Nest site selection and breeding biology of house wrens (Troglodytes aedon parkmanii) using natural cavities in Western Canada

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Nest site selection and breeding biology of house wrens

(Troglodytes aedon parkmanii) using natural cavities in Western Canada

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Nest site selection and breeding biology of house wrens (*Troglodytes aedon parkmanii*) using natural cavities in Western Canada

C.D. Kaluthota and D. Rendall

Abstract

House wrens, *Troglodytes aedon* (Vieillot 1809), are among the best studied songbirds in North America, but most of what is known about this model species derives from studies using artificial nestboxes. Consequently, we know comparatively little about the natural breeding biology of house wrens and whether it corresponds to patterns reported from nestboxes. To address these issues, we report a study of nest site selection and breeding phenology in house wrens using natural cavities in aspen forests in southwestern Alberta, Canada. A total of 96 breeding pairs, representing 77 different banded males, were studied across a four-year period (2011-14). In total, 78% of arriving males paired, with 52% of nests successfully fledging. More than 30% of males attempted polygyny, but only 8% succeeded. Distinct patterns were observed for many characteristics of the nest site and cavity including the type of tree used, and the cardinal direction and dimensions of the cavity entrance, its location on the nest tree and height above the ground some of which were related to pairing and breeding success. Results are compared to studies of house wrens using artificial nestboxes with broader application to many other model species likewise studied primarily using nestboxes.

**Key words:** breeding phenology, breeding success, cavity nesting, house wrens, nest boxes, nest site selection, polygyny, *Troglodytes aedon*
Introduction

House wrens are a new world passerine with the widest latitudinal distribution of any native songbird in the western hemisphere. They are distributed from approximately 58°N in Alberta, Canada to the extreme southern tip of South America at 55°S in Tierra del Fuego (Brewer 2001). Currently, populations across this vast range are recognized as a single species with 31 subspecies (AOU 1998; Dickinson and Christidis 2014). With such a vast distributional range, encompassing a diversity of habitat types, house wrens “present an almost unparalleled opportunity to study how environmental conditions shape the morphology, physiology and, especially, the behavior of birds” (Johnson 2014). Not surprisingly, the species has become one of the best studied model passerines with many hundreds of papers encompassing virtually every aspect of behavior, ecology, and biology (Johnson and Barclay 1996; Cavitt and Thompson 1997; Johnson et al. 2001; Albrecht and Johnson 2002; Masters et al. 2003; Johnson et al. 2005; Forsman et al. 2008; Forsman et al. 2010; Bowers et al. 2011; Masters et al. 2011).

At the same time, the majority of what is known about house wrens derives from studies that involve breeding in artificial nestboxes. Nestboxes can be a tremendous advantage to research. They allow some standardization, and controlled manipulation of core elements of the breeding environment, thereby permitting refined experimental testing of research hypotheses. Because nestboxes are relatively easy to access, they also permit more accurate counts of eggs and chicks and establishment of landmark breeding events (e.g., date of first eggs, date of first hatchlings).

However, nestboxes necessarily also eliminate variation in many factors related to the natural ecology and quality of the types of cavities normally used for nesting and that have
presumably shaped the adapted breeding biology and behavior of the species. For example, it is possible that natural variation in cavity and nest tree characteristics are as important to breeding success as many other ecological characters (Cockle et al. 2015). It is also possible that in selecting where to settle and breed, females place as much, or more, emphasis on characteristics of the nest site and cavity as they do those on the surrounding area or the resident male (Johnson and Kermott 1991, 1994; Eckerle and Thompson 2006; Grana et al. 2012).

It is also true for many bird species that breeding in nestboxes entails advantages over natural cavities in terms of protection from predators and from environmental elements such as wind and rain (Møller 1989; Robertson and Rendell 1990; Purcell et al. 1997; East and Perrins 1988; Fargallo et al. 2001; Brazill-Boast et al. 2013). Such advantages are documented to lead to a variety of improved breeding outcomes, including reduced losses to predators, increased clutch size, improved nestling survival, and higher rates of polygyny (Johnson and Kermott 1991; Purcell et al. 1997; Llambías and Fernandez 2009; Lambrechts et al. 2010).

It is certain, therefore, that studies using artificial nestboxes do not present an entirely accurate picture of a species’ natural behavior and breeding biology. For example, Johnson et al. (1994) argued that although certain strategies of female mate choice (e.g., pairing with already mated males) may appear maladaptive when all males have access to several high-quality nest sites in the form of nestboxes, such strategies may be favored under conditions where males have limited access to natural nest sites that vary substantially in quality. Concerns like this apply not only to house wrens but to other model passerines that also have been studied heavily using nestboxes, including great tits *Parus major* (Linnaeus 1758), blue tits
Cyanistes caeruleus (Linnaeus 1758), pied flycatchers Ficedula hypoleuca (Pallas 1764), tree swallows Tachycineta bicolor (Vieillot 1808) and bluebirds (Robertson and Rendell 1990; Dunn et al. 1994; Barber et al. 1996). Similarly, the effects of artificial nest box supplementation have been studied in non-passerine birds such as owls, kestrels, and wood ducks (Bellrose et al. 1964; Komimiiki 1984; Fargallo et al. 2001).

It is, thus, important that we supplement this body of work with research on species’ natural nesting and breeding behavior to assess the validity and generality of the patterns and conclusions drawn from nestbox studies. To that end, we report here a multi-year study of house wrens breeding in natural cavities to help fill a critical gap in our understanding of the breeding biology of this otherwise well-studied species, and we compare the results with those obtained from nestbox studies of this species. Researchers of other model species should be particularly interested to examine the resulting pattern of similarities and differences for possible application to their own work.

Methodology

General breeding biology and behavior. Our research focused on house wrens in southwest Alberta, Canada, recognized as T. a. parkmannii. This subspecies is broadly distributed throughout western North America, where it is very well-studied in central Illinois, and northern Wyoming, (Johnson and Kermott 1991, 1994; Soukup and Thompson 1997, 1998). A second subspecies, T. a. aedon, is distributed across much of eastern North America where it has been particularly well-studied in south-central New York and Ohio (Llambías 2009; Cramer 2012; Cramer et al. 2013; Llambías et al. 2015).
The two North American subspecies are similar in many aspects of life-history and breeding biology (reviewed in Johnson 2014). Males arrive on the breeding grounds and survey the local area for suitable breeding sites, often moving one or more times locally before settling on a territory that they then defend from rival males (Johnson and Albrecht 1993). Their survey of possible territories includes inspecting various types of natural cavities, foremost among them cavities previously excavated by woodpeckers (Raphael and White 1984; Li and Martin 1991; Haggard and Gaines 2001). However, other sorts of natural cavities are inspected and sometimes used for nesting including natural crevices in bark, tree snags, and broken stumps and branches (see Figure 1 for sample of cavities used by house wrens in southwest Alberta).

Males then begin to make initial preparations to one or more cavities by removing previous nesting material and then adding sticks to the base of the nest cavity (Kendeigh 1941; Johnson 2014).

Females arrive a short time after males and survey available males and breeding sites. In this process, females spend considerable time inspecting cavities in a male’s territory. The male often follows the female during her inspections, at times seeming to lead the female among the candidate cavities by flying ahead and singing loudly at the entrance to a particular cavity. Some females appear to settle relatively quickly (within hours of being first observed on a territory), while others are observed to sample multiple territories before settling. The ‘decision’ to settle often appears to have been made when the female herself begins to make concerted modifications to the contents of one or more cavities by repeatedly removing material and then beginning to add sticks of her own. Females then finish nest construction typically with no
further contributions by the male. However, males are active again later in feeding nestlings (Johnson et al. 1992; LaBarbera et al. 2011; Llambías et al. 2012; Barnett et al. 2012).

Many males also actively court second mates once their first mate has begun incubating eggs, and males resume vigorous singing at this time typically from the location of a second cavity in their territory (Johnson and Kermott 1991; Rendall and Kaluthota 2013). Previously reported rates of successful polygyny vary among populations (10–24%) possibly reflecting variation in the number and quality of additional suitable nest cavities that are available within a male’s territory (Drilling and Thompson 1991; Johnson and Kermott 1991).

**Study sites and subjects.**—Research reported here was conducted between 2011 and 2014 at two sites in the foothills of the Rocky Mountains of southwest Alberta. One site, the Whaleback (WB), was located in the Bob Creek Wildlands of the Whaleback region (49.86°N, 114.27°W; mean elevation = 1 360 m). The second site, Lundbreck Falls (LF), was located on private lands near Lundbreck Falls, Alberta (49.56°N, 114.29°W; mean elevation = 1 280 m). The two sites were separated by 35 km, and both were in montane habitat at similar elevation where the vegetation was a mosaic of open grasslands punctuated by small stands of quaking aspen (*Populus tremuloides*) and occasional Douglas-firs (*Pseudotsuga menziesii*). The Lundbreck Falls site was used occasionally for light cattle grazing, while the Whaleback site was regularly used for more intensive grazing. The primary disturbance from grazing at both sites involved reduction in the understory ground cover. Otherwise, the forest habitats at both sites were largely undisturbed.

Research was conducted at the Lundbreck Falls site in all four years and at the Whaleback site in only two years (2011 and 2012). Each year, we started preliminary surveys in early May.
to find first arrivals in the area. Observations continued until the nestlings of the last active nest had fledged, typically in mid-August.

Once male house wrens started to arrive and settle in territories, we commenced capture using mist nets. Song playback was occasionally used but normally only one or two songs were required because males were highly responsive and aggressive at this time and typically flew straight to the net. When captured, each bird was marked using a numbered metal band and a unique combination of three colored bands to facilitate individual identification. Because females were wary and difficult to capture early in the season prior to nesting, and because this study was part of a larger project focused on male song patterns (e.g. Rendall and Kaluthota 2013), we chose to capture and band only males.

*Monitoring Territories and Breeding Events.* The nest trees of all males were marked, and the territory and male occupant were then monitored regularly (2-4 times/week) for the remainder of the season. During each visit, we spent at least one hour in the territory between 06.00h and 12.00h to confirm male breeding status. Soon after birds were paired, we monitored female behaviour for signs of incubation, such as extended stays in the cavity and less frequent movements away from the nest site. When the first eggs were suspected, we attempted to confirm using a mini-camera fixed on a bendable gooseneck cable to access the nest (Meerkam wildlife inspection camera). Unfortunately, many nests were not accessible either because of their location on the tree, or because the precarious state of the nest tree (dead and leaning) would not allow climbing and would not support a ladder. For more accessible nests it was often possible to confirm the presence of eggs or nestlings, but not always possible to get complete counts of their number because the interior architecture of the nest did not permit
full camera access. For example, the internal architecture of some nests involved sticks piled to the entrance with an overhanging lip or bend at the top. The nest cup was then tucked directly underneath this overhanging lip. The lip may be a design feature to reduce access by some kinds of nest predators, but it also was effective in preventing full access of the nest camera. For nests where it was possible to get a clear view of the nest cup, we found a pattern of adding one egg per day (Bowers et al. 2013). Hence, for these nests it was possible to establish the date of first eggs definitively using the accumulated egg number and counting back one egg per day. In principle, nestling counts also should have been possible for these particular nests, but, in practise, definitive counts were seldom possible because nestlings were often cramped tightly together and piled on top of each other as a consequence of the very tight space available within the cavity. So often it was not possible to clearly delineate among the overlapping bodies.

We defined the incubation period as the interval between the first egg in a nest and the first nestling, while the nestling period was defined from the date that the first egg hatched to the date the first nestling left the nest. Males were considered to have paired if they attracted a female who remained on their territory for multiple consecutive days and began nest-building herself. Males were considered to be polygynous if they started a second nest with another female while the first nest was still active with eggs or nestlings and attended by the first female. Males were considered to have attempted to be polygynous if they were observed singing vigorously again from exposed perches to attract a second female while still active with their first nest. Finally, males were defined as having nested successfully if their nest produced one or more fledglings.
Nest tree and cavity measurements. Data about the nest tree included its species, condition (live or dead), overall height, diameter at breast height (DBH), and the number of suitable cavities it contained. Cavities with unusually large entrances or very shallow cavities are not generally used by house wrens and thus were considered to be unsuitable. Data about the cavity included its height above the ground, tree diameter at cavity height (DCH), and the height, width, and cardinal direction of the cavity entrance. Overall height of the nest tree and the height of the nest cavity were obtained using a clinometer. We subsequently calculated an index of cavity entrance shape as the ratio between the entrance width and height. A value of 1 indicates a perfectly circular entrance, while values greater than 1 indicate a more horizontal entrance, and values less than 1 indicate a more vertical entrance.

Data on nest cavity characteristics were available only for the first three years of the study (2011-2013) and are summarized in Table 2 alongside comparable available data from other studies of house wrens. Statistical testing was done in SPSS v.23. Data normality was evaluated using the Shapiro-Wilk’s test.

Results

A total of 81 different males were captured on the two study sites across the four-year period, though not all of these males ultimately settled and successfully held territories. At the same time, some males returned and thus were present in two (N=15), three (N=4) or all four years (N=1). A total of 65 different cavities were used by this sample of males, many cavities being reused within and across years.
I. Breeding phenology and success

First males arrived on the study sites in mid-May (18-May, 2011; 12-May, 2012; 13-May, 2013; 15-May, 2014) with later arrivals continuing until mid-June. Arrival of new males peaked 9 to 11 days after the arrival of the first male (Figure 2). There was no relationship between male arrival date and the duration of time males remained unpaired (Pearson $R = -0.02, P=0.90$, $N=55$, Figure 3a). However, the duration of the unpaired period was positively correlated with the pairing date (Pearson $R = 0.87, P<0.01$, $N=55$, Figure 3b). In other words, irrespective of the date they arrived, males that paired quickly necessarily also did so earlier in the season.

Collapsed across years, there were 123 male arrivals with 111 attempts to settle and breed. In 96 of these attempts (86%), males paired successfully. For 88 (91% of the paired males), their nests made it further to the egg stage; 63 went on to have nestlings; and 48 ultimately fledged at least one young (Table 1). For first breeding attempts, the mean date of first eggs was 9th June (SD=6.8 days, range 29th May – 28th June, $N=46$ nests) and the mean date of first nestling was 23rd June (SD=4.2 days, range 15th June–6th July, $N=33$ nests). The mean duration of incubation for all broods was 15 days (SD=3.3, Range= 12-22, $N=61$ nests), while the mean nestling period was also 15 days (SD=1.3, Range= 13-22, $N=47$ nests).

We were able to access and obtain complete egg counts for 19 nests with a mean of 7.16 eggs (SD=0.6, Range=6-8). Eggs were arranged in a very regular geometric pattern of 5-7 eggs encircling a center egg. Despite difficulties in getting accurate nestling counts, we recorded a range of 1-7 nestlings across 12 nests where partial counts were possible.

Overall nesting success was 52% across the four-year period, with only slight differences between years (Table 1). This level of nesting success is 10-20% lower than reported for other...
populations of house wrens breeding in natural cavities and approximately 30% lower than reported for house wrens breeding in nestboxes (Figure 4).

A total of 18 males paired more than once within the same season. Six of them did so polygynously while the first nest was still active (further details for these males are provided below). All others did so in succession, not simultaneously (i.e., only one female partner at a time). One male paired four times having failed in each of the previous attempts. The remaining eleven males paired with a second female after either failing, or breeding successfully, in their first attempt (i.e., serially monogamous).

In the 88 breeding attempts that proceeded to the egg stage, 28 males (31.8%) were observed attempting to attract a second mate while their first mate was incubating by singing vigorously from another location in their territory. However, only six males (8.2%) succeeded in pairing with a second mate while the first nest was active. Of those males, five succeeded to the egg stage, while the sixth did not. However, only two males successfully bred polygynously (i.e., fledged young from two overlapping clutches). For the other males, either the primary or secondary nest failed. Finally, another male entirely succeeded with a second brood after completing its first brood successfully (i.e., serially and not polygynously).

II. Nest selection and breeding outcomes

Nest tree characteristics. A total of 91 different nesting attempts in tree cavities were recorded. All involved cavities in quaking aspen which was also by far the predominant tree species available, and 60 (65.9%) involved cavities in dead trees. There was no significant difference in the likelihood of success of cavities in dead (24/60: 40%) versus live (17/31: 55%) trees ($\chi^2=1.82,$
For 87 breeding attempts, we were able to establish the number of suitable cavities available in the nest tree and 60 (68.9%) were in trees that contained only a single cavity (Figure 5). There was a non-significant trend toward higher probability of breeding success in such trees compared to trees that contained more than one suitable cavity ($\chi^2 = 3.14$, $df=1$, $P=0.076$, $N=87$).

Cavity orientation. The cardinal direction of the nest cavity entrance ranged widely from $0^\circ$ to $330^\circ$. Of 81 nests for which cardinal direction could be definitively established, 55 (68%) were oriented within a $90^\circ$ swath from East to South (Figure 6). The mean ($M$) orientation of successful nests ($M=147.1$, SD=83.5) was different from that of failed nests ($M=185.4$, SD=79.9; $F_{1,70} =3.95$, $P=0.051$) with successful nests generally oriented in an E-SE direction (Figure 6).

Cavity dimensions and location. The dimensions of the cavity entrance varied considerably, from circular shaped entrances to vertical slot-shaped entrances (Figure 1) and this variation had some effect on nesting success. Of the 39 cavities whose entrances could be definitively measured, 17 (44%) had circular, or near circular shapes (Cavity shape index = 0.8-1.2).

Focusing only on first nesting attempts, the duration of the period that males spent unpaired following arrival was negatively correlated with the diameter of the tree at cavity height (DCH: Pearson $R=-0.50$, $P=0.026$, $N=20$) and positively correlated with both the height of the cavity on the nest tree (Pearson $R=0.35$, $P=0.013$, $N=50$) and the cavity entrance height (Pearson $r=0.540$, $P<0.01$, $N=22$). Hence, males that paired more quickly had nests on larger trees, located closer to the ground, with smaller nest entrances.

Cavity re-use. A total of 65 different cavities were used for breeding at the two study sites across the study period, many of which were re-used in subsequent years by the same or
different males. Of 22 different cavities used in the first year (2011), 10 (45%) were re-used the following year (2012); and in 2013, 14 of 28 cavities (54%) from the previous year were re-used. Three cavities were used for three consecutive years, while one cavity was used in all four years. In total, there were 26 cases of males returning from one year to the next, and in seven cases the returning males settled in exactly the same cavity they used the previous year.

Discussion

I. Breeding phenology and success

The breeding phenology of house wrens in southwest Alberta was broadly similar to patterns reported for other populations with some natural shifts based on different latitudes. Thus, males breeding in southwest Alberta began arriving in mid-May, and the dates of first eggs and first hatchlings were, respectively, 9th June and 23rd June. These dates are somewhat later than those reported for other populations of house wrens in North America (reviewed in Johnson 2014), but this almost certainly reflects the fact that our study sites, at 49° N latitude, are substantially farther north than most other populations studied and are approaching the northern breeding limit of the species. Hence, migrating males (and females) arrive on the breeding grounds later in the season. The comparatively late start and resulting short breeding season in southwest Alberta has implications for other aspects of breeding phenology, such as the potential for second broods (discussed below), and also the average clutch size observed (7.2 eggs) which was large for the species and affirms a pattern of increasing clutch size with increasing latitude (reviewed in Johnson 2014: Table 4).
The duration of both the incubation (15 days) and nestling periods (15 days) were also broadly similar to other house wren populations (reviewed in Johnson 2014). The mean nestling period, and the overall breeding cycle duration were slightly shorter than reported for more southern latitudes (17 and 33 days, respectively; Johnson 2014), while the duration of the incubation period in southwest Alberta was somewhat longer (15 days versus 12-13 days elsewhere; Johnson 2014).

Overall rates of nesting success (at least one fledgling) averaged 52% across the 4-year period in southwest Alberta. This level is notably lower than success rates reported from the few previous studies of northern house wrens breeding in natural cavities in California, Wyoming and Arizona, where success rates have ranged from 62 – 70% (Li and Martin 1991; Johnson and Kermott 1994; Purcell 1995; Figure 4). This difference may also represent a latitudinal effect but is difficult to assert with confidence because the sample of studies is relatively small and encompasses a range of habitats, from primarily oak-pine vegetation in California, to a more mixed forest habitat in Arizona and Wyoming, to almost exclusive stands of aspen in southwest Alberta. Levels of disturbance from activities like cattle grazing also vary across the populations studied, as do predator communities.

Nevertheless, what is consistent across these populations is that levels of successful breeding in natural cavities are considerably lower than those associated with breeding in artificial nestboxes, which generally exceed 80% (Figure 4). This difference reflects a variety of well-known advantages to breeding in nestboxes in house wrens but also other species including reduced predation risk (by minimizing cavity entrance dimensions) and better protection from environmental factors like wind and rain (East and Perrins 1988; Nilsson 1986;
Lambrechts et al. 2010). Studies of house wrens, in particular, have shown that the birds prefer
nestboxes over natural cavities and that this indeed translates into lower rates of predation,
increased clutch size, improved nestling survival and higher overall breeding success (Johnson

The documented advantages of breeding in nestboxes also include elevated rates of
polygyny, which was very rare in our population. Although many males in our population
(31.8%) attempted to attract a second mate while their first nest was active, only a very few
(6.8% of all males) managed to pair and produce a second brood. This pattern matches reports
for house wrens using natural cavities in Wyoming, where 47% of males attempted to be
polygynous but only 9% (of all males) were successful in pairing with a second mate (Johnson
and Kermott 1991). These outcomes for populations using natural cavities are dramatically
different from nestbox studies which have shown rates of polygyny two to three times higher:
16% in Wisconsin (Poirier et al. 2004) and 24.2% in Illinois (Drilling and Thompson 1991).
Success in acquiring a second mate can be even higher still when territories are supplied with
additional nestboxes: 53.3% in Wyoming (Johnson and Kermott 1991), and 13-40% in New York
(Llambías et al. 2012). Thus, it seems that the distribution of cavities and males’ ability to
defend territories containing more than one suitable cavity limit the natural polygyny potential
of house wrens using natural cavities.

Taken together, the differences in breeding patterns and in the level of successful
breeding in natural cavities compared to nestboxes make it important to consider further the
characteristics of natural cavities used by house wrens and how these may influence natural
breeding patterns.
II. Nest cavity characteristics

One pattern in the natural cavities used by house wrens was the cardinal orientation of the cavity entrance, which involved a disproportionate number facing in easterly to southerly directions. There are very few studies of house wrens with natural cavity orientation data for comparison, one in California reporting the same pattern we observed (Purcell 1995), and another in Arizona finding no such pattern (Li and Martin 1991). In our population, cavities with easterly exposures had higher breeding success, which might be attributable to a variety of factors. For example, cavities with easterly orientations might experience greater morning sun exposure and increased radiant heating of cavity interiors. This might be particularly functional at higher latitudes where overnight temperatures can drop below freezing in early spring. At the same time, the prevailing winds in southwest Alberta are from the west-southwest. In early spring, these winds can be cold and are often accompanied by rain and sometimes even snow, with May and June being by far the wettest months of the year (EnvironmentCanada 2015) which coincides with the primary period of nesting and incubation for house wrens. Hence, cavities with eastern exposures might be multiply beneficial. They may improve rapid radiant heating of cavity interiors in the morning and thereby reduce incubation costs, while also reducing exposure to cold westerly winds and the risk of cavity flooding from accompanying rain, both advantages contributing to improved egg and nestling survival. While intuitive, these possibilities remain speculative.

At the same time, it is not clear that the pattern in cavity orientation that we observed necessarily reflects any kind of preference or bias on the part of house wrens. As secondary
cavity nesters, house wrens rely heavily on cavities originally excavated by woodpeckers (Raphael and White 1984; Li and Martin 1991; Haggard and Gaines 2001). While some studies of woodpeckers have failed to find any orientation pattern in their nests (Stauffer and Best 1982), a meta-analysis involving 23 woodpecker species found that cavities in populations at higher latitudes are disproportionately oriented in southerly orientations (Landler et al. 2014). At the same time, in a study focused specifically on aspen trees, Losin et al. (2006) found that heartwood rotting is higher on the south to southeast sides of the trunk, and that this in turn corresponds with the frequency of cavities excavated by red-naped sapsuckers (Sphyrapicus nuchalis, Baird 1858).

As a result, the pattern in cavity orientation observed for house wrens in our populations may have been largely passive, reflecting only the activities of the woodpeckers that excavated the cavities, which then created a biased distribution of entrance directions available to the house wrens. However, the fact that we nevertheless found differential breeding success within the range of cavity orientations used by house wrens, suggests that the proposed functional advantages of easterly facing entrances might nevertheless apply to house wrens.

There was also a clear pattern of choice in house wrens for cavities with smaller entrances, 81% of nests having widths of 5 cm or less, which agrees well other studies (Raphael and White 1984; Gutzwiller and Anderson 1987; Sedgwick and Knopf 1990; Dobkin et al. 1995), including some using nestboxes (Pribil and Picman 1997). In our population, nests with smaller entrances were also more successful, which is likely a result of reduced predation, as this is the primary reason for nest failures in house wrens in both temperate and tropical populations (Li and Martin 1991; Auer et al. 2007; Llambías and Fernandez 2009). Reported or suspected nest
predators of house wrens include snakes, a variety of small mammals (e.g. rats, racoons, squirrels, chipmunks, weasels, etc.) and birds (reviewed in Johnson 2014), and nests with smaller entrances are almost certainly functional in reducing predation by many of them.

It is also possible that the use of smaller cavity entrances helped to reduce competition for cavities with other secondary cavity nesters (Dobkin et al. 1995; Purcell 1995). A variety of other secondary cavity nesters were common at our field sites in southwest Alberta and were frequently observed harassing house wrens, including European starlings, *Sturnus vulgaris* (Linnaeus 1758), tree swallows (*T. bicolor*), mountain bluebirds, *Sialia currucoides* (Beckstein 1798), red-breasted nuthatch, *Sitta Canadensis* (Linnaeus 1766), white-breasted nuthatch, *Sitta carolinensis* (Latham 1790), black-capped chickadee, *Poecile atricapillus* (Linnaeus 1766), and mountain chickadees, *Poecile gambeli* (Ridgway 1886). Using a cavity with a smaller entrance may reduce competition from some of the larger-bodied competitors among these, such as starlings and bluebirds. The importance of reducing competition from other cavity nesters may also help to account for the pattern observed in house wrens of nesting in trees containing only a single cavity.

Most cavities used by house wrens were located on the main trunk (bole) of trees, relatively close to the ground (*M*=4.68 m). Studies of some other populations have not found such a clear pattern for bole- as opposed to branch-nesting (Gutzwiller and Anderson 1987; Sedgwick and Knopf 1990), but these studies have also been conducted in areas containing quite large species (e.g., floodplain cottonwoods, *Populus deltoids*) with very large branches. In contrast, the predominant tree species at our study sites in southwest Alberta were quaking
aspen which accounted for 96% of the stems and seldom attained sizes large enough to support branches of sufficient diameter to contain cavities.

The pattern we found of cavities located closer to the ground appears to be a general one (Johnson and 2014) and may be functional in allowing rapid escape to the surrounding shrub layer at the approach of danger, and reducing travel time and allowing more cryptic approach from this layer when provisioning nestlings. It is also possible that cavities located lower on the trunk, at a place where trunk diameter is wider, provides a larger interior space for nestling growth.

Finally, all of the nest cavities used by house wrens in our study were on aspen trees, and nearly 2/3 were on dead trees. Aspen was also the predominant tree species available at our site, but even in mixed vegetation types where aspen is not so predominant, there is a clear pattern for use of aspen among excavator species and secondary users (Martin et al. 2004). This pattern seems to reflect the high susceptibility to heartwood decay in aspen compared to other tree species (Basham 1958), which facilitates excavation and promotes the formation of other sorts of natural cavities, and likely for these reasons, woodpeckers show a pattern of excavating in unhealthy live and recently dead aspen trees (Blanc and Martin 2012).

In conclusion, while some elements of the basic breeding phenology of house wrens using natural cavities were broadly similar to reports from nestbox studies, such as the seasonal timing and duration of major events in the breeding cycle (e.g., nest initiation, incubation, nestling period), there were substantial differences in a variety of other aspects of breeding behavior and success. Notably, these included rates of polygyny and the overall level of breeding success which were both substantially lower in our population of house wrens.
breeding in natural cavities compared to those breeding in artificial nestboxes. These differences highlight a key constraint on the natural breeding behavior and success of house wrens arising from limitations in the number and quality of good breeding cavities. Under natural conditions, good quality breeding cavities are likely a critical limiting resource for this and other cavity nesting species, serving to depress breeding success and polygyny potential.

At the same time, the breeding success of house wrens in natural cavities was affected by a number of additional details of those cavities that are also either minimized or eliminated altogether by artificial nestboxes. These include the specific tree species involved and variation in the height, dimensions and cardinal orientation of the nest entrance. Importantly, because house wrens are actually secondary cavity users, the influence of these factors may ultimately be attributable to the behavior of the primary users and excavators of these cavities, namely woodpeckers. As a result, the breeding patterns of house wrens under natural conditions might depend a lot on the particular community of tree and primary excavator species present, and differences in both across populations, factors that are entirely glossed in studies using artificial nestboxes.

Altogether then, there are a number of factors relevant to the natural breeding behavior and success of house wrens, and other species of secondary cavity nesters, that are overlooked or eliminated in studies using artificial nestboxes, with effects on metrics of breeding biology as basic as overall breeding success and polygyny potential. Caution must then be used in extrapolating from nestbox studies to the behavior of a species under fully natural conditions.

Acknowledgements

https://mc06.manuscriptcentral.com/cjz-pubs
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References


Losin, N., Floyd, C.H., Schweitzer, T.E., and Keller, S.J. 2006. Relationship between aspen heartwood rot and the location of cavity excavation by a primary cavity-nester, the red-


Figure captions

Figure 1. A sample of the types of natural cavities used by house wrens (*Troglodytes aedon*) in southwest Alberta. The most common cavities were those previously excavated by woodpeckers with circular (a, b, c) or slot-shaped entrances (e) but house wrens also used other naturally formed cavities on trunks (d) or in snags (f).

Figure 2. Number of male arrivals relative to the date of first male’s arrival (day 1) for the study population of house wrens (*Troglodytes aedon*). Arrivals peak 9 to 11 days after first male arrives.

Figure 3. Relationship of the unpaired period to the arrival (a) and pairing dates (b) of male house wrens (*Troglodytes aedon*) in the study population. The length of time males spent unpaired was not related to when they arrived (a: $r^2=0.00$) but was necessarily positively correlated with the date they ultimately paired (b: $r^2=0.76$).

Figure 4. Nesting success of house wrens (*Troglodytes aedon*) using natural cavities in southwest Alberta compared to other populations of house wrens using either natural cavities or artificial nestboxes. (*E-C California = Purcell et al. 1997; N. Wyoming = Johnson and Kermott 1994; N. Arizona = Clark and Martin 2007*)

Figure 5. Number of nests used by house wrens (*Troglodytes aedon*) as a function of the number of suitable cavities available on the nest tree. There was a strong pattern of nesting in trees containing only a single suitable cavity.

Figure 6. The success or failure of house wrens (*Troglodytes aedon*) nests based on the cardinal direction of the cavity entrance. The outermost (green) line captures the orientation of all
nests, while the inner red and blue lines capture, respectively, the orientation of those that succeeded or failed.
Table 1: The number and proportion of nesting attempts reaching various breeding milestones for the study population of house wrens (*Troglodytes aedon*) in southwestern Alberta.

<table>
<thead>
<tr>
<th>Year</th>
<th>Arrivals</th>
<th>Paired</th>
<th>Eggs</th>
<th>Chicks</th>
<th>Fledged</th>
</tr>
</thead>
<tbody>
<tr>
<td>2011</td>
<td>24</td>
<td>15</td>
<td>15</td>
<td>12 (80%)</td>
<td>8 (53%)</td>
</tr>
<tr>
<td>2012</td>
<td>42</td>
<td>35</td>
<td>32</td>
<td>22 (69%)</td>
<td>17 (53%)</td>
</tr>
<tr>
<td>2013</td>
<td>44</td>
<td>34</td>
<td>31</td>
<td>22 (71%)</td>
<td>18 (58%)</td>
</tr>
<tr>
<td>2014</td>
<td>13</td>
<td>12</td>
<td>10</td>
<td>7 (70%)</td>
<td>5 (50%)</td>
</tr>
<tr>
<td>Total</td>
<td>123</td>
<td>96</td>
<td>88</td>
<td>63 (72%)</td>
<td>48 (55%)</td>
</tr>
</tbody>
</table>

Note: Number of Eggs, Chicks and Fledglings represent number of nests that produced at least one egg, chick or fledgling. Percentage values for chicks and fledglings are calculated relative to the number of nests that produced eggs.
Table 2: Basic characteristics of the habitat, nest site and dimensions of natural cavities used by house wrens (*Troglodytes aedon*) in SW Alberta, compared to available data for other North American populations of house wrens breeding in natural cavities.

<table>
<thead>
<tr>
<th>Study</th>
<th>Location</th>
<th>Latitude (°N)</th>
<th>Vegetation</th>
<th>Sample size</th>
<th>Cavity height</th>
<th>Entrance width</th>
<th>Entrance height</th>
<th>DCH</th>
<th>Nest tree DBH</th>
<th>Nest tree height</th>
</tr>
</thead>
<tbody>
<tr>
<td>Current study</td>
<td>SW Alberta</td>
<td>49</td>
<td>Aspen</td>
<td>117</td>
<td>4.7</td>
<td>4.2</td>
<td>7.0</td>
<td>18.1</td>
<td>21.3</td>
<td>9.4</td>
</tr>
<tr>
<td>Haggard and Gains 2001</td>
<td>Washington</td>
<td>48&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Pine and Fir</td>
<td>18</td>
<td>8.5</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>42.0</td>
<td>18.9</td>
</tr>
<tr>
<td>Gutzwiller and Anderson 1987</td>
<td>Wyoming</td>
<td>42&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Cottonwood-Willow</td>
<td>32</td>
<td>6.9</td>
<td>4.8</td>
<td>-</td>
<td>16.9&lt;sup&gt;c&lt;/sup&gt;</td>
<td>53.9</td>
<td>-</td>
</tr>
<tr>
<td>Dobkin et al. 1995</td>
<td>Oregon</td>
<td>42</td>
<td>Aspen</td>
<td>31</td>
<td>3.6</td>
<td>5.1</td>
<td>5.8</td>
<td>24.5</td>
<td>27.6</td>
<td>12.9</td>
</tr>
<tr>
<td>Stauffer and Best 1982</td>
<td>Iowa</td>
<td>41&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Mixed riparian</td>
<td>82</td>
<td>5.4</td>
<td>-</td>
<td>-</td>
<td>19.6</td>
<td>-</td>
<td>8.4</td>
</tr>
<tr>
<td>Sedgewick and Knopf 1990</td>
<td>Colorado</td>
<td>40&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Cottonwood-Willow</td>
<td>29</td>
<td>4.9</td>
<td>4.9</td>
<td>-</td>
<td>17.4&lt;sup&gt;c&lt;/sup&gt;</td>
<td>52.1</td>
<td>13.1</td>
</tr>
<tr>
<td>Raphael and White 1984</td>
<td>California</td>
<td>39</td>
<td>Pine and Fir</td>
<td>21</td>
<td>4.1</td>
<td>4.4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-</td>
<td>47.6</td>
<td>51.8</td>
<td>9.3</td>
</tr>
<tr>
<td>Purcell 1995</td>
<td>California</td>
<td>37&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Oak-Pine</td>
<td>45</td>
<td>4.5</td>
<td>5.8</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Li and Martin 1991</td>
<td>Arizona</td>
<td>34&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Aspen-Maple</td>
<td>120</td>
<td>9.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>33.6</td>
<td>-</td>
</tr>
</tbody>
</table>

<sup>a</sup> - Latitudes not provided by authors, but estimated based on site names provided in the work.

<sup>b</sup> - n=9 nests

<sup>c</sup> - DCH is low compared to DBH because most nests were on tree limbs not on the main trunk.
828x793mm (72 x 72 DPI)