

A COMPARATIVE STUDY OF REPRODUCTIVE ADAPTATIONS IN HOUSE AND TREE SPARROWS

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ABSTRACT.—I studied the reproductive biology of the House Sparrow (*Passer domesticus*) and the Eurasian Tree Sparrow (*P. montanus*) in a 1.3-ha plot in central Spain during 1985 and 1986. The breeding season of both species overlapped to a great extent, although egg laying began and peaked earlier in Tree Sparrows. Clutch size was slightly larger in House Sparrows, but it varied significantly only with the season in Tree Sparrows. Egg mass of House Sparrows was greater than that of Tree Sparrows (body size effects removed) and largely determined hatching size in both species. Egg mass increased with the laying sequence in Tree Sparrows, and egg-size dependent mortality was recorded only in this species. Tree Sparrows had longer incubation periods but shorter hatching interval than House Sparrows. Growth rates were higher in Tree Sparrows (though the difference was significant only for growth of primary feathers). Fledging mass (as a proportion of adult size) and nestling fat stores also were larger in Tree Sparrows. Nestling mortality rates and productivity did not differ between species, and starvation was dependent on hatching order in both. Fledged House Sparrows grew more rapidly than Tree Sparrows, and reached adult size earlier. Crops of young trapped within 4 months after fledging were fuller in House Sparrows than in Tree Sparrows. Young House Sparrows used abundant human feeding sources, whereas Tree Sparrows fed mainly on small indigenous seeds.

Patterns of clutch size, egg size, and timing of breeding favor the hypothesis that interspecific differences in these traits are determined by energetic limitations, which constrain Tree Sparrows more than House Sparrows. An increase of egg mass with the laying sequence in the species that invested less in the hatchlings supports a brood-survival hypothesis. In both species, only the last hatched was subjected to differential mortality, even though the entire brood frequently starved. This does not support the brood-reduction hypothesis. The nest-failure hypothesis was also unsupported. Greater relative fledging mass and heavier fat stores in the species that suffered more adverse feeding conditions after fledging suggest that the fat accumulation is related to facing higher risks of starvation. Received 27 December 1988, accepted 16 July 1989.

THE COMPARISON of life history traits among different species is a widely used method. Many important issues can be resolved by this method, even though it has many limitations similar to some experimental procedures (Clutton-Brock and Harvey 1984). Most comparative studies of avian reproduction have focused on single traits or on various traits considered independently. It is generally accepted that reproductive traits have evolved in close interdependence (Cody 1966, MacArthur and Wilson 1967, Trivers 1972, Smith and Fretwell 1974, Brockelman 1975, O'Connor 1978). Accordingly, the simultaneous consideration of a cluster of presumably co-adapted traits is considered to be a realistic ap-

proach in the study of reproductive biology (Murphy 1983).

The advantage of comparing a small number of species is that variables can be compared accurately (e.g. Orians 1961, 1980; Ekman and Askenmo 1986). I compared the congeneric House Sparrow (*Passer domesticus*) and the Eurasian Tree Sparrow (*P. montanus*), to examine alternative life history models and to test specific hypotheses regarding the evolution of some major reproductive traits. These species are similar in their habitat use, nesting behavior, number of broods raised each year, and food selected for the young. This similarity excludes many nesting-related factors as determinants of the differences between them in the traits I considered. Likewise, confounding environmental variables had minimal effects because the study area was small.

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I studied seasonal variation in clutch size and egg size to test two major hypotheses: first, that intraspecific variability of clutch size represents an adjustment to prevailing conditions during the brood-rearing period, which can maximize the number of surviving offspring (Lack 1966); and, second, that the variability of clutch size and egg size is a consequence of proximate energetic constraints (Murton et al. 1974, Ankney and MacInnes 1978, Winkler 1985). I used incubation time, hatching asynchrony, intra-clutch variation of egg size, and nestling mortality in relation to hatching order to test three major hypotheses about the consequences of asynchronous hatching. First, the *brood-reduction hypothesis* states that hatching asynchrony imposes a size hierarchy that creates asymmetric competition among siblings. This leads to the death of the last hatched sibling if the food is scarce and enables the parents to match the brood's needs to prevailing environmental conditions (Lack 1954). Second, the *brood-survival hypothesis* states that the pattern of increased egg size over the laying sequence represents an adaptation to counteract hatching advantages of the older sibling and promote the survival of the entire brood (Slagsvold et al. 1984). Finally, the *nest-failure hypothesis* states that, by starting incubation early and hatching asynchronously, the amount of time the eggs and some young are vulnerable to nest predation is reduced (Hussell 1972, Clark and Wilson 1981). I also measured nestling growth rates, post-fledging mass increase, and food habits to estimate the role of feeding conditions after fledging on nestling development.

METHODS

Study area and species.—The main study took place in Collado Villalba (Madrid, Spain) in 1985–1986. Additional clutch size data were collected in 1987. This town is situated on the south slope of the Guadarrama mountain range (approximately in the center of Spain) at an altitude of 900 meters. Nests were observed in an area of 1.3 ha within a cattle ranch of oak (*Quercus rotundifolia*) and ash (*Fraxinus angustifolia*) trees supplied with nest boxes.

During both years the climate was normal and food was abundant. The number of nest predators in the area was large. At least four species (two of snakes, one of lizards, and magpies [*Pica pica*]) frequently preyed upon the nestlings, whereas others (e.g. cats, rats, weasels) probably did so occasionally. To reduce predation, nest boxes were placed in inaccessible areas,

and some predators (mainly snakes) were removed from the study area. As predators in the study area were the same for both sparrows, there are no reasons to think that this procedure biased predation rates toward one species.

The biology of the two species is well known (see Summers-Smith 1963, 1988; Seel 1968a, b, 1970). The diets of both species are qualitatively and quantitatively very similar (J. P. Veiga pers. obs.). At the start of the breeding season, both species fed their young mainly Lepidoptera larvae. The intake of grasshoppers (Orthoptera) and a variety of other insects (Diptera, Coleoptera, Hymenoptera, Hemiptera, etc.) increased in summer. The diets differed slightly during the last fortnight of the breeding period because of the tendency (observed only in House Sparrows) to feed fruits and seeds to the young. Most individuals of both species nested in the nest boxes provided, although other sites (such as holes in buildings, under roof tiles, cane roofs, etc.) were also used. I was able to watch 95% of the nests built within the study area.

Field procedures.—Observations of most nests began as soon as the first egg was laid, although some nests already had a number of eggs when the watches began. Most eggs were numbered and weighed to the nearest 0.05 g on the day of laying. When the laying sequence of the eggs was not known, the eggs were numbered at random. These eggs were excluded when analyzing correlation between egg mass and laying order. Nests were monitored daily until all eggs were laid. When hatching was near, nests were checked every 3 h. Because each nest was checked at least 4 and usually 5 times per day on the day(s) of hatching, I could determine the hatching period of each brood accurately. It was possible also for each nestling to be matched with the egg from which it hatched. Overall, the hatching order of each individual was known, though it was not infrequent for more than one nestling (usually two) to hatch between two nest watches.

For future identification, I marked nestlings with indelible ink. I recorded body mass and tarsus length daily until the end of the nestling period. The length of the outermost primary was measured once it emerged. Mass was recorded to the nearest 0.05 g up to 10 g; above 10 g mass was recorded to the nearest 0.1 g. After the nestlings were 8 days old, fat level was recorded on a scale of 6 values, based on the fullness of the furcular cavity. The mode of all daily records for fat level was used to characterize each nestling. All nestlings 8–11 days old were banded with individually numbered metallic leg bands.

When healthy nestlings exhibiting normal growth disappeared from the nest, I assumed they were preyed upon. When an entire brood disappeared from one day to another, I also considered a predator was involved. Only when a nestling left the nest 11 or more days after hatching was it considered to have fledged successfully.

Postfledging control.—Birds were caught with mist

nets near the breeding site in 1985 from mid-June to the end of October and in 1986 until the end of August. The birds were aged (as first year or adult individuals), weighed, banded, and released. The crops of 1,504 individuals were examined externally (Newton 1967) for information on feeding habits and food consumption rates. Only 408 of these crops contained food.

Data analysis.—I measured growth rates as the regression of mass, tarsus length, and outermost primary length on age. I characterized growth rates of mass and tarsus length for the first 9 days after hatching, and growth rate of primary length for the period between emergence and fledging. I calculated the growth rates of the nestlings killed by predators when at least 6 values were available for the regressions. The linear model gives an adequate description of growth, as all the r^2 values were >0.89 and most were >0.98 . Consequently, I accepted the linear model for descriptive purposes. I averaged growth rates, fledging sizes, and nestling-period lengths for each brood because measurements of individual young in a nest were not independent of one another.

To make egg mass, nestling size, and growth variables comparable between species, they are expressed as a percentage of adult size (e.g. O'Connor 1984). I used as reference the size of the individuals caught during the 12 months of the year (House Sparrow: mass = 27.59 ± 2.11 g, tarsus length = 19.22 ± 0.64 mm, outermost primary = 57.56 ± 1.98 mm, $n = 274$; Tree Sparrow: mass = 19.82 ± 1.48 g, tarsus length = 17.19 ± 0.71 mm, outermost primary = 50.41 ± 1.66 mm, $n = 77$; $\bar{x} \pm SD$ given throughout). Records for both species were distributed similarly over the year, so that seasonal variation did not affect interspecific differences. Percentages relating nestling size or egg size to adult size or to values predicted by specific equations were arcsine square root transformed for statistical comparisons. I chose parametric statistics except when the assumptions of normality and homoscedasticity were not met. Because none of the reproductive traits examined were significantly different between the years (or among the three years in the case of clutch size), I pooled data for each species.

RESULTS

Breeding season and clutch size.—Tree Sparrows began to lay eggs on 23 April 1985 and 3 May 1986. House Sparrows began 10 days later in 1985 and 8 days later in 1986. The egg-laying season did not differ between years in either of the two species ($P > 0.05$, Kolmogorov-Smirnov tests) and was pooled (Fig. 1). The seasonal distribution of the frequencies of clutch initiations differed significantly between species (Kolmogorov-Smirnov test, $D = 0.288$, $n_1 = 59$, $n_2 = 73$, $P < 0.01$), as a result of the early Tree Sparrow

breeding. The intrinsic pattern of seasonal variation (i.e. assuming that both species began their clutches simultaneously) did not differ between species (Kolmogorov-Smirnov test, $D = 0.08$, $P > 0.05$). Clutch initiation by both species peaked within 10 days after the first egg was laid. Approximately 40 days later, a second peak in egg laying due to second clutches occurred in both species. Mean egg-laying dates for first clutches differed significantly between species (House Sparrow: 16.95 days [after the first egg laid by either species] ± 9.83 , $n = 40$; Tree Sparrow: 10.22 ± 7.1 days, $n = 32$; $t = 3.19$, $df = 70$, $P < 0.001$).

The clutch size was larger in House ($\bar{x} = 4.89 \pm 1.06$) than in Tree sparrows (4.69 ± 0.82), but the difference between means was not significant ($t = 1.19$, $df = 131$, $P > 0.05$). The lack of significance was possibly due to small sample size because the addition of the clutches laid in 1987 produced a significant difference between species (House Sparrow: $\bar{x} = 4.90 \pm 1.05$; Tree Sparrow: $\bar{x} = 4.65 \pm 0.86$; $t = 1.97$, $df = 241$, $P < 0.05$). Clutch size varied seasonally in Tree Sparrows (ANOVA: $F = 2.87$, $df = 7, 51$, $P < 0.025$) but not in House Sparrows ($F = 1.39$, $df = 6, 66$, $P > 0.05$) (Fig. 1). In Tree Sparrows, clutch size increased significantly over the first five 10-day periods of the breeding season (Fig. 1; $r = 0.304$, $df = 48$, $P < 0.05$). A sharp decline followed ($r = -0.709$, $df = 18$, $P < 0.01$). I believe that clutch size was more closely tied to environmental factors in Tree Sparrows than in House Sparrows.

Egg size.—House Sparrow eggs averaged 2.95 ± 0.23 g and Tree Sparrow eggs averaged 2.05 ± 0.19 g. Because relative egg mass (percentage of adult mass), on an interspecific level, tends to decline as adult mass increases, I calculated the average egg mass for each clutch as the percentage of the value predicted by the equation: $E = a \cdot W^{0.67}$, where E is egg mass, W is body mass, and a is a constant for each order or family (Rahn et al. 1975). The difference between species was highly significant (House Sparrow: 91.47% of expected egg mass ± 6.21 , $n = 74$; Tree Sparrow: $78.99 \pm 6.02\%$, $n = 56$; $t = 8.62$, $P < 0.001$). Variance and correlation analyses failed to show any significant seasonal trend in egg mass in either species. Similar results were obtained when all clutches were pooled and when clutches of 5 and 6 eggs were analyzed separately. The same type of analyses did not reveal significant variations in egg mass with

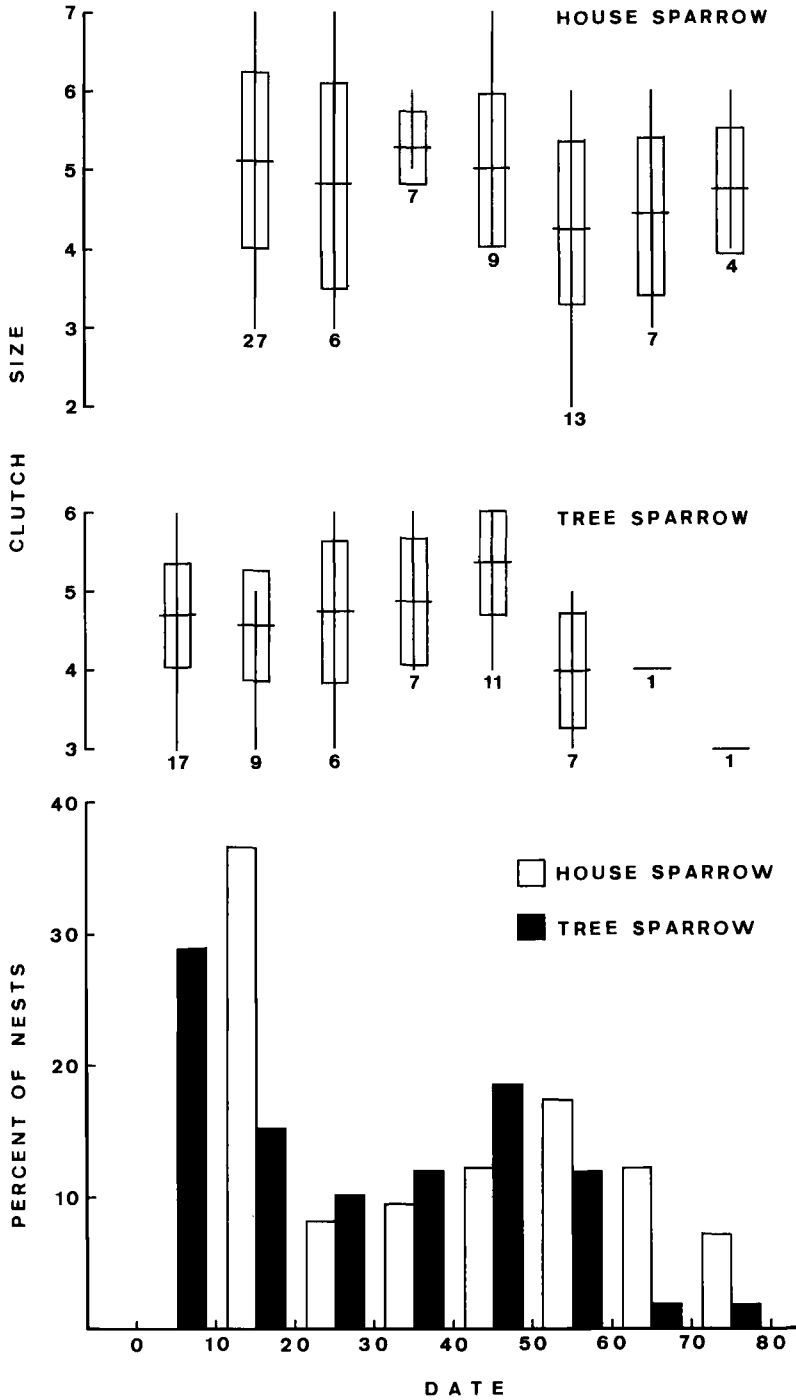


Fig. 1. Pattern of seasonal variation in pooled clutch size for 1985 and 1986. Clutch initiation dates and clutch sizes are grouped in 10-day periods. Horizontal lines indicate the mean, vertical lines the range, and boxes one standard deviation on either side of the mean. Sample sizes (nests) are below the boxes. The abscissa gives days elapsed from the date of the earliest clutch of the year laid by either species.

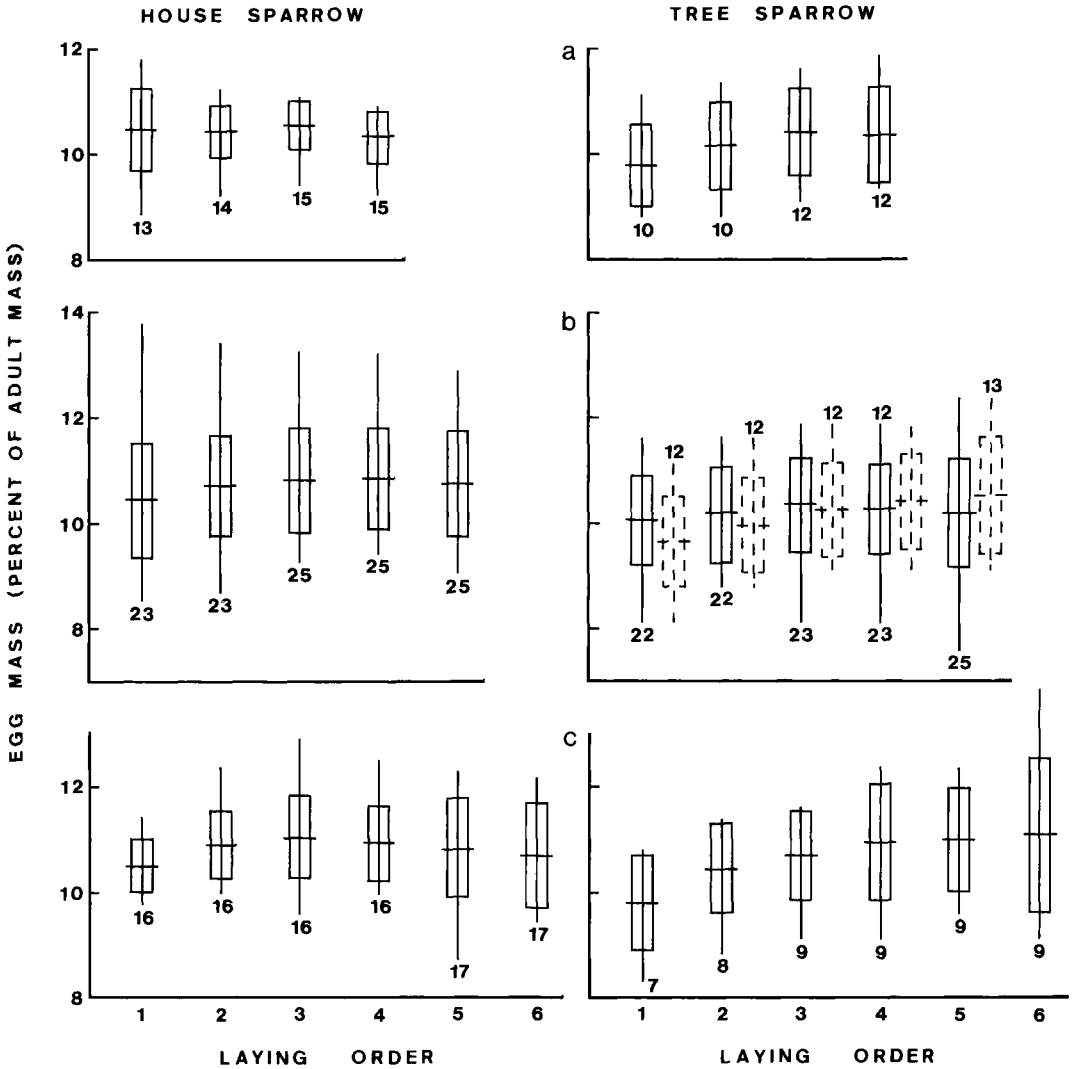


Fig. 2. Egg mass vs. laying sequence in 4-egg (a), 5-egg (b), and 6-egg (c) clutches. Symbols as in Figure 1. Dashed lines in Tree Sparrow 5-egg clutches give egg mass tendency using 1985 data only.

clutch size in either species. Similarly, egg mass did not vary with the laying sequence in House Sparrows at any clutch size. However, Tree Sparrow egg mass was correlated positively with the laying order in clutches of 6 ($r = 0.334$, $df = 49$, $P < 0.02$; Fig. 2). Egg mass and laying order were significantly correlated in clutches of 5 in 1985 ($r = 0.303$, $df = 52$, $P < 0.05$), but not in 1986 ($r = -0.224$, $df = 59$, $P > 0.05$) nor when both years were pooled ($r = 0.037$, $df = 113$, $P > 0.05$). Eggs in clutches of 4 tended to increase in mass with laying sequence, but the correlation was not significant ($r = 0.236$, $df = 42$, $P > 0.05$). Trends for increased egg size with

laying sequence were probably disguised because interclutch variance in egg mass was much larger than intraclutch variance. I adjusted the mean egg mass of each egg by subtracting the mean egg mass for each clutch from the actual egg masses of that clutch. Mean egg mass for each clutch was thus standardized to zero (see Murphy 1983). This procedure increased the correlation coefficient to significant values in Tree Sparrow clutches of 4 eggs ($r = 0.364$, $df = 42$, $P < 0.05$). However, the results did not change qualitatively in other clutch sizes of Tree Sparrows or in any House Sparrow clutches.

Most of the variance in egg mass of both

TABLE 1. Hatching span (mean hours; range) in House and Tree sparrows. Number of clutches is in parentheses.

	Clutch size				
	3	4	5	6	7
House Sparrow	10.7; 0-20 (3)	15.5; 4-26 (5)	28.5; 11-54 (11)	19.7; 3-39 (16)	25.5; 24-27 (2)
Tree Sparrow	10.0; 0-20 (2)	11.6; 2-24 (7)	17.9; 3-38 (10)	14.5; 6-24 (4)	

species remained unexplained. Differences in body size or condition among females are possibly important because the variance of adult body mass and the interclutch variance of egg mass, once standardized, did not differ from each other in either of the two species (House Sparrow: $F = 1.04$, $df = 72$, 273 , $P > 0.05$; Tree Sparrow: $F = 1.06$, $df = 57$, 76 , $P > 0.05$).

Incubation length and hatching span.—Incubation length is expected to decrease as egg mass declines (Rahn and Ar 1974), and I calculated the time elapsed from laying to hatching of the last egg in a clutch as the percentage of the value predicted by the equation proposed by Rahn and Ar. The difference between House Sparrows ($77.73 \pm 6.21\%$, $n = 37$) and Tree Sparrows ($84.59 \pm 6.16\%$, $n = 23$) was significant ($t = 2.64$, $P < 0.025$).

Hatching span was greater in House than in Tree sparrows (Mann-Whitney U -test, $z = 2.3$, $n_1 = 23$, $n_2 = 37$, $P < 0.025$). The differences among Tree Sparrow clutch sizes were not significant (Kruskal-Wallis test, $H = 2.47$, $df = 3$, $P > 0.05$; Table 1), although they did approach significance for House Sparrows (Kruskal-Wallis test, $H = 8.17$, $df = 4$, $P < 0.1$). Furthermore, the pool of House Sparrow clutches of 5, 6, and 7 eggs took longer to hatch than the pool of clutches of 3 and 4 (Mann-Whitney U -test, $z = 1.97$, $n_1 = 8$, $n_2 = 29$, $P < 0.05$).

Hatching size.—Hatching size was studied by

separating the individuals into those that hatched during a nest watch and those that hatched in the interval between consecutive nest watches. In both species body mass and tarsus length were both significantly larger in nestlings that hatched between watches compared with those hatched during a watch (Table 2). This indicates that nestlings were fed very soon after hatching.

In both species, about 80% of the variance in body mass of freshly hatched nestlings was due to differences in egg mass (House Sparrow: $r^2 = 0.841$, $df = 30$, $P < 0.001$; Tree Sparrow: $r^2 = 0.859$, $df = 9$, $P < 0.001$). Egg mass accounted for less of the variance in tarsus length, but in both species the relationships were significant (House Sparrow: $r^2 = 0.170$, $df = 30$, $P < 0.02$; Tree Sparrow: $r^2 = 0.719$, $df = 8$, $P < 0.01$). The relative body mass was larger in House Sparrows than in Tree Sparrows for the two groups of nestlings, but tarsus length did not differ between species in either case (Table 2).

Because the eggs of both species tended to hatch in the same sequence in which they were laid (House Sparrow: $r = 0.999$, $df = 166$, $P < 0.001$; Tree Sparrow: $r = 0.999$, $df = 85$, $P < 0.001$), it follows that hatchling size would increase with laying sequence in Tree Sparrows because the egg mass increased with laying sequence.

Growth, fledging size, and nestling period.—The

TABLE 2. Body mass and tarsus length, expressed as percentage ($\bar{x} \pm SD$) of adult size, of nestlings hatched during a nest watch and between consecutive nest watches. Sample sizes are in parentheses. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$; NS = not significant.

	Body mass			Tarsus length		
	Hatched during nest watch	Hatched between watches	t^a	Hatched during nest watch	Hatched between watches	t^a
House Sparrow	7.90 \pm 0.88 (32)	8.55 \pm 0.95 (192)	3.39***	30.33 \pm 1.57 (32)	30.96 \pm 1.40 (192)	2.52*
Tree Sparrow	7.03 \pm 0.82 (14)	7.59 \pm 0.93 (99)	2.08*	29.80 \pm 1.72 (13)	30.94 \pm 1.59 (99)	2.35*
	3.03**	7.78***		0.91 NS	0.35 NS	

^a t -test comparing time periods.

^b t -test comparing species.

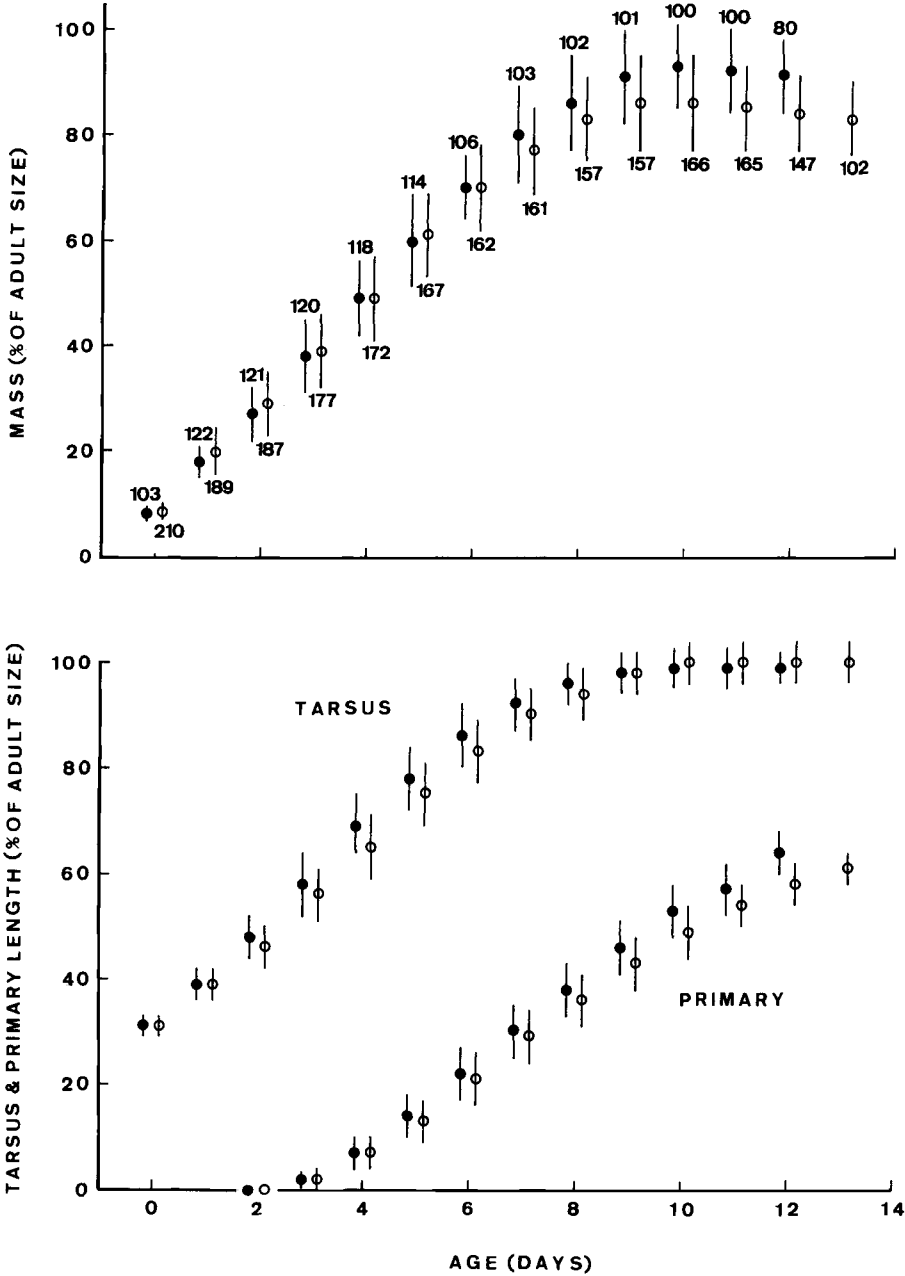


Fig. 3. Upper: nestling mass gain. Lower: growth of tarsus (above) and outermost primary (below). ○ House Sparrow; ● Tree Sparrow. Vertical lines show ±1 SD. Sample sizes are the number of nestlings measured, though average brood values have been used to test differences between species.

rates of increase of body mass, tarsus length, and outermost primary length were higher in Tree than in House sparrows (Fig. 3), although the differences were significant only for the outer primary (body mass: $t = 1.89$, $df = 69$, P

< 0.1 ; tarsus length: $t = 0.89$, $df = 69$, $P > 0.05$; and outermost primary length: $t = 7.00$, $df = 70$, $P < 0.001$). Likewise, Tree Sparrow fledging body mass was greater than in House Sparrows although fledging tarsus length and fledging

TABLE 3. Fledging measurements as percentage ($\bar{x} \pm SD$) of adult size. Number of broods is in parentheses; *** = $P < 0.001$; NS = not significant.

	Mass	Tarsus length	Primary length
House Sparrow	81.8 \pm 6.34 (41)	100.2 \pm 2.96 (41)	58.4 \pm 3.70 (40)
Tree Sparrow	89.0 \pm 7.29 (30)	99.5 \pm 2.51 (30)	59.8 \pm 3.13 (30)
<i>t</i>	4.30***	1.10 NS	0.90 NS

primary length did not differ (Table 3). Fat level was also higher in Tree Sparrows (2.43 ± 0.24 vs. 1.90 ± 0.31 ; $t = 7.49$, $df = 69$, $P < 0.001$).

Neither variance nor correlation analyses for growth rates and fledging sizes among broods of different sizes gave significant trends in either species (Table 4). However, the pool of Tree Sparrow clutches of 5 and 6 eggs averaged larger than the pool of clutches of 3 and 4 eggs for tarsus growth ($t = 2.08$, $df = 23$, $P < 0.05$), primary growth ($t = 2.56$, $df = 24$, $P < 0.025$), and fledging mass ($t = 2.08$, $df = 24$, $P < 0.05$). Growth and fledging size variables in Tree Sparrows were not clearly influenced by hatching order because neither variance nor correlation analyses showed significant trends. This influence was also minimal in House Sparrows; nevertheless, a significant decline in daily body mass gain with hatching order was recorded in 6-egg clutches in House Sparrows ($r = -0.378$, $df = 52$, $P < 0.01$).

Nestling mortality and productivity.—Throughout different stages of the breeding cycle, mortality rates did not differ significantly between the species (Table 5). Both species had high rates of egg loss, most of which (ca. 75%) occurred in nests with total failure. The different mortality factors affected both species equally (Table 6). The relationship between the number of nest-

lings that died in nests with total failure and those that died in nests with partial failure did not differ ($\chi^2 = 0.56$, $df = 1$, $P > 0.05$). Likewise, the proportion of starved nestlings in nests affected by brood reduction did not differ between species ($\chi^2 = 0.77$, $df = 1$, $P > 0.05$). The number of fledged young per successful nest and per breeding attempt was slightly but not significantly larger in House than in Tree sparrows (Table 5).

Mortality was dependent on hatching order in both species (Fig. 4). For all brood sizes together, the proportion of the last hatched sibling that fledged was significantly lower than that of all other nestlings ($\chi^2 = 15.8$ for House Sparrows and $\chi^2 = 13.03$ for Tree Sparrows, $df = 1$, $P < 0.001$). On the other hand, the proportion of the penultimate hatched siblings that fledged did not differ from those hatched earlier ($\chi^2 = 1.49$ for House Sparrows and $\chi^2 = 0.09$ for Tree Sparrows, $df = 1$, $P > 0.05$), indicating that only the last hatched siblings had a reduced chance of survival. Brood reduction due to selective starvation occurred in 22 of 26 cases during the 5 days after the hatching of the first sibling. In neither species was this brood reduction conditioned by the number of siblings. Occurrence of brood reduction was independent of whether brood size was above or below

TABLE 4. Growth rates and fledging measurements ($\bar{x} \pm SD$) for each brood size. Number of broods is in parentheses.

Brood size	Growth rates			Fledging measurements		
	Daily mass gain (g/day)	Tarsus (mm/day)	Primary (mm/day)	Mass (g)	Tarsus length (mm)	Primary length (mm)
House Sparrow						
3	2.67 \pm 0.20 (7)	1.58 \pm 0.07 (7)	3.83 \pm 0.15 (7)	22.9 \pm 1.75 (7)	19.1 \pm 0.60 (7)	33.7 \pm 2.18 (7)
4	2.64 \pm 0.22 (9)	1.54 \pm 0.09 (9)	3.78 \pm 0.22 (9)	23.2 \pm 0.80 (9)	19.3 \pm 0.37 (9)	34.1 \pm 1.19 (9)
5	2.61 \pm 0.26 (13)	1.58 \pm 0.08 (13)	3.65 \pm 0.32 (13)	22.2 \pm 2.29 (12)	19.1 \pm 0.67 (12)	33.5 \pm 2.12 (11)
6	2.60 \pm 0.22 (10)	1.59 \pm 0.10 (10)	3.73 \pm 0.12 (10)	22.5 \pm 1.55 (10)	19.5 \pm 0.40 (10)	33.5 \pm 2.81 (10)
7	2.45 \pm 0.03 (2)	1.60 \pm 0.00 (2)	3.71 \pm 0.08 (2)	22.0 \pm 0.60 (2)	19.1 \pm 0.08 (2)	33.9 \pm 0.94 (2)
Tree Sparrow						
3	1.97 \pm 0.24 (6)	1.41 \pm 0.10 (6)	3.59 \pm 0.19 (6)	17.5 \pm 1.55 (5)	16.9 \pm 0.59 (5)	30.1 \pm 0.84 (5)
4	1.89 \pm 0.24 (6)	1.39 \pm 0.07 (6)	3.54 \pm 0.19 (8)	17.0 \pm 1.36 (8)	17.1 \pm 0.28 (8)	29.7 \pm 1.45 (8)
5	2.05 \pm 0.18 (10)	1.47 \pm 0.07 (10)	3.75 \pm 0.20 (10)	18.5 \pm 1.22 (11)	17.2 \pm 0.36 (11)	30.7 \pm 1.76 (11)
6	1.94 \pm 0.18 (3)	1.49 \pm 0.13 (3)	3.85 \pm 0.10 (2)	17.4 \pm 0.61 (2)	17.3 \pm 0.30 (2)	29.6 \pm 0.50 (2)

TABLE 5. Survival and productivity in House and Tree sparrows. Successful attempts are those producing at least one fledging.

	House Sparrow	Tree Sparrow	
Survival			
Eggs laid/hatched (%)	355/253 (71.3)	281/170 (60.5)	$\chi^2 = 1.50$ NS
Eggs hatched/young fledged (%)	253/175 (69.2)	170/125 (73.5)	$\chi^2 = 0.10$ NS
Eggs laid/young fledged (%)	355/175 (49.3)	281/125 (44.5)	$\chi^2 = 0.43$ NS
Productivity ($\bar{x} \pm$ SD [n])			
No. fledgings/attempt	2.36 \pm 2.32 (74)	2.08 \pm 2.10 (60)	$t = 0.72$ NS
No. fledgings/successful attempt	4.17 \pm 1.40 (42)	3.79 \pm 1.25 (33)	$t = 1.21$ NS

average ($\chi^2 = 0.25$ in House Sparrows, and $\chi^2 = 0.22$ in Tree Sparrows, $df = 1$, $P > 0.05$).

Tree Sparrow nestling mortality was dependent on egg mass. Nestlings that died of starvation hatched from eggs with an average mass significantly lower than that of nestlings that survived to fledge (1.89 ± 0.169 g, $n = 14$, vs. 2.01 ± 0.165 g, $n = 104$; $t = 2.53$, $P < 0.02$). This difference did not occur in House Sparrows (2.94 ± 0.191 g, $n = 30$, vs. 2.94 ± 0.185 g, $n = 170$).

Postfledging body mass and food.—Some banded young were captured after fledging. The time elapsed between fledging and capture was the same in House Sparrows: (22.05 ± 14.82 days, $n = 21$), and Tree Sparrows: (28.12 ± 16.57 days, $n = 17$; $t = 1.16$, $P > 0.05$). The daily increase in body mass, expressed as a percentage of adult body mass, was significantly higher in House Sparrows ($0.53 \pm 0.533\%$) than Tree Sparrows ($0.009 \pm 0.393\%$; $t = 3.26$, $P < 0.01$). The difference between the species in adult size-adjusted postfledging body mass of the young captured in June was not significant ($t = 0.13$, $df = 118$, $P > 0.05$; Fig. 5). Throughout July and August, the body mass of young House Sparrows, which reached adult body mass in August, was greater than the body mass of young Tree Sparrows ($t = 2.94$, $df = 524$, $P < 0.01$, and

$t = 3.21$, $df = 201$, $P < 0.01$, for the 2 months, respectively). During September and October, young Tree Sparrows reached adult body mass, and the differences between the species ended ($t = 1.28$, $df = 86$, $P > 0.05$).

I examined crops externally and classified contents into four types (Table 7). Young House Sparrows used abundant, spatially stable human feeding sources. Young Tree Sparrows fed mainly on small *Dactylis glomerata* seeds, a species with a relatively uniform distribution throughout the region. Throughout June and October, I caught 1,293 House and 211 Tree sparrows. The degree of fullness of their crops (on a scale of 0–3) was markedly higher in House than in Tree sparrows (Kolmogorov-Smirnov test, $D = 0.29$, $n_1 = 211$, $n_2 = 1,293$, $P < 0.001$).

DISCUSSION

Clutch size, egg mass, and seasonal constraints.—The differences in clutch size, egg mass, and timing of breeding are largely determined by energetic limitations that affect Tree more than House sparrows (Table 8). Lack (1966) contended that the seasonal variation of clutch size represents an adjustment to prevailing conditions during the brood-rearing period in order to

TABLE 6. Causes of nestling loss in House and Tree sparrows. Values are the number followed by percentage in parentheses.

	House Sparrow		Tree Sparrow	
	Nests	Nestlings	Nests	Nestlings
Whole brood starvation	4 (7.3)	12 (4.7)	3 (7.0)	10 (5.9)
Partial brood starvation	12 (21.8)	18 (7.1)	8 (18.6)	8 (4.7)
Whole brood predation	9 (16.4)	42 (16.6)	6 (13.9)	26 (15.3)
Partial brood predation*	2 (3.6)	4 (1.6)	1 (2.3)	1 (0.6)
Unexplained	2 (3.6)	2 (0.8)	1 (2.3)	1 (0.6)
Total sample size	55	253	43	170

* Intraspecific infanticide.

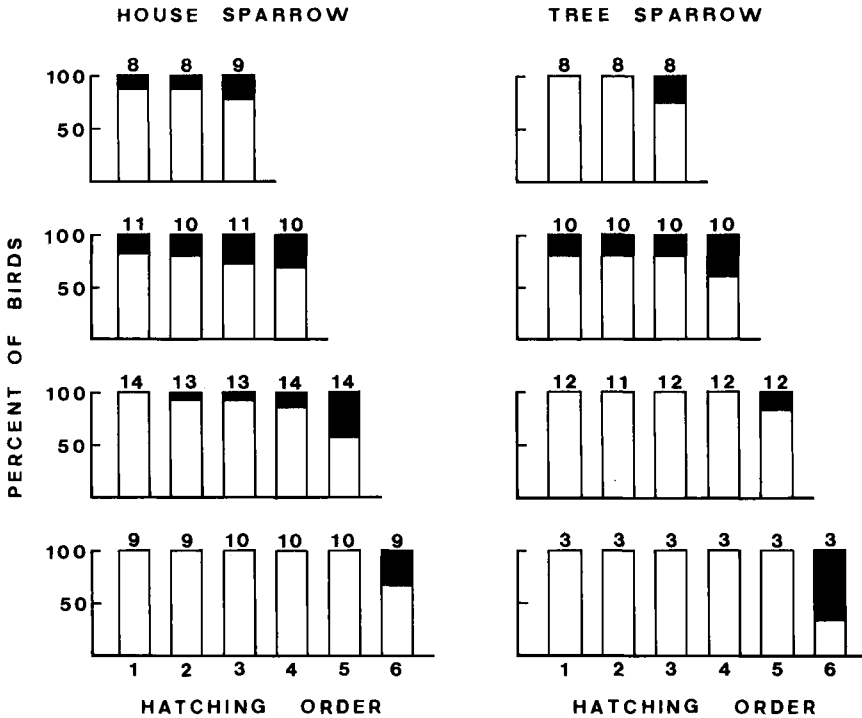


Fig. 4. Fledging and dying frequencies vs. hatching sequence for different brood sizes. I excluded entire broods and individual nestlings whose death was not due to starvation. Unfilled portion of the bars gives the proportion of fledged birds; filled portion gives that of the dead birds. Numbers refer to individual nestlings.

maximize the number of surviving offspring. Reports for several species hold that postfledging survival prospects are dependent on nestling characters, especially fledging mass (e.g. Perrins 1965, Murphy 1978, Garnett 1981, Hedgren 1981, Nur 1984; but see Ross and McClaren 1981, Harris and Rothery 1985). I found that a relatively larger fledging mass is adequate to offset higher risks of starvation (see below). Tree Sparrow broods of 3 and 4 nestlings, generally hatched from clutches laid either early or late in the breeding season, grew slower, and fledged with lower body mass than those of larger mid-season clutches. This implies that most of the seasonal variation of Tree Sparrow clutch size does not maximize offspring survival. Provided that productivity and starvation rates were similar between species, the interspecific contrast in clutch size tendencies cannot be explained by constraints related to the rearing of the offspring.

A possible explanation of the differences between species in clutch size and seasonal vari-

ation is that Tree Sparrow egg production is constrained by proximate factors. This has been observed in several species, including House Sparrows (Murphy 1978, Ankney and MacInnes 1978, Hogstedt 1981, Newton and Marquiss 1981, Winkler 1985, Askenmo and Unger 1986). Nevertheless, House Sparrow egg formation requires only 26–42% of the energy delivered when feeding the young (Krementz and Ankney 1986). Clutch size in House Sparrows is not determined by a shortage of energy during egg production (Krementz and Ankney 1986). Though this could also hold for Tree Sparrows, the food availability during egg formation is possibly much lower than when feeding the young, especially in early spring when environmental conditions rapidly change. Consequently, the comparison of energetic constraints in either of the two periods by calculating only caloric requirements is questionable.

In many birds larger eggs produce larger hatchlings, greater survival expectancies, or both

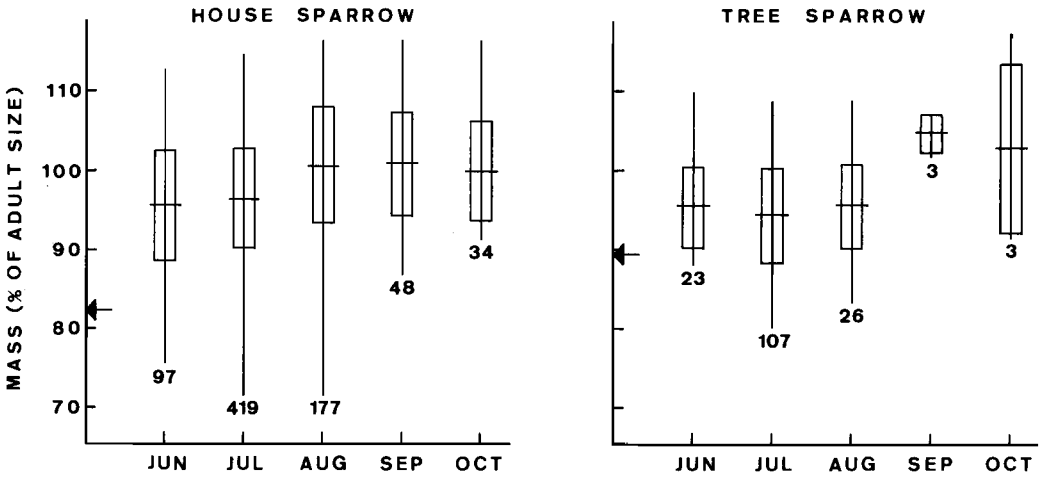


Fig. 5. Pattern of seasonal variation in postfledging mass. Masses are grouped into monthly periods. Symbols as in Figure 1. Arrows show the average fledging value.

(Davis 1975; Parsons 1975; Howe 1976, 1978; Nisbet 1978; Noordwijk et al. 1981; Bancroft 1984; Järvinen and Ylimaunu 1984; Richter 1984). I found that egg mass largely determined hatchling size, but that egg-size dependent mortality occurred only in Tree Sparrows, which laid smaller eggs. If egg size-dependent survival selects for larger eggs, the smaller average egg size indicates that Tree Sparrows suffer greater energy limitations during egg formation. Additionally, a longer Tree Sparrow incubation period possibly reflects a longer time spent by the females out of the nest during incubation because of poorer body conditions after laying.

Earlier Tree Sparrow egg laying might well be a way to counteract House Sparrow dominance. Although some House Sparrow pairs defended nests long before egg laying, others settled after the main peak of Tree Sparrow laying. An early start in breeding requires better environmental feeding conditions (Yom-Tov 1974, Högstedt 1981, Newton and Marquiss 1981, Davies and Lundberg 1985). Hence, laying smaller

eggs may be advantageous to Tree Sparrows because of reduced energetic requirements to produce the clutch. This would allow earlier laying. It is possible that low egg mass is a response to chronic energy stress derived from disadvantageous competition. The relatively constant egg size as the season progresses in spite of changes in environmental conditions better supports this hypothesis, which implicates fixed evolutionary differences between species. The alternative hypothesis proposes a proximate limitation of egg size (Murton et al. 1974, Nisbet 1978, Järvinen and Väisänen 1983, Wiklund 1985, Winkler 1985, Murphy 1986).

I cannot expand this to other geographical areas where these species coexist. My results do not parallel those of Seel (1968a, b, 1970) in a comparative study of House and Tree sparrows in Britain. Contrary to conditions in Spain, clutch size and reproductive success were lower in House than in Tree sparrows. Seel suggests that environmental conditions were relatively adverse for House Sparrows, and he contends that Tree Sparrows were not limited by nesting

TABLE 7. Food of House and Tree sparrows in the postfledging period. Values are percentage of crops that contained food type indicated in the column heading.

	Human sources*	Indigenous seeds	Insects	Fruits	Total crops with food
House Sparrow	72.9	21.6	20.0	4.9	384
Tree Sparrow	12.5	87.5	16.7	0	24

* Bread and cereal seeds fed to cattle.

TABLE 8. A summary of life history traits of House and Tree sparrows breeding in central Spain. All values are means.

Trait	House Sparrow	Tree Sparrow	Comments
Timing (days) of breeding ^a (first clutches)	16.9	10.22	Difference also significant for first and second clutches.
Clutch size	4.89	4.68	Difference significant adding data from 1987.
Egg mass (%) ^b	91.47	78.99	Mass increased with laying sequence in Tree Sparrows. Egg mass closely determined hatching mass in both species.
Incubation (%) ^c	77.73	84.59	
Hatching span (h)	21.3	14.7	
Hatching mass (%) ^d	7.90	7.03	Difference not significant for tarsus length.
Nestling growth		Faster than in House Sparrows	Differences significant only for primary length.
Postfledging mass increase	Faster than in Tree Sparrows		
Fledging mass (%) ^d	81.8	89.0	Difference apparently determined by larger fat accumulation in Tree Sparrow nestlings, and possibly related to more favorable feeding conditions for fledged House Sparrows.

^a Values are days elapsed from date of the earliest clutch laid by either species.

^b Values are percentages of the values predicted by Rahn et al. (1975).

^c Values are percentage of values generated by Rahn and Ar (1974) equation.

^d Values are percentages of adult mass.

sites as indicated by late occupation of nest boxes. If reproductive success and population size of House Sparrows was lower in areas other than my study area, then interspecific competition, which I claim is a major determinant of differences between the two sparrows in several reproductive traits, becomes relaxed or does not exist.

Hatching asynchrony and hatching provisioning.—A number of hypotheses have been advanced to explain asynchronous hatching (see introduction). Empirical and theoretical approaches tend to favor the brood-reduction hypothesis (Howe 1976, 1978; Hahn 1981; Richter 1982, 1984; Shaw 1985; Wiklund 1985; Husby 1986; but see Slagsvold 1986; Skagen 1987, 1988; Amundsen and Stokland 1988). According to this hypothesis, siblings are expected to starve in succession. However, I showed that in both species only the last hatched sibling was subjected to differential mortality though frequently the entire brood died of starvation. I surmise that asynchronous hatching was only partially capable of inducing brood reduction.

A number of species that exhibit hatching asynchrony also show a pattern of increasing egg size with laying sequence (Howe 1976, 1978;

Clark and Wilson 1981; Murphy 1983; Slagsvold et al. 1984; Haftorn 1986) as I found in Tree Sparrows. This has been interpreted as a mechanism to minimize sibling size asymmetries and promote the survival of the entire brood. Advocates of the brood survival hypothesis claim that hatching asynchrony is not an adaptation to induce brood reduction (Slagsvold et al. 1984). My comparison between species indicates that egg mass increased with laying sequence only in Tree Sparrows, which also lay smaller eggs and rear young with egg-size dependent survival. Perhaps this trend evolved in this species only as a result of the greater handicap the last hatched sibling suffers. Consequently, my results are more in accordance with the brood-survival hypothesis than with the brood-reduction hypothesis, although they do not explain unequivocally the adaptive basis of hatching asynchrony.

Hussell (1972), and Clark and Wilson (1981), tried to explain hatching asynchrony based on selective pressures to minimize nest failure due to predation. A corollary of this hypothesis is that the younger sibling undergo a competitive disadvantage which is an unavoidable cost of attempts to reduce exposure time in the nest.

My data do not allow testing this nest-failure hypothesis directly. Nevertheless, the fact that the hatching period is shorter and invariable with clutch size in Tree Sparrows, which invest less in their hatchlings, suggests that the risk of losing handicapped siblings limits the hatching period. Consequently, the stage of the laying period at which incubation begins (i.e. the determinant of the hatching asynchrony) would not depend on predation risks, contrary to the prediction of the nest-failure hypothesis.

Fledging size and postfledging food conditions.—Tree Sparrows invest less in their hatchlings than House Sparrows, and nestling Tree Sparrows fledged at a relatively greater body mass and with larger fat stores than nestling House Sparrows. The diet and rate of food ingestion suggest that Tree Sparrows suffer more adverse feeding conditions after fledging. The rapid postfledging body mass gain in House Sparrows may allow them to compensate quickly for the advantage of Tree Sparrow fledging body mass and thus reach adult size earlier. Perhaps the higher postfledging mass gain in House Sparrows depends upon a relatively recent association with civilized humans. Morphological differentiation of this species in North America in the last 100 yr has demonstrated its potential for rapid evolution (W. Richter pers. comm.). Tree Sparrow nestling fat accumulation may offset higher risks of postfledging starvation. My results imply that nestlings with higher body mass have higher survival prospects after fledging.

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