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DIVISION OF LABOR: INCUBATION AND BIPARENTAL CARE IN HOUSE SPARROWS (*PASSER DOMESTICUS*)

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ABSTRACT.—In the great majority of animal taxa, males do not participate in parental care, but substantial paternal care is common across avian species. We examined male and female incubation contributions in House Sparrows (*Passer domesticus*), quantifying the incubation behavior of free-living, individually color-banded parents during 47 nesting cycles. We also measured the relative warmth of male and female incubation surfaces. Females spent more time incubating than their male partners, and female time incubating served as the best single predictor for hatching success. Considered alone, male time incubating correlated negatively with hatching success, but that effect was nullified when female incubation was taken into account. Females had warmer abdomens than males, a difference that may reflect greater development of brood patch and effectiveness of incubation in that sex. Here, male badge size was not demonstrably associated with either male or female incubation patterns or hatching success. *Received 5 March 2004, accepted 3 January 2005.*

Key words: division of labor, House Sparrow, incubation, parental care, *Passer domesticus*.

División de Labores: Incubación y Cuidado por Ambos Progenitores en *Passer domesticus*

RESUMEN.—En la mayoría de los taxa animales los machos no participan en el cuidado parental; sin embargo, un cuidado paterno substancial es común en las aves. Examinamos las contribuciones de los machos y las hembras durante la incubación en la especie *Passer domesticus*, cuantificando el comportamiento de incubación de parejas en libertad y marcadas individualmente con anillos de colores durante 47 ciclos de nidificación. También medimos la temperatura relativa de las superficies de incubación de las hembras y de los machos. Las hembras permanecieron incubando por un periodo de tiempo mayor que sus parejas macho y el tiempo de incubación por la hembra fue la variable única que mejor predijo el éxito de eclosión. Al considerar sólo el tiempo de incubación de los machos, éste se correlacionó negativamente con el éxito de eclosión, pero este efecto se anuló cuando se tomó en cuenta la incubación por parte de la hembra. Las hembras tuvieron abdómenes más cálidos que los machos, una diferencia que puede reflejar un mayor desarrollo del parche de incubación y una mayor efectividad de la incubación por parte de las hembras. En este estudio, el tamaño del parche del macho no se asoció con los patrones de incubación del macho ni de la hembra, ni con el éxito de eclosión.

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ABOUT 95% OF all birds are at least socially monogamous (Lack 1968, Black 1996), with both male and female partners typically providing substantial parental care in nidicolous species. Nevertheless, considerable variation exists in the type and magnitude of male contributions. Males may or may not incubate eggs, brood nestlings, deliver food, stand watch, actively deter predators, and assist the fledglings after they have left the nest (e.g. Ketterson and Nolan 1994, Liker and Szekely 1999, Currie et al. 2001). The diversity in paternal care presumably stems from balancing offspring care against other means of enhancing fitness, especially time and energy expenditure allocated to the incompatible activities of foraging for self-maintenance, seeking additional mating opportunities, or both (Maynard Smith 1977, Jönsson et al. 1998, Wright et al. 1998)

Most research on biparental care in birds has focused on nestling food-provisioning activities, rather than on contributions of each sex during alternative forms of care, such as incubation and brooding (Whittingham and Dunn 2001). Studies that have addressed the process of incubation, in turn, have focused primarily on its physiological aspects (heat transfer, energy costs, hormone variation, etc.; e.g. Biebach 1984, Jones 1987, Chaurand and Weimerskirch 1994, Minguez 1998). Nevertheless, behavioral studies of species with biparental incubation (e.g. Drent 1970, Hatch 1990, Pinxten et al. 1993, Reid et al. 2002) have the potential to explore the specific role of males in this form of parental care and hence the relative importance of male investment at this early stage of the reproductive cycle.

Embryo survival, proper embryo development, and length of the developmental period are all affected by the necessity of keeping eggs within a given temperature range (Farmer 2000). Failure to maintain eggs within the temperature range for embryonic development can cause hatching failure (Webb 1987). In general, most avian embryos must be maintained between 30°C and 40°C, with the average temperature for passerines being ~32°C (Webb 1987). Because temperatures >40.5°C can kill embryos (Conway and Martin 2000), incubation also insulates eggs against excessively high temperatures.

Although no morphological specializations are required for transferring body warmth

from parents to eggs, and only modest physical modifications have evolved (e.g. increased vascularization and feather loss to create a "brood patch"), incubation has been shown to carry a variety of costs (Visser and Lessells 2001). In males, decreased circulating levels of testosterone, in tandem with increased levels of prolactin, may curtail the number of extrapair copulations or additional social mates a male can obtain while incubating. Specifically, such fluctuations in those hormones may reduce sexual behavior in male birds (Ketterson and Nolan 1994, Moreno et al. 1999). Incubation is also likely to carry nontrivial energetic costs associated with heat generation and transfer to eggs (Siikamaki 1995, Heaney and Monaghan 1996). Finally, incubation is simply more time-consuming and spatially confining than most other forms of parental care (Ketterson and Nolan 1994), automatically limiting time for foraging (Webb 1987, Siikamaki 1995) and other valuable activities, while simultaneously rendering the immobile parent more vulnerable to predators (Stoleson and Beissinger 2001, Amat and Masero 2004). When summed, those costs may explain why males do not incubate in many avian species (Ketterson and Nolan 1994).

In taxa in which males contribute to incubation, females may benefit from being able to predict the magnitude and value of that contribution early in the process of mate choice (Johnstone 1997). The color intensity, pattern, and size of patterns in male plumage have often been investigated as possible indicators of genetic, physical, and parental quality (e.g. Griffith 2000, Poiani et al. 2000). In male House Sparrows (*Passer domesticus*), the most conspicuous sexually dimorphic plumage trait is the badge, a black patch that extends from the throat into a roughly circular shape on the chest. A variety of relationships between male badge size and male parental care have been found. Reyer et al. (1998) determined that large-badged males engaged in a greater share of risky nest defense than smaller-badged males, and Voltura et al. (2002) found badge size to be positively associated with both male share of nestling feeding and subsequent fledging success. By contrast, Václav and Hoi (2002) suggested that male House Sparrows with average-sized badges contributed most to incubation, and subsequently experienced the greatest incidence of hatching failure.

Our study's first objective was to examine the incubation contributions of male House Sparrows as a function of time and effectiveness in helping embryos develop properly. Specifically, male incubation contribution was quantified and tested as a predictor of hatching success, and male brood-patch development was compared with that of females. The second objective was to explore whether male badge size covaries with male contributions to incubation, such that it might inform females about that form of cooperation.

METHODS

The incubation behavior of House Sparrows was studied in a population containing 38 nest boxes located on University of Oklahoma property (North Base) in Norman, during May–July 2000 and April–July 2001. Data on sex differences in brood patch temperatures were collected in 2002. Nest boxes at the site are attached to fences, buildings, or utility poles; a study of variation among individual nest boxes in relation to hatching success and fledging success revealed no significant consistency in those measures of box “quality” across a span of five years (Alig 2003). Nest boxes were equipped with a 10-cm hardware cloth “corridor” that prevented larger avian species from entering the boxes and preying on eggs or nestlings. In all years, we censused nest boxes twice a week from mid-March through early August to determine clutch size, brood size, and fledging success. We supplemented those censuses with additional checks of nest contents as the projected hatch date for each clutch approached, which provided further resolution of hatch date and hatching success. The House Sparrow is a predominantly socially monogamous (averaging 9.6% polygyny in a Spanish population; Veiga 1992) multibrooded passerine with biparental care. Both sexes feed and defend young. During the incubation stage, females alone remain in the nest box at night; males have been reported to contribute approximately one-third of the total diurnal incubation performed by a pair (34%: Summers-Smith 1963; 40%: Hegner and Wingfield 1986).

Daytime incubation patterns were quantified for 47 pairs. Because the population was also the focus of other studies and all adults occupying nest boxes were banded, detailed

records (including regular identification of the individually banded resident pair at each nest box) were kept across years, and no individuals were observed during more than one nesting cycle. House Sparrow incubation begins when the next-to-last egg is laid (Anderson 1997), and in Oklahoma lasts ~11 days from the day the last egg is laid (Whitekiller et al. 2000). Clutch size in Oklahoma ranges from two to six eggs, with most clutches containing four or five eggs. Our observations of incubation began the day the fourth egg was due to appear (± 1 day). Hour-long samples of parental visits were made every second morning over the ensuing seven days, for a total of four sample hours per nest. In those samples, we recorded the identity of the parent and the times (to the nearest second) it landed at, entered, exited, and departed from the nest box. In the absence of information on how quickly effective incubation begins after a parent enters the nest, we included all time a parent spent inside the nest box as potentially contributing to incubation. Number of visits per hour included only those visits where the parent entered the nest box (excluding, for example, those spent on the box's roof); as such, visits included very brief trips into the nest by either parent to add nesting material, but their cumulative duration is probably negligible. For estimates of mean incubation duration of each sex per hour and the mean maximum duration of incubation bouts, we included only the time that each parent spent inside the nest box during each sample. Mean incubation duration was the total amount of time an individual spent in the nest box during the four one-hour samples divided by four to produce an average across the samples. Mean maximum duration was calculated by summing the longest single incubation bout from each of the four one-hour samples and dividing that total by four to find an average maximum. (Lengthy incubation bouts may contribute to overall incubation effectiveness by reducing any negative effects associated with fluctuations in egg temperature.) Observations were made only in the morning to capitalize on lower ambient temperatures (so parental warmth was more likely to be needed) and generally higher avian activity. Sampling times were systematically distributed for each pair across the morning hours to minimize possible time-of-day effects. Observations were made using a spotting scope

in a vehicle parked a minimum of 40 m from the nest box and partially concealed, whenever possible, behind local obstructions (trees, other cars, buildings, etc.). Each sample began as soon as the observer was in position and ended 60 min later, without respect to whether either or both parents were in sight or inside the nest box at the time.

Most of the males whose behavior was observed (42 of 47) were socially monogamous, at least during the nesting cycle when their incubation was sampled. Both monogamously and polygynously mated males incubated and did not differ in the mean duration of incubation ($t = 0.46$, $df = 6.8$, $P = 0.66$). Similarly, male incubation duration did not differ between years ($t = -1.21$, $df = 46$, $P = 0.23$), so data were pooled across mating systems and years.

To estimate male badge size, we videotaped each male using a camera with a long focal-length zoom lens. No measurements were taken of the so-called "hidden" male badge (i.e. black sections concealed by overlying light-colored feather tips), which begin to abrade during the breeding season (Møller and Erritzøe 1992, Veiga 1996). Visible badge size during the breeding season has been reported to correlate highly with the size of the portions hidden before the breeding season (Griffith et al. 1999). Furthermore, all males were videotaped during the height of the breeding season (late May to mid-July) to minimize individual variation from differential abrasion of the light-colored feather tips. Each video image included a nearby measurable object (board width, entrance hole diameter, etc.) that allowed subsequent calibration of scale. The most head-on images from each piece of video footage were digitized using frame-grabbing software, and each badge was analyzed with IMAGE software, a public domain National Institutes of Health (NIH) program (see Acknowledgments). Each image was analyzed three times, and the average area was used for analysis. Estimates of the same male's badge area derived from two different scorers (each independently choosing a still frame from video footage and measuring it) were highly correlated ($r = 0.90$, $P < 0.001$, $n = 15$).

We assessed the degree of sex differences in brood patch thermal effectiveness by measuring the lower abdomen and back temperatures from a sample of male and female parents. During April to June 2002, each captured adult

was restrained on a Plexiglas board with narrow Velcro straps across the bird's thorax and adhesive tape to secure full extension of the wings. (A small blood sample was taken from a brachial vein for use in a separate study of genetic relatedness.) The lower abdomen was then bared by pushing the feathers aside so that a thermocouple (Digi-Sense T-type; Geneq, Montreal, Quebec) head could be placed flat against the abdominal skin. After 30 s of timed contact, the surface temperature was recorded. We then removed the bird from the Plexiglas board and turned it over so its back was up. A small apterium was bared between one wing and the spinal feather tract, from which a dorsal skin temperature was taken after another 30 s of contact. Back temperatures allowed correction for variation in ambient and general body temperature. For analysis, the back temperature was subtracted from the abdominal temperature to give a single value (i.e. the difference) for each bird. Only data from color-banded adults (9 females, 13 males) that were known to be tending clutches or newly hatched broods <6 days old (when nestlings are still ectothermic) were included in the analysis.

Statistical analyses were performed using SAS, version 8.1, and SPSS 10.1 statistical software. Behavioral variables were converted to a single average value for each individual and for each pair. To examine factors predicting hatching success, we used the events-trials syntax for logistic regression in SAS, so the number of chicks hatched was weighted by the number of eggs in the clutch. All P -values are two-tailed with alpha (α) set at 0.05, and means are presented with standard deviations (means \pm SD). Daily and hourly temperature data for North Base were obtained from the Oklahoma Mesonet (The Oklahoma Climatological Survey), and an average temperature during each pair's sample hours was calculated and used in analyses of hatching success and incubation behavior. Seasonal effects on incubation behavior and hatching success were further evaluated in relation to mean Julian date (number of days elapsed since 1 January) on which each pair had been sampled.

RESULTS

Females incubated an average of 28.4 ± 9.0 min h^{-1} , whereas males incubated less than half as much (13.5 ± 7.1 min h^{-1}) (paired $t =$

8.48, $df = 46$, $P < 0.0001$). Each parent's mean incubation duration was correlated negatively with that of its partner ($r = -0.43$, $P = 0.002$, $n = 47$). On average, a clutch was left with neither parent incubating for 18.2 ± 17.9 min h^{-1} . The mean maximum duration of incubation bouts differed between the sexes (paired $t = 15.11$, $df = 46$, $P < 0.0001$), with females' maximum bouts (15.4 ± 4.9 min, range: 6.8–25.8 min) double those of males (7.6 ± 4.3 min, range: 0.0–16.3 min). Number of bouts per hour did not differ between males and females (paired $t = 1.36$, $df = 46$, $P = 0.18$). Numbers of nest visits by males correlated positively with both their mean incubation duration ($r = 0.44$, $P = 0.002$, $n = 47$) and their maximum incubation duration ($r = 0.36$, $P = 0.01$, $n = 47$). Numbers of visits by females similarly correlated positively with their mean incubation duration ($r = 0.44$, $P = 0.002$, $n = 47$), but not with their mean maximum duration ($r = -0.08$, $P = 0.55$). The average time a clutch was left without either parent incubating correlated negatively with both male mean duration ($r = -0.46$, $P = 0.001$, $n = 47$) and female mean duration ($r = -0.54$, $P < 0.001$, $n = 47$), and was not a significant predictor of hatching success (Wald $\chi^2 = 2.00$, $P = 0.16$, $n = 47$).

There was no strong evidence that incubation behavior varied in response to seasonal shifts. The mean summed incubation time for both parents could not be shown to correlate with Julian date ($r = 0.24$, $P = 0.10$, $n = 47$), ambient temperature ($r = -0.03$, $P = 0.84$, $n = 47$), or clutch size ($r = -0.06$, $P = 0.66$, $n = 47$). Logistic regression showed that hatching success was not predicted by date (Wald $\chi^2 = 0.11$, $P = 0.74$, $n = 47$) or ambient temperature (Wald $\chi^2 = 0.71$, $P = 0.40$, $n = 47$).

Percentage of eggs within a clutch that did not hatch averaged $10.6 \pm 15.0\%$ among nests. When controlling for clutch size, logistic regression showed that female incubation duration was positively associated with hatching success (Wald $\chi^2 = 9.52$, $P = 0.002$, $n = 47$), but male incubation duration was negatively associated with hatching success (Wald $\chi^2 = 4.73$, $P = 0.03$, $n = 47$). When both male and female times were included in multivariate logistic regression, only female incubation duration served as a significant predictor of hatching success (Wald $\chi^2 = 10.22$, $P = 0.006$, $n = 47$).

Body-surface temperature measurements showed that females' lower abdomens were

warmer than their backs (mean difference = $2.09 \pm 2.06^\circ\text{C}$; paired $t = 2.86$, $df = 7$, $P = 0.024$), whereas males' lower abdomens were cooler (mean difference = $-0.83 \pm 1.19^\circ\text{C}$; paired $t = -2.51$, $df = 11$, $P = 0.027$). A sex disparity exists for temperature differences between abdomen and dorsum ($t = -3.64$, $df = 9.76$, $P = 0.005$), with females averaging 2.92°C warmer ventrally than males.

Male badge size did not vary with either mean male incubation duration per hour ($r = 0.03$, $P = 0.84$, $n = 45$) or mean incubation duration by the female partner ($r = 0.11$, $P = 0.86$, $n = 45$). Badge size also was not a significant predictor of hatching success, either when analyzed as a continuous variable (Wald $\chi^2 = 0.76$, $df = 1$, $P = 0.38$) or when categorized as small, medium, or large (Kruskal-Wallis $\chi^2 = 0.74$, $df = 2$, $P = 0.69$).

DISCUSSION

On average, females spent half again more time incubating than their male partners, and female variation in contribution was positively correlated with hatching success. By contrast, male incubation time was not correlated with hatching success once female investment was considered. Although studies of European Starlings (*Sturnus vulgaris*) have indicated that contributions by males of that species play a crucial role in the pre-hatching care of young (Pinxten et al. 1993, Reid et al. 2002), our results suggest that greater incubation contributions by male House Sparrows have either a neutral or even detrimental consequence for offspring. That association may have several components, including the sex difference in brood patch development. The brood patch of male House Sparrows has been described by some authors as reduced (Bailey 1952) and by others as absent (Summers-Smith 1963). Our skin-temperature results indicate that the lower abdomen of females is certainly warmer (in relation to the rest of the body) than is the corresponding region of males. That implies a reduced effectiveness of males in incubation.

The incubation effectiveness of male and female birds appears to differ across species in various ways. For example, male European Starlings incubate eggs at slightly lower temperatures than females, though males rewarm clutches more rapidly (Reid et al. 2002). Conversely, males of the Moustached Warbler

(*Acrocephalus melanopogon*) and male Reed Warblers (*A. scirpaceus*) were both shown to rewarm clutches more slowly than females (Kleindorfer et al. 1995). Male American Kestrels (*Falco sparverius*) have smaller brood patches than females (Wiebe and Bortolotti 2000). Thus, the benefits to offspring of male incubation may be reduced in various species.

Hatching failure averaged ~11%. Failure to hatch has a number of causes, including unsuccessful fertilization and developmental defects arising from gene interactions (e.g. Kempenaers et al. 1999). On the basis of microscopic examination of the perivitelline layers of House Sparrow eggs, Birkhead et al. (1995) estimated that 85% of hatch failures involve embryonic mortality, with the remaining 15% stemming from infertility. Thus, most hatching failure observed here may be attributed to embryonic mortality, rather than lack of fertilization. Furthermore, although the effects of parental genetic compatibility on embryonic viability have not been specifically addressed in this species, other studies have provided evidence that parental incubation regimes are closely tied to hatching success. Cordero et al. (1999) found that first-laid eggs, which are subjected to the greatest degree of incubation neglect, are at highest risk of hatch failure; similarly, Veiga and Viñuela (1993) determined that asynchronously hatching broods (in which incubation presumably was started relatively early) had better hatching success than synchronous broods. Because appropriate temperatures must be maintained to promote normal embryonic development, proper incubation is allied with avian hatching success. For example, in chickens (*Gallus domesticus*), eggs experiencing temperatures <30.0°C for prolonged periods suffered developmental abnormalities; likewise, eggs experiencing temperatures >40.5°C experienced malformations and even death because of organ failure (Webb 1987).

The apparent difference in how male and female incubation affects hatching success cannot be interpreted unambiguously from a correlative study alone. In particular, it was not clear that increased male incubation played any causal role in hatching failure. High male incubation may imply that better-quality attendance by the female partner was unavailable. That is, males may incubate more only when the female does not incubate as much as she typically

would, in which case the male may have to do the best he can. In support of this view, we note that our multivariate analysis showed that female incubation was the only significant predictor of hatching failure. However, it is possible that male incubation provides other advantages by allowing additional foraging time for females or serving as a deterrent to potential predators, intraspecific brood parasites, or competing conspecific males.

Finally, our study found male badge size to be a poor indicator for prehatching paternal care, at least in the form of incubation. However, inasmuch as male incubation does not appear to improve hatching success, that result does not detract from the hypothesis that badge size may serve as an indicator of male parental quality. Previous studies of House Sparrows in Oklahoma have shown that male badge size correlated positively with male feeding share during nesting provisioning and with nestling survival (Voltura et al. 2002). Female choice of males based on their parental quality (or indicators of such) might be expected to target those aspects of male parental care that contribute positively to offspring welfare. Because male contribution to incubation does not appear to do so, at least in terms of hatching success, other forms of parental care may play a greater role in shaping House Sparrow mating systems and female choice.

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