or parental care; thus, although behavioral plasticity may reduce immediate risk, it may also lead to fitness-related costs (DeWitt et al. 1998; Lind and Cresswell 2005; Cresswell 2008).

Previous research demonstrates that birds are able to express different degrees and forms of behavioral plasticity in response to perceived predation risk. Birds change their incubation patterns (Ghalambor and Martin 2002; Kovařík and Pavel 2011; Zanette et al. 2011; LaManna and Martin 2016), provisioning behaviors (Ghalambor and Martin 2001; Fontaine and Martin 2006; Tilgar et al. 2011; Zanette et al. 2011; LaManna and Martin 2016), vigilance behavior (Morosinotto et al. 2013), and nest-site selection behavior (Forstmeier and Weiss 2004; Eggers et al. 2006; Peluc et al. 2008; Beckmann et al. 2015) in response to a change in the level of perceived risk. These studies also demonstrate that there are species-specific differences in plasticity. For example, female pied flycatchers (*Ficedula hypoleuca*) provisioned nestlings at higher rates under conditions of high perceived risk compared with females provisioning under conditions of low perceived risk (Thomson et al. 2010), but song sparrows (*Melospiza melodia*) decreased parental provisioning rates under similar conditions (Zanette et al. 2011). In other species, the magnitude of behavioral responses to offspring and adult predator models differed depending on the adult survival probability and the clutch size of the species (Ghalambor and Martin 2001), suggesting that risk-management strategies may differ among species depending on life history (Hua et al. 2014; LaManna and Martin 2016). To complicate the matter further, breeding birds must manage both self-risk and risk to offspring (Mahr et al. 2014), where the appropriate response to one may differ from that to the other.

Fewer studies have explored potential fitness-related costs of the behavioral and life-history responses to changes in perceived predation risk (DeWitt et al. 1998). Focusing on the costs of these responses may yield additional insight into the evolution of behavioral plasticity among avian taxa. If costs are low relative to benefits, then plasticity is likely to evolve. It is also necessary to study potential fitness-related costs of behavioral plasticity to determine nonlethal effects (i.e., indirect; any effect that does not involve death of the prey) that predators may have on birds. An increasing number of studies have shown that nonlethal effects of predation, such as behavioral changes and fitness costs that may be associated with such changes, may be just as common, or even more common, than lethal effects (e.g., Lima 1998; Preisser et al. 2005; Creswell 2008).

Research exploring fitness-related costs of behavioral plasticity in response to perceived predation risk has yielded mixed results, with some studies finding that fitness-related costs may be steep and others that they may be negligible. In some cases, when perceived predation risk was heightened, significantly fewer offspring (Scheuerlein et al. 2001; Zanette et al. 2011; Hua et al. 2014) and lower quality offspring (Thomson et al. 2006a) were produced, females were less likely to initiate a second brood (Scheuerlein et al. 2001), and males spent more time nest-guarding and less time foraging, resulting in deterioration of their body condition (Komdeur and Kats 1999). In contrast to such results, significant costs of behavioral plasticity have not been detected in other studies. Wheelwright and Dorsey (1991) found that nestlings raised under heightened perceived risk did not significantly differ in fledging mass from those raised under conditions of lower perceived risk, despite a significant drop in parental provisioning visits under high-risk conditions. A recent study even showed that increased perceived predation risk leads to earlier breeding, resulting in significantly larger clutches (Mönkkönen et al. 2009). Such conflicting results could be attributable to differences in the protocols employed to manipulate perceived risk as well as individual differences in response to risk (Abbey-Lee et al. 2016) and in how parents respond to changes in self-risk or risk to offspring (Hua et al. 2014; Mahr et al. 2014). Alternatively, this seemingly bewildering variation in behavioral and life-history responses could be attributable to life-history differences between species; for example, species with a lower probability of future breeding (e.g., single-brooded species) should be less responsive to changes in perceived predation risk than species with a higher residual reproductive value (e.g., multi-brooded species) (LaManna and Martin 2016).

In this study we explored behavioral plasticity in response to perceived nest-predation risk, as well as potential fitness-related costs of such plasticity, in a small passerine bird, the house wren (*Troglodytes aedon*). Annual adult mortality is high in north temperate populations of house wrens (Ghalambor and Martin 2001; Martin et al. 2015), so they should be more responsive to risk to offspring than to self-risk (Ghalambor and Martin 2001). However, because house wrens commonly produce two broods within a single breeding season in the study population, their response to risk might be expected to vary over the course of a breeding season, with a stronger response to self-risk during the first than the second brood. Because this study focused on the response during the first brood, we framed our predictions based on the possibility that either risk to offspring or self-risk might predominate in the parents’ response, as behavioral predictions may differ depending on what kind of risk is considered (Hua at al. 2014). We tested the hypotheses that (1) breeding house wrens show behavioral plasticity in breeding behaviors in response to increased perceived nest-predation risk to reduce the immediate risk to themselves or to their offspring, and (2) that these behavioral changes, if they occur, incur fitness-related costs. Specifically, we predicted that in response to an increase in perceived risk, females would increase time spent in vigilance if acting to reduce either self-risk or risk to offspring compared with females under control conditions. We also predicted that incubating females would increase incubation effort if acting mainly to reduce risk to offspring, because this would enhance embryonic development and, thus, potentially reduce the length of the incubation period, and that they would do the opposite if acting mainly to reduce self-risk. We further predicted that females would increase brooding time early in the nestling stage if acting mainly to reduce risk to offspring, thereby hastening nestling development and fledging (Bowers et al. 2015), and would decrease brooding time if acting mainly to reduce self-risk. We also predicted that both males and females would lower their provisioning rates if acting to reduce either self-risk or risk to offspring because parental activity around the nest can attract the attention of predators (Martin et al. 2000, Lima 2009). Finally, we predicted that nests exposed to increased perceived risk would suffer greater fitness-related costs compared with nests under control conditions.

## Materials and Methods

### Study Species and Study Site

Migratory house wrens in the north-central Illinois study population are double-brooded, and breed from May through August (see Fig. 3 in Johnson 2014). They are small (10–12 g), insectivorous, and prefer open woodland areas with dense herbaceous ground cover and few understory trees (Belles-Isles and Picman 1986; Finch 1989; Eckerle and Thompson 2006). Females typically select a mate based partly on the number and quality of potential nest-sites on his territory (Eckerle and Thompson 2006; Grana et al. 2012). In the first brood (May–June), clutch size is 6–8 eggs (mode = 7 eggs), and in the second (July–August), 4–7 eggs (mode = 6 eggs). Females incubate eggs constantly at night and for approximately half of the daylight hours; males do not incubate and typically do not provision the incubating female (Johnson 2014; Lothery et al. 2014), but they do provision the nestlings. The incubation period is approximately 12 days, and females brood their altricial nestlings for at least five days after hatching. During this time, males usually assist females in provisioning nestlings, but they never brood the nestlings. Males and females carry only single prey items back to the nest on each provisioning trip (Greenwalt and Jones 1955; Barnett et al. 2012). Nestlings fledge 15–17 days after hatching (Johnson 2014). The main cause of reproductive failure in house wrens is nest depredation and intraspecific infanticide (Belles-Isles and Picman 1986; Finch 1989; Johnson 2014).

This study was conducted on the Mackinaw Study Area in McLean County, Illinois (40.668 ° N, 88.892 ° W) during the 2014 and 2015 breeding seasons in the isolated, northernmost section of the study area, which contains 115 nestboxes at a density of 5.4 boxes/ha (see DeMory et al. 2010 for map showing the location and spatial arrangement of the nestboxes). Nestboxes were mounted on 1.5-m metal poles with a 48.3-cm diameter aluminum disk abutting the bottom of the nestbox to deter nest predators. Potential predators of house wren nests on the study area include the suite of diurnal and nocturnal mammalian, reptilian, and avian predators described in Nolan (1963). Predators observed taking house wren eggs or nestlings from nestboxes on the study area over the previous 35 years are red-bellied woodpecker (*Melanerpes carolinus*; Neill and Harper 1990), raccoon (*Procyon lotor*), eastern fox squirrel (*Sciurus niger*), eastern fox snake (*Pantherophis vulpinus*), and deermouse (*Peromyscus* sp.). Circumstantial evidence suggests nest depredation also by striped skunk (*Mephitis mephitis*), weasel (*Mustela* sp.), Virginia opossum (*Didelphis virginiana*), eastern chipmunk (*Tamias striatus*), and blue jay (*Cyanocitta cristata*). Addition of the predator baffles, begun in 2004 and completed in 2010, reduced snake and mammal depredation, so that most losses of eggs and nestlings during this study are likely attributable to weather, abandonment, and intraspecific infanticidal behavior (see Johnson 2014).

## Field Procedures: Incubation and Provisioning Behaviors

The newly constructed nestboxes used in the 2014 experiment were identical, with one exception, to those used on the rest of the study area (see Lambrechts et al. 2010 for details on nestbox dimensions and materials). All nestboxes on the study area have a trap consisting of a sliding, metal trapdoor with a 3.2-cm diameter hole mounted behind a wooden panel covering the 3.2-cm entrance hole in the side wall of the box. All nestboxes on the study area also have a 3.2-cm hole in the side directly opposite the entrance that is permanently blocked with a cork. The exception was that each of the boxes involved in this experiment had the standard trap with its 3.2-cm hole fastened over an enlarged, 5.0-cm hole in the side of the nestbox. Being new, the boxes did not contain old nesting materials, and were placed on the site with their entrances facing east before the wrens returned in the spring, thereby controlling for potential effects of evidence of previous nesting attempts (Thompson and Neill 1991; Merino and Potti 1995) and for effects of nestbox orientation on nest-site selection and nestbox microclimate (Ardia et al. 2006).

All boxes were identical in entrance-hole diameter (3.2 cm) at the time that house wrens settled on the study area; therefore, each nestbox was of the same perceived quality and perceived predation risk with respect to entrance-hole size, as well as all other features, at the time males and females selected a box. Beginning in early May, boxes were visited at least twice weekly to monitor settlement and nest building. All nestboxes were visited daily after settlement to determine clutch initiation date, clutch size, and the start of incubation.

Forty-six nests were assigned to control (small-hole boxes) or experimental (large-hole boxes) treatments by randomly assigning the first nest of the season in which a clutch was initiated to a treatment and then alternating treatments as new clutches were initiated (24 small-hole; 22 large-hole). The diameter of the entrance of small-hole boxes was 3.2 cm, whereas that of large-hole boxes was 5.0 cm, representing an increase of nearly 150 % of the area of the entrance while still being within the range of diameters of natural cavities used by house wrens (Johnson 2014).

The prescribed treatment at each box was applied on incubation-day 1 once all eggs were laid and incubation had begun (incubation-day 0 is the day the last egg is laid). The wooden cover panel and metal trapdoor were removed from boxes assigned to the large-hole treatment, increasing the entrance diameter. This treatment also eliminated any influence of the 1.5-cm tunnel created by the cover panel, a difference that could have further exacerbated any increase in perceived predation risk (the primary objective of the treatment). Small-hole box entrance diameter and the tunnel effect remained unchanged, but approximately the same amount of time was spent at small-hole boxes to create a disturbance similar to that which occurred when the panel was removed at large-hole boxes on incubation-day 1 (see Morosinotto et al. 2013).

Males and females were caught after the mid-point of the incubation period (approximately incubation-day 6) by using the sliding trap door or a mist net near the nestbox. Females were banded with a numbered, aluminum U.S. Geological Survey band. Males were given four bands, including one numbered, aluminum band and three colored, Darvic bands (2 bands/ leg) in a unique color combination to aid in their identification during video scoring.

Activity at small-hole and large-hole boxes was video-recorded twice during incubation, once on incubation-day 2 or 3 and once on incubation-day 7 or 8, and once during the nestling period (see below). Recordings were made using pocket-sized, digital video cameras (Kodak Zx1, Eastman Kodak Company, Rochester, NY, USA) positioned about 1.5 m from the nestbox and secured in a cell-phone holster at the top of a 1.5-m length of 1.5-cm-diameter metal conduit. Adults were habituated to the camera by setting out a dummy camera 24 h before the actual recording began. Nests were video-recorded for approximately1–2 h between 06:30 and 11:00 h Central Daylight Time; this ensured that we had at least 60 min of undisturbed recording for subsequent analysis, sufficient time to obtain reliable data (see Murphy et al. 2015). Adults typically returned to the nestbox within 5 min of setting up the camera.

The recordings made during the incubation period were later scored for female nest attentiveness, female mean on- and off-bout duration, and female vigilance behavior (defined below). As hatching approached, nests were visited daily to record when the first egg hatched, hereafter brood-day 0. Cameras were used to record female brooding behavior and male and female provisioning for 1–2 h during the nestling period on brood-day 4 or 5, the time during the nestling period when nestling growth rate is maximal and per-capita provisioning rate is positively related to nestling mass prior to fledging (Bowers et al. 2014a). Nestlings and unhatched eggs were counted at each nest after the recordings had been made to determine hatching success.

On brood-day 11, all nestlings were banded with a numbered, aluminum band, and mass and tarsus length were measured using a portable digital scale (Acculab Pocket Pro PP-401, Sartorius Group, Bohemia, NY, USA) to the nearest 0.1 g and dial calipers to the nearest 0.5 mm, respectively. Mass and tarsus length measurements were later used to assess nestling body condition (see Statistical analyses, below), a trait that is positively associated with recruitment and longevity (Bowers et al. 2014b). Nests were monitored daily starting on brood-day 13 to determine fledging success.

## Video Scoring

Video scoring began at the time when the female first returned to the box after the camera had been substituted for the dummy, and ended after 60 min. If recordings were <1 h because of camera malfunction or inclement weather (10.1 % of the recordings; mean = 51.5 min), data were extrapolated to 1 h. Female vigilance was calculated as the proportion of the hour the female spent scanning the surroundings of the nestbox, either from the entrance hole or while perched outside on the lid of the nestbox or on the predator guard. Female nest attentiveness was calculated as the proportion of the hour spent inside the nestbox. Females that are in the nestbox after egg-laying is complete are incubating, as the eggs are always warm to the touch when the female is flushed from the box (pers. obs.). Mean on-bout duration was calculated as the average length of time of each incubation session. On-bouts were defined as any time the female was inside the nestbox for at least 20 sec. Mean off-bout duration was calculated as the average length of time between each on-bout session. Off-bouts were defined as any times during which the female was not incubating (i.e., not in the nestbox) and was not engaging in vigilance behavior at the nestbox. Male and female provisioning rates were calculated as the number of trips that males and females made to the nest with a prey item, and prey items were classified as either small (< 10 mm in length), medium (10–20 mm in length), or large (> 20 mm), based on comparison with house wren mean bill length of 12 mm (Barnett et al. 2011).

## Estimating Fitness-related Costs

Hatching success was calculated as the number of eggs that hatched divided by the number of eggs present at the end of incubation. Early hatchling survival was calculated as the number of nestlings on brood-day 4 divided by the number of eggs that hatched. Fledging success was defined as the proportion of nestlings that fledged out of the total number of nestlings that hatched, and was calculated as the number of nestlings that were ringed on brood-day 11 divided by the number of eggs that hatched. No nestlings were found dead in any nests after the nestlings were processed on brood-day 11, so it was assumed that the number of nestlings banded was equal to the number that fledged, as adults do not remove fully grown dead nestlings (pers. obs.). Nests that failed because of depredation or intraspecific infanticide and those from which nestlings fledged prematurely before ringing were excluded from this analysis (4 small-hole and 6 large-hole nests). Nestling body condition was calculated using mixed-model ANCOVA (see Data Analysis, below).

## Nestbox Preference

In the spring and summer of 2015 on the same part of the Mackinaw study area used in 2014, we performed a follow-up experiment to confirm that the house wrens in the study population preferred boxes with small entrance holes (3.2-cm diameter) over those with large holes (5.0 cm), as was the case in a Canadian population (Pribil and Picman 1997). The nestbox in the northeast corner of the tract was randomly assigned to the large-hole treatment by the flip of a coin, after which treatments were alternated along each north-south row to ensure that there was an even distribution of each type across the study area. In mid-March 2015, well before the return of the wrens from their wintering grounds, the wooden cover panel and sliding trapdoor of each box assigned to the large-hole treatment was removed to expose the enlarged hole; the wooden cover panel and trapdoor of each box assigned to the small-hole treatment was left in place. All old nesting material was removed from each nestbox, and all nestboxes were oriented so that the entrance faced east, as in 2014. Additionally, in 2015, all nestboxes had been in place for one year, controlling for any effects of nestbox age on nest-site selection (Ekner-Grzyb et al. 2014).

All nestboxes were monitored at least every other day to determine the timing of male and female settlement during the first brood of the 2015 season. Male settlement date was the date on which the male was heard singing near the nestbox, and at least 45–50 % of the bottom of the nestbox was covered with sticks (Eckerle and Thompson 2006; Grana et al. 2012). Female settlement date was the date on which the female laid the first egg of her clutch (egg-1 day), and male time to pairing was defined as the difference between the female and male settlement dates (Eckerle and Thompson 2006; Grana et al. 2012).

## Nestbox Microclimate

Nestbox microclimate was examined in a subset of nestboxes during the incubation period in 2014 and during the male-settlement period in 2015 to determine if the size of the entrance hole affected the microclimate within the nestbox, which could, in turn, influence female incubation behavior independent of any effect of perceived predation risk. Thermocron sensors (iButtons, Maxim Integrated, San Jose, CA, USA) were attached using Velcro to the end of the corks that blocked the hole opposite the entrance hole, positioning the iButtons within the box usually just above the rim of the nest. The iButtons were programmed to record temperature (° C) once every hour. In 2014, iButtons were placed in 12 small-hole boxes and 12 large-hole boxes on 26 May when females were incubating their clutch; data were collected over 72 consecutive hours (27–29 May) and the iButtons were removed on 30 May. In 2015, the iButton sensors were installed in nestboxes on 05 May in the same manner as described above in 12 small-hole and 12 large-hole nestboxes that had been settled by males but had no evidence of female nest-lining activity. Because there were fewer than 12 boxes of each type that met this criterion on 05 May, two small-hole boxes and one large-hole box that contained some sticks, but fewer than the 45–50 % criterion, were included, as were four large-hole boxes without sticks. The latter were randomly assigned to receive iButtons using a random number generator. Data were collected over 72 consecutive hours (06–08 May), and the iButtons were removed on 09 May.

## Data Analysis

All statistical analyses were conducted in SAS (version 9.3), and all tests were two-tailed ($\alpha = 0.05$). Data met assumptions of normality and homogeneous variances for parametric tests unless otherwise specified. When ANCOVA was performed, interactions between the main effect and the covariate(s) were removed from the model when non-significant (i.e., $P > 0.05$; Engqvist 2005). Data from one female that re-nested after nest failure were dropped from vigilance and incubation analyses because of the non-independence of her nests. In all mixed-models, degrees of freedom were calculated using the Satterthwaite method. All means reported are least-squares means ± SE.

Male settlement and male time to pairing were both analyzed using failure-time analysis (proportional hazards regression; PROC PHREG) to determine whether the size of the entrance affected timing of male settlement (i.e., indicative of a male preference), and the time it took a male to obtain a mate (i.e., indicative of a female preference). Data were right-censored in the time-to-pairing analysis when males that had settled at a box did not obtain a mate.

Nestbox temperature data from 2014 and 2015 were analyzed separately using repeated-measures, mixed-model ANOVA (PROC MIXED), including treatment and hour as main effects, hour as the repeated measure, and nestbox as a within-subject, random effect. Four temperature readings were included per nestbox per day for three consecutive days at the following hours: 02:00, 08:00, 14:00, and 20:00 Central Daylight Time. One iButton in 2014 and one iButton in 2015 malfunctioned and their data were not included in any analyses.

Female vigilance during the incubation stage was analyzed using repeated-measures ANCOVA (PROC GLM), including treatment as a main effect, clutch size as a covariate, and time (early and late incubation) as the repeated measure. Data were log-transformed to meet the assumptions of normally-distributed residuals and homogeneous variances. All means reported are back-transformed, least-square means with asymmetrical standard errors.

Nest attentiveness, mean on-bout duration, and mean off-bout duration were analyzed using repeated-measures MANCOVA (PROC GLM), with treatment as a main effect, clutch size as a covariate, and time (early and late incubation) as the repeated measure. The three incubation behaviors were all included as response variables (Scheiner 2001). Female brooding behavior was analyzed using ANCOVA (PROC GLM), with treatment as a main effect and brood-day 0 and brood size as covariates.

Male and female provisioning trips were analyzed using a mixed-model ANCOVA (PROC MIXED), with treatment and sex included as main effects, brood size as a covariate, parental identity as a random effect to account for the fact that two males had mates at two nestboxes, and nest as a random effect to account for non-independence of males and females provisioning at the same nest. Prey-item size, calculated as the proportion of total food items that were small items (Bowers et al. 2014a), was also analyzed in this manner.

We analyzed hatching success in events/trials syntax, using a generalized linear mixed model (GLMM; PROC GLIMMIX) with a binomial error structure and logit link function; brood-day 0 was included as a covariate to control for any seasonal effects. We similarly analyzed early hatching survival and fledging success.

Nestling body condition was analyzed using mixed-model ANCOVA (PROC MIXED), which accounts for the correlation between body size (i.e., tarsus length) and body mass (García-Berthou 2001). Nestling mass was included as the dependent variable, treatment as a main effect, nestling tarsus length as a covariate, and nest as a random effect to account for the non-independence of nestlings raised in the same nest.

## Results

### Nestbox Preference and Microclimate

In the 2015 choice experiment, males settled at 98 of 115 nestboxes and were equally likely to at settle small-hole and large-hole boxes (50 small-hole, 48 large-hole; $\chi^2_1 = 0.04$; $P = 0.840$). However, the diameter of the nestbox entrance hole significantly affected the timing of male settlement, with small-hole boxes settled significantly earlier than large-hole boxes ($N = 98$ boxes; $\beta = -0.72$; Wald $\chi^2_1 = 11.83$; $P = 0.001$; Fig. 1a). Males with small-hole boxes obtained mates significantly sooner than males with large-hole boxes ($N = 98$ boxes; $\beta = -0.88$; Wald $\chi^2_1 = 12.54$; $P < 0.001$; Fig. 1b), and males at small-hole boxes were less likely to be unmated at the end of the first brood (5 small-hole, 21 large-hole; $\chi^2_1 = 9.85$; $P = 0.002$). Returning males from the 2014 experiment and males that were newly banded in 2015 did not show different settlement patterns, as there was no association between male status (i.e., returning male from 2014 experiment vs. new 2015 male) and nestbox type ($N = 36$ males; $\chi^2_1 = 2.21$; $P = 0.137$).

Although time-of-day influenced nestbox temperature in both 2014 ($N = 23$ nestboxes; $F_{11,\,128} = 697.96$; $P < 0.001$) and 2015 ($N = 23$ nestboxes; $F_{11,\,120} = 228.55$; $P < 0.001$), there was no significant treatment effect (i.e., entrance hole size), nor was there any significant treatment-by-hour interaction in either year (all $P > 0.1$).

### Nest Success, Clutch Size, Incubation Period, and Nestling Period

Nest success (percentage of nests that fledged at least one nestling) was 87.5 % (21 of 24 boxes) for small-hole boxes and 72.7 % (16 of 22 boxes) for large-hole boxes ($\chi^2_1 = 1.59$; $P = 0.207$). Clutch size did not differ between treatments (median = 7 eggs in each case; Wilcoxon two-sample test, PROC NPAR1WAY: $N = 46$ nests; $z = 1.49$; $P = 0.136$). The length of the incubation period (median = 12 days in each case; failure-time analysis, PROC PHREG: $N = 46$ nests; Wald $\chi^2_1 = 1.73$; $P = 0.188$) and the length of the nestling period (control: median = 16 days, experimental: median = 15 days; failure-time analysis, PROC PHREG: $N = 46$ nests; Wald $\chi^2_1 = 0.64$; $P = 0.423$) did not differ between treatments.

### Female Vigilance and Incubation Behaviors

There was a significant interaction between treatment and incubation period in their influence on the proportion of time that females spent vigilant ($N = 44$ nests; $F_{1,\,38} = 7.26$; $P = 0.010$). During early incubation, there was no effect of treatment (small-hole: 0.017 + 0.003, − 0.003; large-hole: 0.018 + 0.004, − 0.003; $F_1 = 0.07$; $P = 0.791$) or clutch size ($F_1 = 0.08$; $P = 0.772$). However, during late incubation, there was a significant effect of treatment (mean ± SE, small-hole: 0.028 + 0.005, − 0.004; large-hole: 0.013 + 0.003, − 0.002; $F_1 = 9.05$; $P = 0.005$; Fig. 2), with large-hole females spending less time being vigilant than small-hole females. There was no effect of clutch size on vigilance ($F_1 = 0.08$; $P = 0.783$). There was no effect of treatment, time, clutch size, or any interactions among these factors on female incubation behaviors (Table 1 and Table 2).

### Female Brooding Behavior

There was a significant interaction between time of season (as measured by brood-day 0) and brood size ($N = 30$ nests; $F_1 = 6.26$; $P = 0.019$) on the proportion of time females spent brooding, but there was no effect of treatment (mean ± SE, small-hole: 0.496 ± 0.032; large-hole: 0.489 ± 0.035; $F_1 = 0.02$; $P = 0.883$) or significant interactions involving treatment.

### Male and Female Provisioning Behavior

There was a significant three-way interaction among treatment, sex, and brood size ($N = 30$ nests; $F_{1,\,50.6} = 6.73$; $P = 0.012$) with respect to the number of provisioning trips made by adults. To determine the source of this interaction, a mixed-model ANCOVA was conducted within each treatment to examine effects of sex, brood size, and their interaction. For pairs provisioning at small-hole boxes, there was no effect of sex ($F_{1,\,28} = 0.04$; $P = 0.843$) or brood size ($F_{1,\,28} = 1.00$; $P = 0.326$) on the number of provisioning trips/h, nor was the interaction between sex and brood size significant ($N = 16$ nests; $F_{1,\,28} = 0.59$; $P = 0.447$; Fig. 3a). For pairs provisioning at large-hole boxes, however, there was a significant interaction between sex and brood size ($N = 14$ nests; $F_{1,\,24} = 7.10$; $P = 0.014$), with large-hole males increasing and large-hole females decreasing provisioning rates with increasing brood size (Fig. 3b).

With respect to the size of prey items supplied by male and female parents, there was no effect of treatment (mean ± SE, small-hole: 0.380 ± 0.050; large-hole: 0.530 ± 0.060; $F_{1,\ 22.5} = 0.10$; $P = 0.750$), sex ($F_{1,\ 39.5} = 0.22$; $P = 0.643$), or brood size ($F_{1,\ 11.9} = 1.26$; $P = 0.284$); none of the interactions among these effects was significant (all $P > 0.05$).

### Fitness-related Costs

There was no significant effect of treatment on hatching success (least squares mean ± SE (95% confidence limits), small-hole ($N = 24$): 0.94 ± 0.02 (95% CL = 0.14 – 1.00), large-hole ($N = 16$): 0.95 ± 0.02 (95% CL = 0.09 – 1.00); $F_{1,1} = 0.10$; $P = 0.805$), nor was there any effect of brood-day 0 ($F_{1,1} = 3.08$; $P = 0.329$). Similarly, there was no significant effect of treatment (small-hole, $N = 24$: 0.95 ± 0.02 (95% CL = 0.89 – 0.98); large-hole, $N = 16$: 0.99 ± 0.01 (95% CL = 0.94 – 1.00); $F_{1,37} = 2.72$, $P = 0.107$) or brood-day 0 ($F_{1,37} = 0.23$; $P = 0.633$) on early hatchling survival. Finally, there was no significant effect of treatment (small-hole, $N = 20$: 0.95 ± 0.02 (95% CL = 0.88 – 0.98); large-hole, $N = 16$: 0.99 ± 0.01 (95% CL = 0.93 – 1.00); $F_{1,33} = 2.72$; $P = 0.108$) or brood-day 0 ($F_{1,33} = 0.15$; $P = 0.697$) on fledging success.

Although nestling body mass increased with nestling tarsus length ($N = 223$ nestlings; $F_{1,\ 218} = 49.84$; $P < 0.0001$), there was no effect of treatment on nestling body mass ($F_{1,\ 218} = 0.47$; $P = 0.496$) after accounting for body size (least squares mean ± SE, small-hole: 10.5 ± 0.09 g (95% CL = 10.3 – 10.7 g); large-hole: 10.5 ± 0.09 g (95% CL = 10.3 – 10.7)).

## Discussion

Both males and females strongly preferred nestboxes with small rather than large entrances, a result similar to previous findings in another house wren population (Pribil and Picman 1997). This preference is consistent with the assumption that both males and females perceive large-hole boxes as riskier than small-hole boxes, or, at least, less desirable, because of increased likelihood of depredation and brood parasitism (Stanback et al. 2013). Furthermore, the experimental manipulation to the diameter of the nestbox entrance hole did not affect internal nestbox temperature, either before females occupied the boxes or when they were incubating. Thus, differences between treatments were unlikely to have been caused by differences in nestbox temperature.

### Evidence of Behavioral Plasticity

House wrens exhibited behavioral plasticity in two important respects to an increase in the perceived risk of nest predation during a breeding attempt: (1) the time that females invested in vigilance, and (2) plasticity in the provisioning behavior of both males and females. Although we cannot be certain that the time females spent scanning from the vicinity of their nestbox was devoted exclusively to vigilance per se, it seems reasonable to assume, given the prevalence of nest predation, that at least some of this time is directed at detecting predators. Female vigilance, as assessed here, was significantly affected by an increase in perceived nest-predation risk, during late, but not early, incubation. Unexpectedly, large-hole females spent less time being vigilant than small-hole females, in contrast with other studies showing that birds typically increase, not decrease, vigilance time with increasing perceived risk (Scheuerlein and Gwinner 2006; Zanette et al. 2011; Morosinotto et al. 2013).

There are several possible reasons for this surprising result. First, the increase in entrance-hole diameter experienced by the large-hole females may have provided a wider range of vision from inside the nestbox, making it possible for them to monitor their surroundings while still inside the nestbox. If this was the case, we may not have been able to detect all of their vigilance behavior, and, thus, underestimated the time they devoted to surveying the area around the nestbox. A second possibility is that large-hole females were more exposed and perceived themselves in a riskier situation than small-hole females, both when incubating and when scanning their surroundings while perched in the large entrance hole. This may have caused large-hole females to perceive that any benefits they might gain from scanning their surroundings to gather information were outweighed by the potential costs of high vulnerability (Mönkkönen et al. 2009; Dall 2010), leading them to reduce vigilance time when perceived risk was increased. If so, then females may have been acting primarily to reduce self-risk. Finally, this difference in vigilance between treatments occurred only in late incubation, perhaps because it simply took longer than 24 hours to respond to the increase in perceived vulnerability. After all, a sudden enlargement of the entrance to a nesting cavity is not likely to occur under normal circumstances. Following removal of the trapdoor, females may have become more wary as they gradually perceived that they and their nest’s vulnerability had increased.

With respect to their provisioning behavior, males and females responded differently to both treatment and brood size as evidenced by a significant three-way interaction among treatment, sex, and brood size. There were no effects of sex or brood size in small-hole birds, nor any interaction between sex and brood size; however, there was a significant interaction between sex and brood size in large-hole birds, with males increasing provisioning visits with increasing brood size and females decreasing provisioning visits. Thus, females behaved in accordance with our prediction that when perceived risk was increased females would reduce their provisioning rates to reduce the risk to themselves. This result is consistent with the hypothesis that multi-brooded species of high residual reproductive value such as the house wren should respond to an increase in perceived predation risk so as to enhance their prospects of breeding again (LaManna and Martin 2016). This result is also in agreement with that of a previous study on a house wren population in north-temperate Arizona (Ghalambor et al. 2013), which found that females reduced provisioning visits when vocalizations of nest predators were played near the nest. In contrast, males did not behave in accordance with the prediction that they would reduce their provisioning rates, and this result was opposite that found in the Arizona population (Ghalambor et al. 2013), suggesting that males in different populations are responding differently to perceived risk.

The sharp increase in large-hole male provisioning visits with brood size may seem unusual, because parental activity around the nest may attract the attention of predators, thereby increasing risk to themselves and their offspring (Martin et al. 2000; Lima 2009). However, an increase in provisioning rates with increased perceived risk has been reported in some other species, such as the pied flycatcher (Thomson et al. 2010). Additionally, activity levels around the nest may not always be correlated with predation risk (Roper and Goldstein 1997). It is unlikely that males increased provisioning to increase nestling growth in an effort to reduce the time that the nestlings were exposed to the risk of nest predation, because the length of the nestling period did not differ between broods in large-hole and small-hole boxes. Another possibility is that large-hole males were compensating for the reduction in provisioning visits by their mates. The strong negative correlation between male and female provisioning rates suggests that this could be the case (see Fig. 3). A similar negative correlation between male and female provisioning rates was found in an earlier experiment on the study population that manipulated male attractiveness (DeMory et al. 2010); however, in another study that manipulated only brood size, there was a trend for a positive association (Bowers et al. 2014a). It is difficult to be certain if males in our study were compensating for the effort of their mates because changes in provisioning rates within individual birds over the course of the nestling period were not assessed. Where changes within individuals have been assessed in this study population, changes in male and female provisioning rates were not associated, suggesting that males and females do not directly compensate for the effort of their mates (Bowers et al. 2014a). It is important to note, however, that the correlations reported by both Bowers et al. (2014a) and DeMory et al. (2010) came from nests that were all under identical perceived-risk conditions (i.e., all entrance holes had a trapdoor with an entrance-hole diameter of 3.2 cm); such results may not obtain when perceived risk changes. We think the most likely explanation for increasing provisioning by males with increasing brood size was to silence begging nestlings to reduce risk to offspring, as increased begging is well known to increase predation risk (Redondo and Castro 1992; Leech and Leonard 1997; McDonald et al. 2009).

In contrast to the plasticity revealed in female vigilance and provisioning behaviors of both males and females, an increase in perceived nest-predation risk did not influence female incubation or brooding behavior. These results are in agreement with a number of studies showing a lack of plasticity in these behaviors in some species (Ghalambor and Martin 2002; Morosinotto et al. 2013; Basso and Richner 2015), but contrasts with those that have documented such plasticity in others (Fontaine and Martin 2006; Kovařík and Pavel 2011; Zanette et al. 2011). These conflicting results may not be surprising when one considers differences in life histories, environmentally-imposed constraints, and whether females respond mainly to self-risk or risk to offspring.

The lack of plasticity in the incubation behavior of females may reflect constraints imposed by their life history. House wrens in north temperate populations have a high adult mortality rate (Ghalambor and Martin 2001; Martin et al. 2015), so many reproduce in only one breeding season. Thus, investing in their current clutch may outweigh potential survival costs of increased vulnerability. Furthermore, females must spend some of their time away from the nest to find food for themselves. Females in this study population increase nest attentiveness when they are experimentally supplemented with food (Lothery et al. 2014), which suggests that there is a trade-off between time spent incubating and finding food for themselves. In addition to the demands of self-maintenance, females may have difficulty reducing incubation effort because of the deleterious effect that reduced egg temperature has on hatching success (Reid et al. 2000; Hepp et al. 2006; Nord and Nilsson 2011) and because of the energetic cost of rewarming cooled eggs (Vleck 1981). Furthermore, any energy saved during the incubation period has the potential to improve reproductive success by allowing birds to allocate extra energy to activities during the nestling stage (Reid et al. 2000).

As in the case of incubation behavior, constraints may play a role in limiting flexibility in brooding behavior. Large-hole females may not have reduced the time spent brooding relative to small-hole females because, by the nestling period, the benefits of investing in their current brood outweigh potential costs, even if the clutch fails. The probability of producing another clutch after a predation event decreases as the breeding season progresses, clutch sizes are smaller, and offspring raised later in the season are in poorer condition and less likely to survive to breeding age than those produced earlier (Bowers et al. 2014b). It is also essential that females brood their altricial nestlings, which cannot thermoregulate until they are older than four or five days (Johnson 2014). Conversely, brooding time may not be able to be increased because nestlings must be fed at a high rate, and provisioning rates and brooding time are negatively associated in female house wrens (Newhouse et al. 2008).

Notwithstanding the behavioral plasticity revealed by increasing perceived nest-predation risk, treatment had no effect on hatching success or early hatchling survival, nor did it affect nestling body condition or fledging success. That hatching success was unaffected by the perceived-risk treatment is not surprising, as females did not change their incubation behaviors in response to perceived predation risk. Given the lack of a treatment effect on the other fitness-related traits, it is not surprising that there was no effect of treatment on either the size of prey or on the total amount of food that nestlings received. When large-hole females decreased provisioning with increasing brood size, large-hole males increased provisioning and likely compensated for the decrease in the amount of food brought to the nest by their mates.

Negative fitness effects of perceived predation risk may only be apparent when food is limited, because when food is plentiful parents may still be able to provide enough food for their nestlings even if they change their provisioning rates (Dunn et al. 2010). Food availability and predation risk can have synergistic effects on songbirds (Zanette et al. 2003), so perhaps when food availability is high, potential fitness-related effects of perceived risk are much lower than if food availability is low and perceived risk is high. We did not measure food availability, but nestlings that hatch early in the breeding season in this study population are much more likely to survive than those that hatch later in the season (Bowers et al. 2014b), suggesting that early in the breeding season, when the experiment was conducted and when insect prey is most abundant, parents have little difficulty provisioning their offspring. Nevertheless, other studies have demonstrated that increased perceived predation risk can significantly reduce fledging success (Zanette et al. 2011; Hua et al. 2014) and nestling body condition (Thomson et al. 2006a; Thomson et al. 2006b) in other species. It is likely that fitness-related costs of behavioral plasticity vary with species and ecological conditions (e.g., local food availability).

### Future Directions

It is important to reiterate that this experiment assumed that increasing the diameter of the entrance hole increased the birds' perception of predation risk, as was assumed by Morosinotto et al. (2013) using a similar manipulation. The strong, convergent male and female preferences for small-hole boxes over large-hole boxes seen in this study population support this view. It is also known, however, that presence of predators is positively associated with plasma corticosterone levels in birds, suggesting a powerful, independent physiological measure for assessing the birds' perception (Silverin 1998; Scheuerlein et al. 2001; Cockrem and Silverin 2002). If males and females perceive the increase in entrance diameter as an increase in risk, large-hole males and females with large-hole boxes should have higher plasma corticosterone levels than those with small-hole boxes. Future experiments that alter entrance diameter to manipulate perceived predation risk should examine corticosterone levels of the parents to assess the extent to which they experience stress.

## Conclusions

This study provides further support to a growing body of evidence showing that birds exhibit behavioral plasticity in response to perceived nest-predation risk to reduce risk to themselves and their offspring. It also demonstrates that the size of the brood can influence parental behavioral responses, and that life-history and environmental factors likely constrain plasticity in some behaviors. However, results from this study do not provide evidence for strong short-term fitness-related effects of changes in perceived predation risk, which is important because it suggests that nonlethal predation effects may not be important determinants of fitness in the short term in some bird species. Finally, these findings highlight the need for further research both among and within species because behavioral responses and fitness-related costs likely differ depending on variation in life histories and environments.

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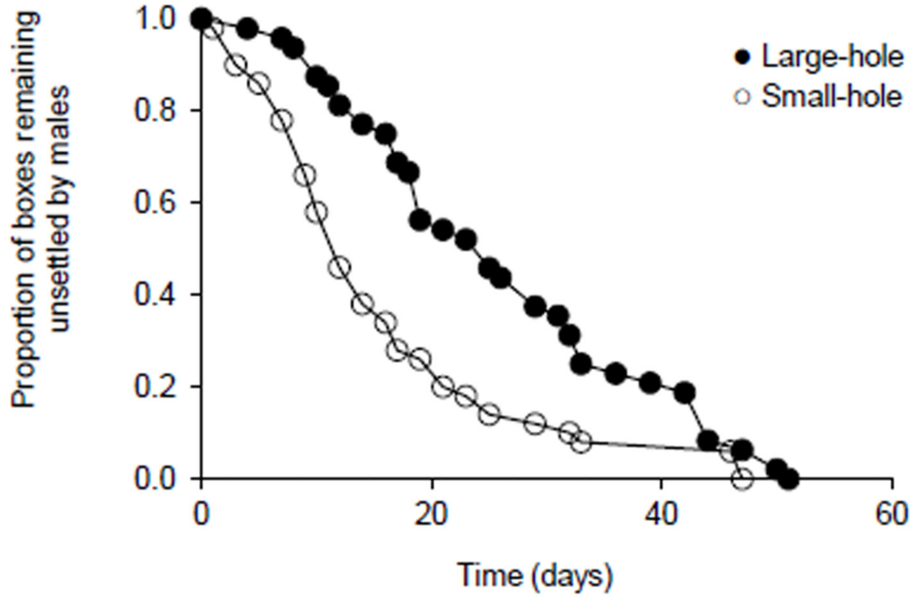
a) Time to male settlement



b) Time to pairing

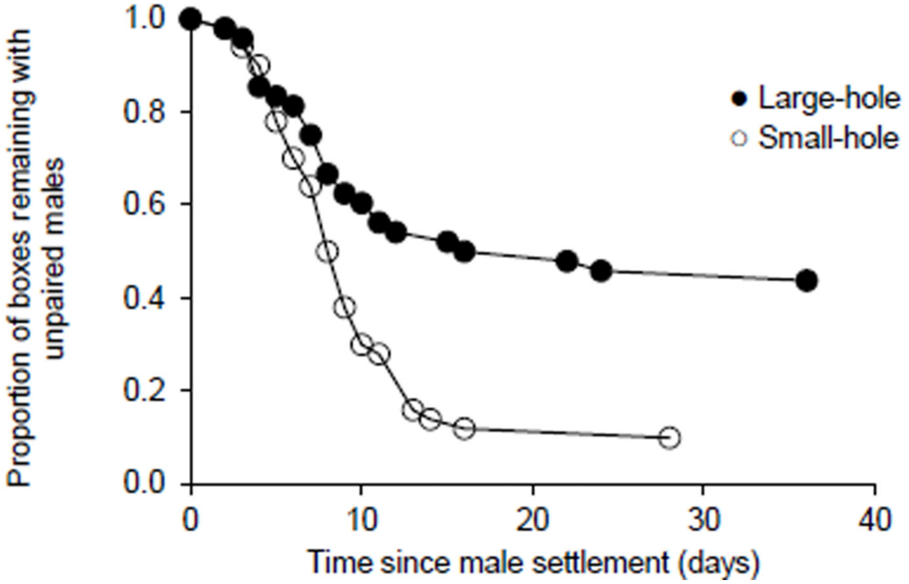


**Fig. 1.**

Failure-time plots showing: **a** time to male settlement and **b**) time to pairing following male settlement in relation to treatment.

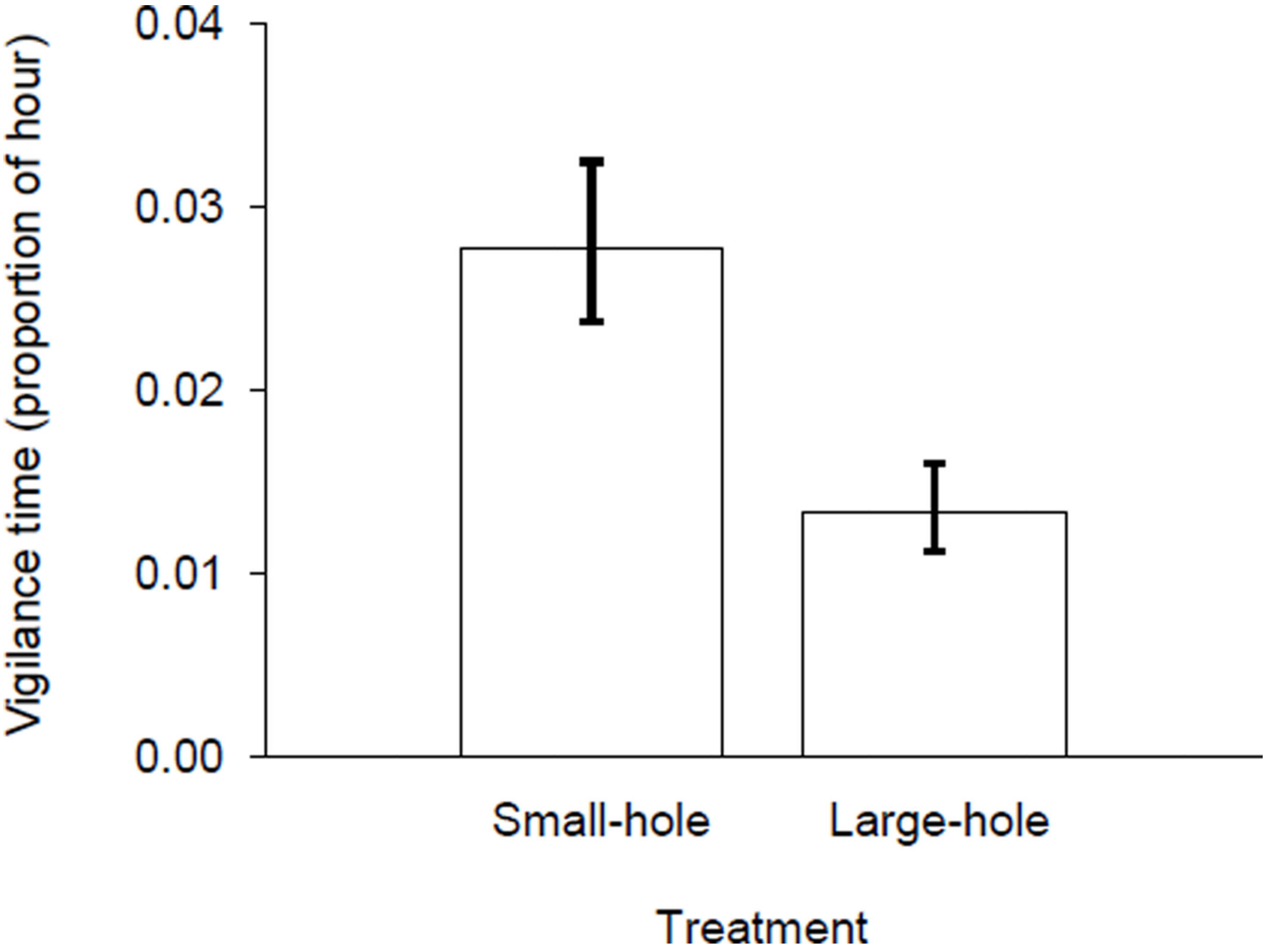
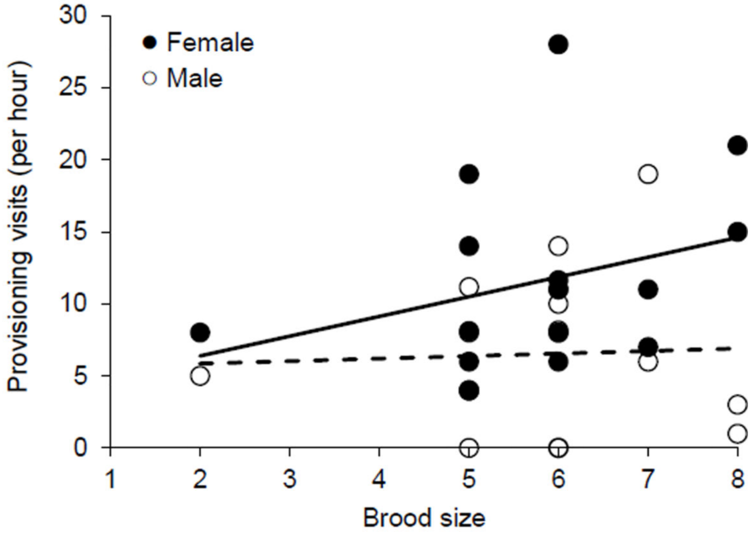


**Fig. 2.**

Proportion of time spent in vigilance during late incubation in relation to treatment. Shown are back-transformed least-squares means with asymmetrical standard error bars.

a) Small-hole treatment



b) Large-hole treatment

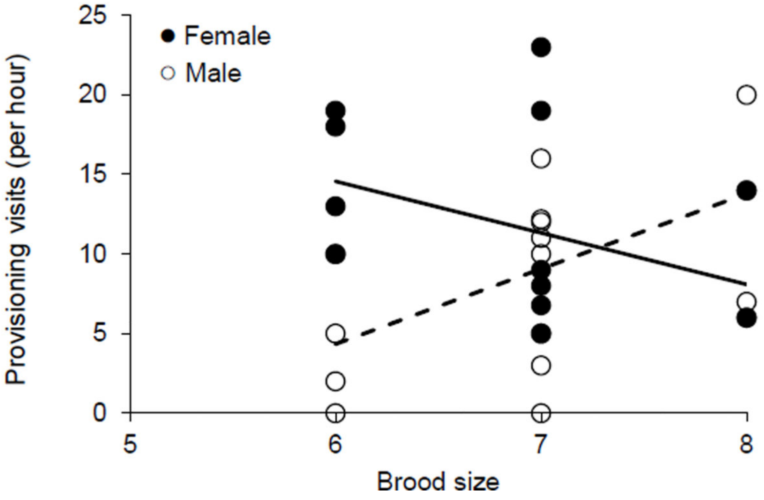


**Fig. 3.**

Nestling provisioning rates in relation to brood size in **a** small-hole treatments and **b** large-hole treatments. Note that the scale differs on the two *x*-axes. Each point represents an individual bird at an individual nestbox. Trend lines derived from linear regression (females are designated by solid lines and males by dashed lines).

### Table 1

Estimates of nest attentiveness (proportion of hour), mean on-bout duration (sec), and mean off-bout duration (sec) in relation to treatment. Estimates are least-squares means. See Table 2 for analyses

| **Behavior** | **Early incubation estimate ± SE** | | **Late incubation estimate ± SE** | |
|---|---|---|---|---|
| | Small-hole | Large-hole | Small-hole | Large-hole |
| Nest attentiveness | 0.74 ± 0.02 | 0.71 ± 0.03 | 0.72 ± 0.02 | 0.70 ± 0.02 |
| Mean on-bout duration | 636.96 ± 57.37 | 573.95 ± 70.62 | 548.57 ± 55.40 | 535.17 ± 68.20 |
| Mean off-bout duration | 279.54 ± 24.88 | 272.37 ± 30.63 | 275.44 ± 18.67 | 264.11 ± 22.98 |

## Table 2

Repeated-measures MANCOVA of incubation behaviors (nest attentiveness, mean on-bout duration, mean off-bout duration) with respect to treatment, clutch size, and time of season. None of the interactions was significant (all $P > 0.05$)

| **Effect** | **df** | **Wilk's λ** | ***F*-value** | ***P*-value** |
|---|---|---|---|---|
| Treatment | 3, 35 | 0.95 | 0.63 | 0.602 |
| Time | 3, 35 | 0.97 | 0.35 | 0.790 |
| Clutch size | 3, 35 | 0.92 | 1.03 | 0.392 |