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GONADAL DEVELOPMENT DURING AUTUMN AND WINTER IN HOUSE SPARROWS[1]

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Abstract. In free-living House Sparrows, *Passer domesticus,* resident in central New York, gonadal development is initiated in the autumn and continues throughout the winter months. Partial recrudescence in the early autumn is associated with transient increases in circulating levels of luteinizing hormone, dihydrotestosterone, and testosterone in both sexes. In females, concentrations of estradiol also increase at this time. There are no seasonal changes in body mass in males, but females are heavier in late autumn and early winter. In both sexes, fat depots and concentrations of corticosterone increase by winter and decrease again by early spring. Autumnal gonadal recrudescence is associated with the initiation of social competition for nesting sites and mates. Adults return to nest sites, rates of intrusion by conspecifics increase, and agonistic interactions are more frequent. Darkening of the male beak, an androgen-dependent secondary sex characteristic, occurs rapidly in the autumn, perhaps in response to social competition. In contrast, development of the cloacal protuberance, also dependent on androgens, does not occur until later in the winter. House Sparrows that initiate nesting early in the spring produce more fledglings during the entire season than do pairs that begin later. Hence, acquisition of a nesting site in the autumn may allow earlier nesting and consequently greater reproductive output during the ensuing nesting season.

Key words: House Sparrows; Passer domesticus; *gonadal recrudescence; reproductive hormones; breeding biology.*

INTRODUCTION

The role of day length in the development and function of the gonads of avian species inhabiting temperate zones has long been the subject of much study (e.g., Rowan 1926, Wolfson 1954, Farner 1985). Many investigations, particularly in the past two decades, have demonstrated the influence of day length on the annual cycles of gonad size, plasma concentrations of reproductive hormones, and expression of sexual and territorial behavior (e.g., Farner and Lewis 1971; Murton and Westwood 1977; Farner and Follett 1979; Farner and Gwinner 1980; Wingfield 1980, 1983; Wingfield and Farner 1980). These investigations have been focused on vernal increases in the physiological and behavioral aspects of avian reproduction.

It is becoming increasingly evident, however, that the wintering strategies of temperate-zone birds are also crucial to their survival and eventual reproduction (e.g., Fretwell 1972). In this report, we focus on an adaptation that may mark the beginning of breeding and involves an increase in gonad size, hormone titer, and territorial and reproductive activity in the autumn, many months before nesting begins (Morley 1943, Marshall 1952, Marshall and Coombs 1957, Lofts and Murton 1968, Gorman 1974, Spurr and Milne 1976, Lincoln et al. 1980, Schwabl et al. 1980, Röhss and Silverin 1983). We present evidence here for autumnal gonadal recrudescence in the House Sparrow (*Passer domesticus*) and some suggestions for the adaptive significance of this phenomenon in this and other temperate-zone avian species.

METHODS

STUDY SITES AND ANIMALS

From September 1982 to October 1984, birds were captured in mist nets at several barnyards and villages in Dutchess County, New York (42°N). Shortly after capture (8.5 ± 5.7 min), approximately 300 to 400 μl of blood was collected from a wing vein into heparinized microhematocrit capillary tubes. Sampling was conducted almost entirely in the morning hours (0700 to 1200) to minimize variation due to diel fluctuations in hormone levels. Plasma samples were stored at −20°C until analyzed.

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All birds were marked with numbered aluminum Fish and Wildlife Service bands and a unique combination of plastic color bands. Before release, length of the cloacal protuberance was measured to the nearest 0.5 mm, and body mass was measured to the nearest 0.1 g. Fat depots in the furculum and abdomen were estimated on an arbitrary scale of 0 to 5, where 0 = no fat and 5 = gross bulging fat bodies. Beak color was estimated on an arbitrary scale of 1 to 4, where 1 = uniform light yellow or horn color and 4 = jet black (following Keck 1934). Laparotomies were performed to provide an indication of gonadal development. Testis mass was estimated by visual comparison with a scale constructed from a series of testes of known weight, and the diameter of the largest ovarian follicle was estimated to the nearest 0.1 mm. Most of these sampling techniques have been described in detail by Wingfield and Farner (1976, 1978).

At all study sites, nest boxes (inner dimensions = 20 × 14 × 10 cm) were provided to monitor nesting activity. From early March through late September, an effort was made to check each box at least twice each week to record clutch size, brood size and age, and fledging success. From the 1982–1984 records, we selected all cases (n = 101) in which the pair bond remained intact for the entire nesting season. In the majority of these cases, one or both members of the pair was color banded. When both birds were unbanded, we used egg spot size and pattern to confirm the continuity of at least the female in successive broods (Dawson 1972). These records were used to determine the total seasonal production of young by each pair according to the date at which the first egg of the season was produced.

BEHAVIORAL OBSERVATIONS

During September and October 1984, activities of adult House Sparrows at nesting boxes were monitored using a focal-nest protocol. During 1- to 2-hr observation periods, the behavioral activities of each adult were monitored continuously. Data recorded included the time of arrival at and departure from the nest box, singing activity, intrusions by other conspecifics, and instances of aggressive responses (threat displays, agonistic supplantings, chases, and fights) to these intrusions. Time of each event was recorded to the nearest min. All observations were conducted from 0700 to 1200 to minimize diel variation and to coincide with hours in which blood samples were collected. The focal-nest protocol allowed unbiased estimates of rates of intrusion at nesting boxes, rates of agonistic responses to these intrusions, and the allocation of time to each type of activity during each observation period (Altmann 1974).

RADIOIMMUNOASSAY OF CIRCULATING HORMONE LEVELS

Plasma levels of luteinizing hormone (LH) were measured by the post-precipitation, double-antibody radioimmunoassay (RIA) for chicken LH, as developed by Follett et al. (1972) and modified for use on small plasma samples by Follett et al. (1975). This assay has been applied extensively to measure LH in a wide variety of avian species including House Sparrows (Donham et al. 1982), and a large body of evidence suggests that it measures primarily LH (Follett et al. 1978). Details of accuracy and inter-assay variation can be found in Hegner and Wingfield (in press [a]).

The following steroid hormones were measured by RIA after separation and partial purification on celite : glycol microcolumns: 17β-hydroxy-5α-androstan-3-one (dihydrotestosterone, DHT), testosterone (T), estradiol-17β (E2), and corticosterone (B). The chromatography procedure and RIA have been described in detail by Wingfield and Farner (1975) and Wingfield et al. (1982). Briefly, plasma samples were equilibrated overnight with approximately 2,000 cpm of each ^{3}H-labeled steroid to determine percentage recovery of steroid after chromatography. Plasmas then were extracted in 5 ml of redistilled dichloromethane. Dried extracts were redissolved in a total of 1.0 ml of 10% redistilled ethyl acetate in isooctane and transferred to the top of a celite : propylene glycol : ethylene glycol (6:1.5:1.5 w:v:v) columns, each of which was fitted with a celite :water (3:1 w:v) trap to prevent the elution of glycols. Steroid fractions then were eluted in order of polarity with increasing concentrations of a mobile phase of ethyl acetate in isooctane. Each steroid fraction was evaporated under a stream of nitrogen, and the dried extract was redissolved in assay buffer (phosphate-buffered saline with 0.1% sodium azide and gelatin) overnight. Fractions then were assayed by RIA using standard curves over the range of 2 to 500 pg (DHT, T, E2) and 4 to 1,000 pg (B). After equilibrium, bound and unbound hormone were separated by addition of 0.5 ml of dextran-coated charcoal for 10 min and centrifugation at 1,500 g for 10 min at 4°C. Further details can be found in Hegner and Wingfield (in press [a]).

DATA ORGANIZATION AND STATISTICAL ANALYSES

All data were organized into a seasonal calendar including a stage of postnuptial (prebasic) molt, actual calendar dates (October

TABLE 1. Dates of blood samples. Values shown are mean ±1 standard deviation.

Stage	Males		Females	
	Date	*n*	Date	*n*
Post-nuptial molt	25 Sep ± 18 days	25	21 Sep ± 20 days	24
October	10 Oct ± 4 days	20	12 Oct ± 5 days	16
November	18 Nov ± 3 days	44	25 Nov ± 10 days	34
December	16 Dec ± 12 days	13	19 Dec ± 8 days	10
January	21 Jan ± 6 days	29	20 Jan ± 6 days	30
February	22 Feb ± 6 days	23	21 Feb ± 7 days	21
March	22 Mar ± 6 days	22	19 Mar ± 9 days	18
Pre-breeding	16 Apr ± 12 days	29	14 Apr ± 12 days	30

through March), and a prebreeding stage (individuals sampled during April and May that had not initiated nesting). Stage of molt was determined for each individual captured from August through October. Prebreeding status was determined by behavioral observations of color-banded birds in the field and by inspection of the nesting boxes. Each stage is positioned along the temporal axis according to average calendar date. Dates and sample sizes for each stage are given in Table 1.

Plasma levels of LH, DHT, E2, and T were not correlated significantly with time after capture. Levels of B, however, rose significantly following the moment of capture ($r = 0.55, P < 0.01, n = 444$ for all adults sampled in a three-year period). Consequently, values of B were corrected for capture time using the following least-squares regression line for all samples pooled: ng B/ml = 5.11 + 0.96 time (min). This regression line was highly significant ($F = 92.5$, $P < 0.005$). Corrected values assume a linear rise in B after capture (e.g., Dawson and Howe 1983) and were obtained by subtracting from each measured value 0.96 ng/ml for each minute that elapsed between capture and collection of blood.

Seasonal changes were analyzed by nonparametric one-way analysis of variance (Kruskal-Wallis ANOVA) to determine overall significant differences. Means were compared with Dunn's multiple comparison test for unequal sample sizes (Hollander and Wolfe 1973). Reported significant differences are at the 0.005 level (ANOVA) or at the 0.05 level (Dunn test).

RESULTS

PHYSICAL AND ENDOCRINE CHANGES

Males. There were significant changes in testis mass, beak color, length of the cloacal protuberance (CPL), and plasma levels of reproductive hormones during the autumn and winter (Fig. 1). Annual minima for each occurred at the end of the postnuptial molt and for several weeks thereafter. By November, however, significant testis recrudescence had begun, and the gonads continued to increase in weight at a moderate rate until the early part of January. During January and February, testicular development entered a phase of rapid growth, reaching maximum size by the beginning of the nesting season. Testes remained at or near maximum size until termination of reproduction in August or early September (Hegner and Wingfield, in press [a]). Autumnal recrudescence of the testis was associated with a significant, although moderate, increase in plasma levels of LH in November. LH concentrations then declined until January and did not increase again until the end of the phase of rapid testicular development. Plasma levels of T increased moderately in the late autumn and more markedly during the phase of rapid testicular growth. DHT levels also increased by March.

Partial gonadal recrudescence in autumn also was associated with a significant darkening of the beak (Fig. 1). By January nearly all males had jet-black beaks. An increase in CPL was not associated with autumn gonadal recrudescence. However, during the phase of rapid testicular development, there was a marked development of CPL, reaching near maximal length just before egg laying commenced.

Seasonal changes in body mass, fat depots, and plasma levels of B are shown in Figure 2. There was no significant change in body mass throughout the study period, even though fat reserves increased to an annual maximum during the colder months of the year and declined by early spring. Fat reserves then showed a slight increase just before reproduction was initiated. Plasma levels of B increased during the autumn and, except for a slight decline in February, continued to increase during the prebreeding stage.

Females. Changes in follicle size and circulating levels of reproductive hormones in females throughout the autumn and winter are presented in Figure 3. During the postnuptial molt, the gonads were completely regressed, and levels of reproductive hormones were low.

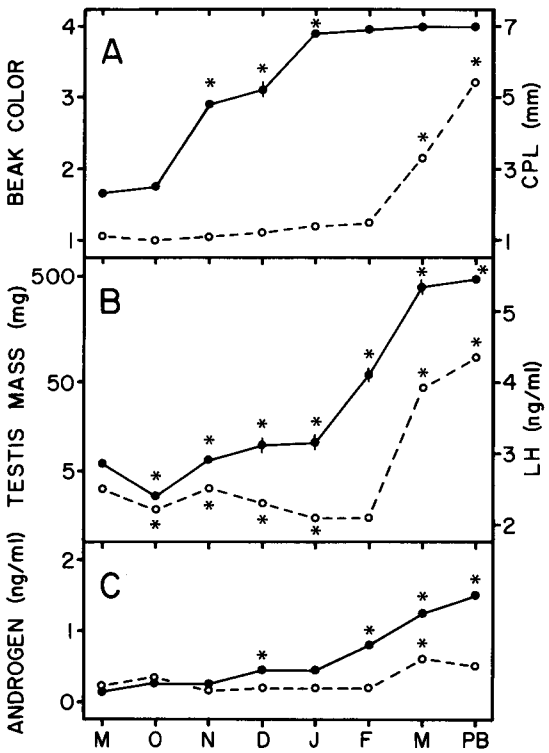

FIGURE 1. Seasonal changes in (A) beak color (solid circles) and length of the cloacal protuberance (open circles), (B) mass of the left testis (solid circles) and plasma levels of LH (open circles), and (C) plasma levels of T (solid circles) and DHT (open circles) for male House Sparrows. Gonad mass is shown on a logarithmic scale; all others are arithmetic. Values are mean ± 1 standard error; error bars not visible are within the circles. Points marked with an asterisk represent values that differ significantly from the preceeding stage ($P < 0.05$, Dunn test). All data are organized into a schematic calendar representing a stage of postnuptial molt (M), individuals sampled during the autumn and winter months (O, N, D, J, F, M), and a prebreeding stage (PB). Sample sizes for each stage are given in Table 1.

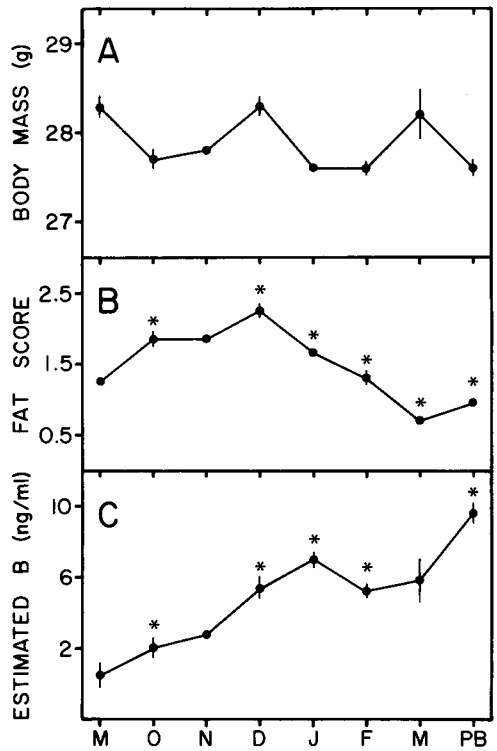

FIGURE 2. Seasonal changes in (A) body mass, (B) fat depots, and (C) estimated plasma concentrations of corticosterone for male House Sparrows. This figure follows the format of Figure 1.

By November, ovarian recrudescence had begun, and the ovarian follicles continued to enlarge at a constant rate during the autumn and winter. By March, follicles were 1 to 2 mm in diameter and were devoid of yellow yolk. This condition has been termed the pre-yolk deposition stage and represents maximum development prior to activation of the yolk deposition, ovulatory, and oviposition sequence (King et al. 1966; Wingfield 1980, 1983; Wingfield and Farner 1980). Rapid vitellogenesis and follicular development occurred just prior to the onset of oviposition (Hegner and Wingfield, in press [b]).

Initiation of gonadal recrudescence was associated with moderate, but significant, peaks of LH and sex steroid hormones. LH concentrations then declined until January, rose during the remainder of the winter, and remained high during the prebreeding stage. After an initial rise, circulating levels of E2 remained relatively constant during the autumn and fluctuated irregularly during the winter and early spring. DHT concentrations declined sharply from October to November, remained low throughout the winter, and reached a second maximum in March, only to decline again just before egg laying was initiated. Plasma levels of T, although low, were constant during the autumn. In January, T levels first declined and then rose again in late winter, only to decline again just before the nesting season commenced. Note that levels of DHT were higher than those of T.

Over-winter changes in body mass, fat reserves, and levels of B in females are presented in Figure 4. Body mass was lowest for several weeks after the molt, increased during the autumn, and remained high during the winter prebreeding period. Changes in fat reserves showed a similar rise but then declined during late winter and early spring. Concentrations of B rose moderately as gonadal development was initiated, increased sharply in December, declined during the winter, and rose again sharply during the prebreeding stage.

BEHAVIORAL CHANGES DURING THE AUTUMN

During the molt, House Sparrows rarely visited the nesting boxes, and few visits were re-

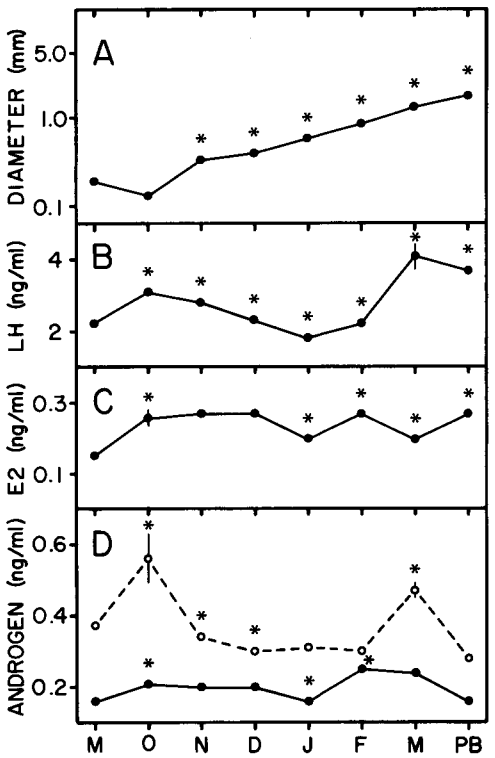

FIGURE 3. Seasonal changes in (A) diameter of the largest ovarian follicle, (B) plasma concentrations of LH, (C) levels of estradiol (E2), and (D) levels of T (solid circles) and DHT (open circles) for female House Sparrows. Follicle diameter is shown on a logarithmic scale; all others are arithmetic. This figure follows the format of Figure 1.

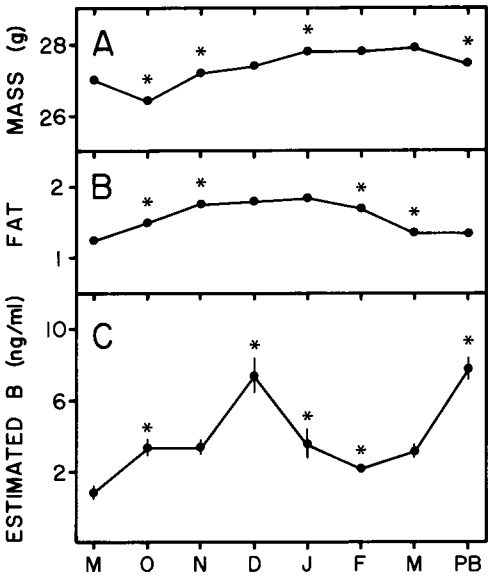

FIGURE 4. Seasonal changes in (A) body mass, (B) fat depots, and (C) estimated plasma concentrations of corticosterone (B) for female House Sparrows. This figure follows the format of Figure 1.

corded in 21 nest-hours of observation. Instead, flocks of up to 200 individuals were seen foraging in fields adjacent to the breeding areas. In October, when the molt was completed, birds returned to the breeding areas and the activities of the adults again began to be centered around their nesting site and mate (Table 2). Both males and females spent increased amounts of time at the nest, were more likely to be present at nests simultaneously, and showed an increased tendency to arrive or depart together. Males occasionally sang, but no courtship displays were seen. Intrusion rates by conspecifics, notably other adult males, increased dramatically to a level comparable to egg-laying stages during the nesting season (Hegner and Wingfield, in press [a]). As a result, males were more likely to become involved in agonistic interactions.

REPRODUCTIVE OUTPUT

House Sparrows that initiated breeding earlier in the spring completed more broods, laid more eggs, and fledged more young over the course of the entire nesting season. This is illustrated in Figure 5, which shows the total number of fledglings produced by a pair according to the date the first egg of the season appeared in their nest. Although this figure pools data collected over three seasons, similar relationships were seen in each year separately. A least-squares regression fitted to these data indicated a decline of one young fledged for every nine days that nest initiation was delayed. Pairs that initiated nesting early, however, were not more successful at any one time during the season than were pairs that initiated nesting later ($r = -0.06$, $F = 0.36$, $P > 0.25$). Instead, early nesting allowed individuals to make more nesting attempts each season.

DISCUSSION

Following Lincoln et al. (1980), we consider the initiation of gonadal recrudescence in the autumn months as marking the start of the breeding period. Viewed from this perspective, the annual cycle of House Sparrows in central New York is characterized by a brief nonbreeding period (September to October) occupied almost entirely by the postnuptial molt, and a prolonged breeding period spanning the remaining 10 to 11 months of the year. The breeding period is divided into a preparatory phase in which gonadal development is initiated and completed (October to March) and several nesting phases during the warmer months of the year (March to September). The gonads remain at or near maximum development for nearly six months before regressing rapidly at the end of the breeding period. They are completely regressed only for a few weeks

TABLE 2. Activity at nesting boxes during the molt and in early autumn. Shown are the proportion of time males, females, and both members of a pair were present; the proportion of simultaneous arrivals to, and departures from, the nest by the male and female (% following activity); rates of intrusion at nesting boxes by all conspecifics and adult males; and the frequency of agonistic interactions involving the male. Values shown are mean ±1 standard error.

	Post-nuptial molt ($n = 7$)	October ($n = 23$)	Mann-Whitney U-test
% time male at box	1 ± 1	15 ± 9	$P < 0.005$
% time female at box	1 ± 1	9 ± 1	$P < 0.005$
% time male and female at box	0 ± 0	4 ± 1	$P < 0.025$
% following activity	0 ± 0	12 ± 1	$P < 0.005$
Total intrusions/hour	0.1 ± 0.1	1.2 ± 0.9	$P < 0.005$
Intrusions by males/hour	0 ± 0	1.0 ± 0.9	$P < 0.005$
Agonistic interactions/hour	0.1 ± 0.1	0.6 ± 0.1	$P < 0.005$

during the postnuptial molt, and then begin to recrudesce shortly after the molt is completed.

In our study area, gonadal development in males occurs in two qualitatively different stages. The autumnal stage (from late October to early January) is characterized by a relatively slow rate of gonadal growth and a significant darkening of the beak, accompanied by a transitory increase in plasma levels of LH and T. During these months, the interstitial volume of the testis increases, but no spermatogenesis occurs (Threadgold 1960). The winter stage (January to March) is characterized by more rapid gonadal growth, lengthening of the cloacal protuberance, and rapid increases in circulating levels of reproductive hormones. This stage is marked by a further increase in interstitial volume and complete spermatogenic activity (Threadgold 1960). A similar two-stage pattern of testis development was seen by Polikarpova (1940). In females, gonadal development appears to occur more gradually during the autumn and winter. Moderate but more sustained increases in plasma LH, E2, and androgens are associated with initiation of follicular development. The autumnal increases in LH and androgens are transitory, but E2 remains elevated throughout the autumn.

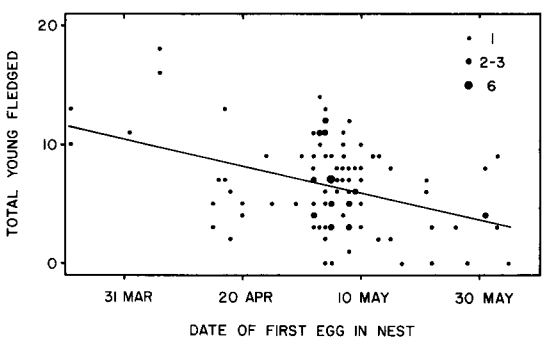

FIGURE 5. Annual production of fledglings from $n = 101$ nest boxes monitored during 1982–1984. A least-squares regression indicated a decline in total young fledged in later-starting nests [No. fledged = 20.6 − 0.113 (No. days from first nest), $r = -0.397$, $F = 18.50$, $P < 0.005$]. Similar results were obtained from analysis of each year separately.

Although the annual cycle we report refers strictly to our study population in central New York, there is evidence that gonadal development during autumn and winter occurs in other north-temperate House Sparrow populations. Threadgold (1960) found significant gonadal growth in January and February in populations resident in California and Oklahoma. Successful nesting in January has been observed in Utah (Cottam 1929). In northern Mississippi, oviposition may occur in late February (Sappington 1977). In one population from the Soviet Union, gonadal development begins by late December or early January (Polikarpova 1940). Hence, there is no reason to suspect that our study population is atypical in this regard.

Sexual activity in the autumn also has been recorded in a number of other avian species inhabiting north-temperate regions (for reviews, see Morley 1943, Marshall 1952, Marshall and Coombs 1957, Spurr and Milne 1976, Lincoln et al. 1980, Röhss and Silverin 1983). Several studies have found an increase in plasma androgens (Gorman 1974, Temple 1974, Balthazart and Hendrick 1976, Paulke and Haase 1978, Lincoln et al. 1980, Schwabl et al. 1980, Röhss and Silverin 1983) or plasma LH (Sharp et al. 1974, Scanes et al. 1974, Haase et al. 1975, Donham 1979, Lincoln et al. 1980, Dittami 1981, Röhss and Silverin 1983) associated with this activity, but others have not (Haase 1983, Dawson 1983). Several histological studies have reported changes in testis morphology during the autumn, and all have found increases in the androgen-secreting interstitial portion of the gonad (Leydig cells) but no initiation of spermatogenesis (Marshall 1952, Marshall and Coombs 1957, Temple 1974, Paulke and Haase 1978, Lincoln et al. 1980, Röhss and Silverin 1983).

Several authors have suggested that the

physiological basis of gonadal recrudescence in the autumn is a recovery of photosensitivity at a time when day length is still long enough to stimulate gonadal development (e.g., Höhn 1947, Marshall and Coombs 1957, Lofts and Murton 1968, Gorman 1974). House Sparrows have a well-developed photoperiodic mechanism, and typical October day lengths (approximately 11 hours) may be experimentally photostimulatory (Farner et al. 1977). Captive male House Sparrows held continuously on long days (16L or longer) reinitiate gonadal growth shortly after completing postnuptial molt, suggesting that this species does not require short days to break photorefractoriness (M. C. Moore, pers. comm.). In tropical and subtropical areas, House Sparrows breed in 10 or more months of the year, pausing only during severe monsoon rains and during the period of molt (Naik and Mistry 1980). During the annual cycle of the House Sparrow, there thus is a potential for gonadal recrudescence to begin any time after the molt. Particularly in higher latitudes, the rate of this recrudescence may be influenced by other factors such as day length, ambient temperature or social interactions (Threadgold 1960, Hegner and Wingfield 1984). Hence, autumnal recrudescence in north-temperate regions in some cases may simply reflect the continued operation of a regulating mechanism that evolved in lower latitudes.

There are suggestions that the initiation of gonadal development in the autumn depends at least partially on abundant trophic resources available as the result of the commensal relationship between House Sparrows and humans. Nesting is initiated later in the migratory race *P. d. bactrianus* breeding in Soviet central Asia than in the sedentary race *P. d. domesticus* breeding at 55°N. *Passer d. bactrianus* also exhibits an annual cycle of fat deposition and locomotor activity typical of north-temperate migrants (Dolnik and Gavrilov 1975). Trophic resources provided by humans are also a major factor allowing the extremely prolonged nesting season of House Sparrows (Hegner and Wingfield, in press [a], in press [b]). However, the occurrence of autumnal sexual activity in many other north-temperate avian species, none of which are commensal with humans, requires a more general explanation.

Photoperiodic and other regulatory mechanisms have evolved because they allow individuals to anticipate the time of year favorable for breeding and thus to initiate gonadal development in advance of the ensuing nesting season (Farner and Lewis 1971; Farner and Follett 1979; Farner and Gwinner 1980; Wingfield 1980, 1983; Wingfield and Farner 1980). Any mechanism or other character will remain in a population only as long as it continues to be of selective advantage to individual members of that population. There thus must be some selective advantage associated with the autumnal resurgence of reproductive activity in House Sparrows and other species.

Most authors have suggested that autumn sexuality is adaptive because it allows individuals to initiate reproduction earlier in the subsequent spring, a factor that normally correlates with increased breeding success (e.g., Lack 1968, Perrins 1970). Species resident in their breeding areas during the autumn and winter may gain this advantage through the opportunity to establish pair bonds and nesting sites in the autumn, thus being able to take advantage of favorable conditions as soon as possible in the following spring (Morley 1943, Marshall 1952, Lincoln et al. 1980). In both migratory and resident species, females that form pair bonds in the autumn also may be able to survive the winter months with greater amounts of protein and fat reserves because they are able to feed with less interruption from unpaired males (Gorman 1974, Spurr and Milne 1976, Krapu 1981, McLandress and Raveling 1981). Females with greater nutrient reserves at the end of the winter are able to lay larger and earlier clutches of eggs (Gates and Woehler 1968, Ankney and MacInnes 1978).

The above arguments seem likely for single-brooded species or those that rely primarily on endogenous nutrient reserves to initiate reproduction. For species that produce more than one brood per season, advantages gained from early nesting may accrue over the course of the entire season. In House Sparrows, for example, the earliest clutch of the season is not usually the most productive (McGillivray 1983, Hegner and Wingfield, unpubl.). Instead, the advantage for early reproduction is the ability to rear more young during the entire nesting season. Pairs that initiate breeding earlier, fledge more young over the course of the entire season but are not more successful at any one time during the season than are pairs that initiate nesting later. Instead, early nesting allows individuals to attempt more broods each season.

Reproductive advantages of early nesting may be offset by a resulting increased risk of mortality, because in some populations most adult annual mortality occurs during the nesting season (Summers-Smith 1963). However, McGillivray (1983) found no evidence that reproductive effort increased as the probability of surviving to the next breeding attempt decreased. Also, Schifferli (1976) found that females terminated reproduction when fat re-

serves were well above the threshold for survival.

Even if no measurable reproductive advantage to early nesting is evident, competition for safe nesting sites (such as nest boxes) may be severe enough that only those individuals establishing control of one during the autumn will be able to utilize it in the following season. The autumnal stage of gonadal recrudescence in House Sparrows is associated with the initiation of social competition for nesting sites and mates. In the early autumn, House Sparrows begin to establish nesting sites and pair bonds that will be maintained throughout the colder months of the year. During this stage of gonadal recrudescence, adults spend significantly more time at their nesting sites, and rates of intrusion by other conspecifics and aggressive responses to these intrusions increase significantly. Some nest building occurs, and sexual displays are seen, but copulation generally is absent. There also is an increase in the frequency of communal courtship displays (Marshall 1952; Summers-Smith 1954, 1963; Hegner and Wingfield, unpubl.). Experimental evidence also suggests that competition for nesting boxes and/or mates stimulates the rate of gonadal development during the autumn and winter in both sexes (Hegner and Wingfield 1984).

Towards the end of the autumn, as day length and environmental temperature decrease, the frequency of reproductive activities also wanes; but on warm, sunny days such activity increases spontaneously. The winter stage of gonadal recrudescence is associated with preparation for the initiation of reproduction. At this time there is an increase in singing, courtship activities, and nest-site defense, and also additional pair-bond formation, nest-building, and sexual activity, including copulation (Summers-Smith 1963).

The blackened beak of males is an androgen-dependent secondary sexual characteristic (Keck 1934, Fevold and Eik-Nes 1962, Lofts et al. 1973, Haase 1975, Donham et al. 1982) important in agonistic interactions (Summers-Smith 1963, Watson 1970). This characteristic develops rapidly in the autumn when agonistic interactions over nest sites and mates are initiated. An important contrast, however, is the delay until the winter stage of recrudescence in the development of the cloacal protuberance, which is also an androgen-dependent secondary sexual characteristic (Farner and Wingfield 1980). This character is necessary for successful reproduction, not at the time when nesting sites are established, but rather several months in the future, when environmental conditions are favorable for reproduction. Hence, the autumnal stage of recrudescence appears to allow individual males to compete for mates and nesting sites without wasting energy on the production of sperm or development of a copulatory organ until the appropriate time of year. The endocrine mechanism(s) responsible for the separate development of beak color and cloacal protuberance are unknown at this time.

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