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MALE MORPHOLOGY AND NEST-SITE QUALITY IN HOUSE SPARROWS

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ABSTRACT.—Previous research on House Sparrows (*Passer domesticus*) in Europe indicated that males with larger bibs are more likely to obtain nest sites with multiple potential nests. To test this observation experimentally, I created nest sites containing either one or two nest boxes. I found no morphological differences, including bib size, between males at single-box nest sites (SBNS's) and those at double-box nest sites (DBNS's). Pairs in DBNS's were more likely to renest than pairs in SBNS's in 1992, leading to increased seasonal reproductive success for pairs at DBNS's. Although pairs at DBNS's fledged more young over the season, I could not detect a strong preference for DBNS's. Pairs in DBNS's did not begin reproducing prior to those in SBNS's, as might be expected if birds preferentially occupied DBNS's prior to SBNS's. More DBNS's than SBNS's were occupied in 1991, but this was not true in 1992 when sample sizes were larger. *Received 2 Dec. 1996, Accepted 11 May 1997.*

Multiple nest sites on a territory may be beneficial, possibly allowing pairs to choose the best site for nesting, to renest in a clean site free of ectoparasites, or to reduce the interval between broods (Møller 1993, Meek and Robertson 1994). Experimental manipulation of the number of nest boxes on a territory indicates that Eastern Bluebirds (*Sialia sialis*) are more likely to occupy or respond from territories with multiple nest boxes (Meek and Robertson 1994, Plissner and Gowaty 1995). If multiple nest sites are beneficial, then dominant or high quality males should be more likely to occupy territories with multiple cavities than will subordinate or low quality males, and females should prefer to nest with males holding territories with multiple cavities.

House Sparrows are facultative cavity nesters and will utilize nest boxes, as well as construct open nests. Cavity nest sites are preferred to sites with no cavities (Cink 1976, Møller 1988). Pairs that nest in cavities or nest boxes have greater reproductive success (Cink 1976, McGillivray 1981), in part because these nests are less likely to be destroyed during storms (Møller 1988). In Europe, bib size is under sexual selection, with large-bibbed males being dominant (Møller 1987a, b), being preferred by females (Møller 1988) and having greater reproductive success (Møller 1988). Large-bibbed males are more likely to obtain nest sites with multiple cavities (Møller 1988), and males with experimentally enlarged bibs occupied nest sites with more nest boxes than did control males (Veiga 1993). House Sparrows may switch nest boxes between nesting attempts

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within a season (Naik and Mistry 1980), so multiple cavities within a nest site may allow pairs to renest without incurring the costs associated with locating and defending a new nesting site.

I manipulated nest site quality in a population of House Sparrows by placing either one or two nest boxes on a tree. Since I expected nest sites with two nest boxes to be preferred, I determined whether males occupying double-box nest sites (DBNS's) had larger bibs or exhibited other morphological differences as compared with males at single-box nest sites (SBNS's). Since multiple nest boxes may be beneficial, I expected that pairs at DBNS's would have greater reproductive success than pairs at SBNS's. I also expected that pairs at DBNS's would begin breeding prior to pairs at SBNS's and that more DBNS's than SBNS's would be occupied.

METHODS

I mistnetted House Sparrows in the spring of 1991 and 1992 and banded them with a unique combination of leg bands—one aluminum Fish and Wildlife Service band and two plastic color bands. I measured wing chords (unflattened), tarsi lengths, bill lengths, and bill depths. I photographed males and digitized the photos. Bib areas were measured using NIH Image (developed at the U.S. National Institutes of Health, available by anonymous FTP from zippy.nimh.nih.gov). I included a ruler in each photograph to convert measurements to mm^2. Sample sizes for the male morphology data were large enough for analysis only in 1992.

To manipulate nest site quality, I placed either one or two nest boxes on the bole of a tree on the Univ. of New Mexico campus, Albuquerque, New Mexico. Trees with nest boxes were clustered in a few areas on campus. This meant that nest box trees were never more than 28 m from another nest box tree, with most trees being no more than 10–16 m away from another nest box tree. Many of these trees contained previously used natural nests, so the dispersion of the nest boxes should have been similar to that of House Sparrow nests in natural nest sites in this area. Birds may have considered both natural nest sites and nest box sites when assessing nest site quality. However, all natural nest sites I observed in these trees were much higher than nest boxes, and were generally on lateral branches away from the bole. Given the small nest sites defended by sparrows, it is unlikely that natural and box nest sites would be considered simultaneously. In addition, after nest boxes were erected, I observed only one natural nest elsewhere in a nest box tree, suggesting that the sparrows focused on nest boxes once they were available.

Nest boxes were 11.4 × 11.4 × 22.9 cm and had a hinged door to allow access to the nest. The hole was 3.8 cm in diameter which prevented use of the boxes by European Starlings (*Sturnus vulgaris*), the only other cavity nesting species in the area. I placed nest boxes 3.0 to 3.7 m above the ground, a height suitable for House Sparrows (Weaver 1939, North 1973). This also ensured that humans could access the boxes only by use of a ladder. To prevent overheating of the nest contents, I placed nest boxes on the north sides of the trees with the hole facing north.

For DBNS's, I placed one box directly above the other so that the entrances to the two boxes were between 23 and 25 cm apart. This close proximity allowed the two boxes to be defended by one male. At no time during the two years did I observe two males simultaneously occupying a single DBNS. Males utilized the roofs of the nest boxes for display, always displaying from the top nest box in DBNS's. However, when nesting in DBNS's, there did not appear to be a preference for top or bottom boxes, with many pairs using both boxes within a season. I created 20 SBNS's and 20 DBNS's in January 1991. An additional 20 SBNS's and 20 DBNS's were created in January 1992 for a total of 80 nest sites in 1992.

In 1991, I checked nest box contents after external signs of occupancy, such as nesting material, were detected. Occupied boxes were then checked every two to three days until the young were banded at 10 to 12 days of age. After all nesting had ceased in 1991, I removed nest material from all nest boxes which had been used and sprayed them with an insecticide (0.1% pyrethrin flea and tick spray). In 1992, all nest boxes were checked weekly beginning in March. Once an egg had been laid, the nest box was checked every other day until the young were banded. After banding the young, at 10 to 12 days of age, nests were left undisturbed for two weeks before being checked again. If the nest was abandoned directly after I disturbed the female while she sat on the nest, the nest was deleted from analyses.

I recorded the date, number of eggs laid, number hatched, and number of young banded (referred to as the number of young fledged). Juveniles were weighed with a 50 g Pesola scale at this time.

Due to the high population density and the large number of nest sites, I could not always determine the date when a nest site became occupied or a male obtained a mate. However, when I observed that a male had obtained a mate, nest building and egg laying always followed rapidly. In this population, pairs which began reproducing earlier had higher reproductive success (Kimball 1995), so it is unlikely that pairs delayed breeding once pairing occurred. Therefore, I used date of the first egg laid as a relative estimate of when a male attracted a mate to his territory.

Variables which were not normally distributed, as determined by a Shapiro-Wilks test, were analyzed using non-parametric statistics, as indicated in the results. Since I expected that DBNS's would be occupied by large-bibbed males, would have greater reproductive success, and would be preferred, I used one-tailed tests for all comparisons between SBNS's and DBNS's. Pairs which nested in both a SBNS and a DBNS in the same season were deleted from these analyses. Power analyses were performed using GPOWER (Faul and Erdfelder 1992). Power analysis depends upon estimating the effect size or the expected relative difference between two means (Cohen 1969). Since it is difficult to estimate effect size, I report power results for both a small ($d = 0.2$) and a large ($d = 0.8$) effect size (Cohen 1969).

The data from 1991 and 1992 differed in several respects (Table 1). Therefore, I analyzed data from the two years separately.

RESULTS

Male bib size did not differ between males occupying DBNS's and those at SBNS's (Table 2), contrary to my expectations. The power of the tests was low ($power_{d=0.2} = 0.11$; $power_{d=0.8} = 0.43$), so I could not conclusively accept the null hypothesis that bib size is the same between males at SBNS's and those at DBNS's. However, the difference in mean bib size between the two types of nest sites was small (18 mm^2, Table 2), particularly considering the variability of bib sizes I observed in this study ($\bar{x} = 387.1$ mm^2, SD = 139.3 mm^2, range = 175.3–589.7 mm^2).

TABLE 1

DIFFERENCES IN REPRODUCTIVE SUCCESS BETWEEN 1991 AND 1992

Variable	1991	1992	*z* or *t* (df)	*P*
Number of sites occupied	22	61		
Percent of sites occupied	55%	76%		
Date of first egg[a,b]	17 May	22 April	3.90 (81)	<0.001
Number fledged (brood)	1.8	3.0	−3.63 (81)	<0.001
Number fledged (season)	2.5	4.8	−3.26 (81)	0.002
Number of nesting attempts[b]	1.3	1.6	−1.71 (81)	0.086

[a] Analyzed as Julian date. Only first nesting attempts were used.
[b] Analyzed using Wilcoxon rank sum test.

Therefore, it is unlikely that a larger sample size would have led to a significant difference in bib sizes between males at SBNS's and DBNS's.

I also found no other morphological differences between males in DBNS's as compared to those in SBNS's (Table 2). The power of these tests also was low ($power_{d=0.2}$ = 0.11; $power_{d=0.8}$ = 0.54). However, for all traits except bill length, the differences between SBNS males and DBNS males was quite small, making it unlikely that significant differences would have been found with larger sample sizes. For bill length, a larger sample size might have indicated significant differences between males at SBNS's and those at DBNS's.

More young fledged during the season from DBNS's than SBNS's in 1992 but not in 1991 (Table 3). The increased reproductive success of pairs in DBNS's was due to an increased number of nesting attempts by DBNS pairs in 1992 and not to an increase in the number of young fledged per brood (Table 3). Data from 1991 also showed that pairs in DBNS's had greater reproductive success, and a larger sample size may have indicated significant differences in 1991 as well.

TABLE 2

DIFFERENCES IN MALE MORPHOLOGY BETWEEN MALES IN SBNS'S AND THOSE IN DBNS'S (1992 ONLY)

Variable	SBNS (N)	DBNS (N)	*t* (df)	*P*
Bib area (mm^2)	378.8 (8)	396.6 (7)	0.24 (13)	0.408
Wing chord (mm)	77.8 (12)	76.9 (9)	−1.02 (19)	0.159
Tarsus length (mm)	17.7 (12)	17.8 (9)	0.51 (19)	0.309
Bill depth (mm)	8.0 (12)	8.0 (9)	0.03 (19)	0.487
Bill width (mm)	7.4 (12)	7.4 (9)	−0.23 (19)	0.412
Bill length (mm)	9.8 (12)	10.4 (9)	1.70 (19)	0.077

TABLE 3

DIFFERENCES IN REPRODUCTIVE SUCCESS BETWEEN SBNS'S AND DBNS'S (1991: $power_{d=0.2} = 0.11$, $power_{d=0.8} = 0.54$; 1992: $power_{d=0.2} = 0.19$, $power_{d=0.8} = 0.93$)

Variable	SBNS	DBNS	*z* or *t* (df)	*P*
1991				
Number of sites occupied	8	14		
Percent of sites occupied	40	70		
Date of first egg[a,b]	12 May	19 May	−0.78 (20)	0.217
Number fledged (brood)	1.4	2.0	1.21 (20)	0.120
Number fledged (season)	1.6	2.9	1.43 (20)	0.085
Number of nesting attempts[b]	1.1	1.4	−0.89 (20)	0.188
1992				
Number of sites occupied	32	29		
Percent of sites occupied	80	73		
Date of first egg[a,b]	24 April	20 April	−1.23 (59)	0.109
Number fledged (brood)	2.9	3.1	0.45 (50)	0.328
Number fledged (season)	3.9	5.7	2.37 (59)	0.011
Number of nesting attempts[b]	1.3	1.8	2.64 (50)	0.004

[a] Analyzed as Julian date. Only first nesting attempts were used.
[b] Analyzed using Wilcoxon rank sum test.

Males occupying DBNS's did not obtain mates and begin reproducing prior to pairs at SBNS's (Table 3), contrary to what would be expected if the sparrows considered DBNS's superior to SBNS's. Significantly more DBNS's than SBNS's were occupied in 1991 (Fisher's Exact Test, N = 39, *P* = 0.036) but not in 1992 when sample sizes were larger (N = 80, *P* = 0.378). If DBNS's are more likely than SBNS's to be occupied, the trend is either weak or variable among years. Unoccupied DBNS's were always available in both years, indicating that at least some males chose to nest in SBNS's instead of DBNS's.

Pairs nesting in SBNS's could obtain clean nest boxes for renesting by moving to another nest site. Seven (of 11) SBNS pairs switched to another nest site before renesting. Although DBNS pairs had more nesting attempts than did SBNS pairs (Table 3), no DBNS pairs switched nest sites between nesting attempts. Therefore, while DBNS's were not consistently preferred, pairs in SBNS's often switched to new nest sites to renest, while pairs in DBNS's switched to the other nest box within the same nest site. The time between nesting attempts was the same for pairs which remained in a nest site and those which switched nest sites ($t = 1.12$, df = 38, $P = 0.271$), suggesting that there was little cost, as measured by delayed renesting, when pairs switched to a new nest site.

If switching nest boxes between nesting attempts is advantageous, one would expect it to occur between most nesting attempts. Unused nest sites were always available on the study site, making such a strategy feasible. However, many pairs renested in the same nest box. In SBNS's, four of 11 pairs which renested did so in the original box. One SBNS pair nested successfully three times in the same box. Even in DBNS's, where a second nest box was already available on the nest site, a similar proportion (5 of 12 pairs) nested twice in the same box. Six DBNS pairs nested three times, and one of those pairs used only one of the two boxes in the nest site. Therefore, switching boxes between nesting attempts was neither a universal strategy nor necessary for successful reproduction.

DISCUSSION

Cavity nest sites are rare in many habitats (Martin 1993, Newton 1994), so cavities are an important resource for cavity nesting species unable to excavate their own cavity. If cavity nests are a scarce resource, (1) territories which contain multiple cavities may be preferred to territories with only a single cavity, (2) dominant or high quality males should be more likely to occupy territories with multiple cavities than will subordinate or low quality males, and (3) females should prefer to nest with males holding territories with multiple cavities.

In Europe, male House Sparrows with large bibs are dominant (Møller 1987a, b) and are more likely to obtain nest sites with multiple cavities (Møller 1988). In addition, male House Sparrows with experimentally enlarged bibs occupied more nest boxes than did control males (Veiga 1993). Contrary to those results, I did not find that males with large bibs were more likely to occupy nest sites with two boxes. Large-bibbed males fledged significantly more young during the breeding season than did small-bibbed males (Kimball 1995), suggesting that bib size does reflect at least some aspects of male quality in this population. There were also no other morphological differences between males in DBNS's and those in SBNS's. Although bib size was measured differently in all three studies, variance in bib sizes is large and it is unlikely that small differences in measurement technique would account for the different results.

In this study, I stacked nest boxes to create DBNS's which were likely to be defended by only one male. Veiga (1993) studied nest boxes placed 0.4–2.0 m apart, while Møller (1988) assessed potential natural nest locations, which would have been randomly distributed in the nesting site. The difference in nest dispersion between my study and those of Møller (1988) and Veiga (1993) may have affected the results. For example, separate nest boxes within a site might allow males to mate polygynously. About 10% of the males studied by Veiga were polygynous (Veiga 1990, 1992), while I only observed one polygynous male in two years (in this case the nests sites were in separate trees). Veiga (1992) experimentally decreased the distance between boxes, to about 15 cm, and did not find that polygyny increased. This suggests that closely spaced boxes do not promote polygyny in House Sparrows, though polygyny may occur at sites with more distantly placed nest boxes. Therefore, the close placement of boxes in this study may have prevented males from attracting additional mates, and hence DBNS's were not preferred. Alternatively, a physical separation between multiple nests within a nest site may limit transmission of ectoparasites between nests, while nest boxes in physical contact may provide no such benefit.

Differences between the results I obtained and those of Møller (1988) and Veiga (1993) may be due to behavioral and ecological differences among populations. House Sparrow behavior is plastic, and other behavioral differences have been observed among different populations. For example, female choice for bib size has been demonstrated in Denmark (Møller 1988), but females do not prefer large-bibbed males in New Mexico, USA (Kimball 1996), and may not in Spain as well (Veiga and Puerta 1996).

Pairs in DBNS's had greater reproductive success in both 1991 and 1992, although results were only significant in 1992 when sample sizes were larger. These pairs gained a reproductive advantage because they were more likely to have multiple nesting attempts than were pairs in SBNS's. A clean nest box, which would have been readily available in DBNS's, may have increased the likelihood that a pair would renest. Supporting this idea, the majority of SBNS pairs which renested did so by switching to a new nest site. House Sparrows in other populations have also been observed to switch nest boxes between nesting attempts (Naik and Mistry 1980), indicating that it may be a common, although not necessary, occurrence.

In spite of the greater reproductive success of pairs in DBNS's, I could not detect a strong preference for DBNS's. DBNS's were not occupied prior to, or more commonly, than SBNS's. A preference for territories with two nest boxes has been demonstrated in Eastern Bluebirds (Meek and Robertson 1994, Plissner and Gowaty 1995). Eastern Bluebirds are obligate cavity nesters, whereas House Sparrows can nest successfully in non-cavity nests. Therefore nest boxes may be a more valuable commodity for Eastern Bluebirds than for House Sparrows. Other characteristics of the nest site, such as foliage structure, levels of human disturbance, or proximity to a food source may be more important for House Sparrows than number of nest boxes, which may not be true of species such as the Eastern Bluebird. In addition, unoccupied nest-box sites, as well as sites capable of supporting natural nests were always available, switching to a new nest site may have involved relatively little cost, particularly when compared to the advantages some of the SBNS's may have offered.

There were several differences between 1991 and 1992. In 1991, when the boxes were new to the study site, seasonal reproductive success was lower and the breeding season began later relative to what I observed in 1992. These differences may indicate that the nest boxes were primarily occupied by younger birds in 1991 (Saether 1990), a phenomenon which may occur in House Sparrows (Lowther 1983). Therefore, the large proportion of DBNS's occupied in 1991 could indicate that DBNS's were easier for the inexperienced breeders to locate. The results from 1992, which included both young and old breeders, may therefore be more representative of typical House Sparrow populations in New Mexico.

I could find no morphological differences between males occupying DBNS's and those occupying SBNS's, suggesting that there are ecological and behavioral differences between this population and those in Europe (Møller 1988, Veiga 1993). DBNS's were not occupied prior to SBNS's, indicating that these nest sites may not have been preferred. Although DBNS's did not appear to be preferred, pairs in DBNS's had greater seasonal reproductive success, as pairs in these nest sites were more likely to renest. This paper emphasizes the need to study multiple populations to understand the constancy or plasticity of behavioral and ecological parameters.

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