

BREEDING ECOLOGY OF HOUSE SPARROWS: SPATIAL VARIATION

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Studies of the introduced House Sparrow (*Passer domesticus*) have provided unique insight into the nature and rate of phenotypic change of an avian species in novel environments. Several investigators (e.g. Calhoun 1947, Johnston and Selander 1973a, b) have documented rapid geographic differentiation in body size since the species was first introduced to North America a little over a century ago. The geographic patterns in body size and dimensions, and those in plumage characters (Johnston and Selander 1964), agree with Bergmann's, Allen's and Gloger's ecogeographic rules, respectively. Geographic trends in thermal tolerances (Hudson and Kimzey 1966), lipid deposition (Blem 1973), insulation and metabolism (Blem 1974, Kendeigh and Blem 1974, Kendeigh 1976) have been documented also.

Anderson (1973:44) noted that clutch size of House Sparrows is positively correlated with latitude in North America. Studies of breeding ecology at several localities in North America (Weaver 1939, 1942, 1943, North 1968, 1973a, Will 1969, 1973, Anderson 1973, Mitchell et al. 1973, Sappington 1975, present study) allow documentation of geographic differentiation in breeding phenology and reproductive output. In this paper, differences between two localities, Calgary, Alberta and Lawrence, Kansas, will be examined in detail.

North American House Sparrows "have descended almost exclusively from English inocula" (Johnston and Selander 1973a:383, also see Barrows 1889, Summers-Smith 1963). Studies of breeding ecology in England (Summers-Smith 1963, Seel 1968a, b, 1970, Dawson 1972) together with those in North America permit comparison of reproductive ecology of ancestral and descendent populations.

Several studies in temperate regions (e.g. Nice 1937, Kendeigh 1963) have suggested that both photoperiod and temperature are proximate factors which cue or control breeding phenology. In contrast, Jones and Ward (1976:573) suggested that breeding of the Red-billed Quelea (*Quelea quelea*) is controlled simply by body condition of adults and that no environmental cues are necessary to trigger breeding at the appropriate time of year. I will evaluate the role of photoperiod and temperature in timing the initiation of House Sparrow breeding seasons.

Numerous factors have been implicated in variation in reproductive ecology, particularly clutch size, of birds (e.g. reviews by Klomp 1970, Cody 1971). Studies of House Sparrow reproduction have revealed significant micro-geographic variation. Reproduction begins earlier if the nest is inside, rather than outside, a building (Will 1969). Reproductive output is inversely related to distance between the nest and feeding sites (Dawson 1972). I have separated variation between localities into study site and nest site effects, gaining insight into the contribution of micro-habitat effects to overall variation in reproductive ecology.

STUDY AREAS AND METHODS

The study sites were nine farms located about 8 km NE of Lawrence, Kansas, and six farms, a granary complex and a rural residence near Conrich, Alberta, 5 km E of Calgary (Fig. 1). Study sites are coded with a letter corresponding to the first letter of the locality and a number corresponding to the site numbers of Figure 1. Thus C2 denotes site 2 in Calgary.

Cattle were raised on all of the farms. Principal crops on the Calgary farms were oats (*Avena sativa*) and barley (*Hordeum* spp.), while those at Lawrence were corn (*Zea mays*), wheat (*Triticum* spp.), soybeans (*Glycine soja*), and milo (*Sorghum vulgare*). Feed grain was stored at or near all study sites, and generally several thousand bushels of seed were stored at each Calgary site.

CLIMATIC FACTORS

I did not record climatological data on the study sites themselves. The Calgary International Airport, 10 km W of Conrich reports detailed weather summaries. In the Lawrence area two stations record maximum and minimum temperatures. I used records maintained by H. Fitch at the University of Kansas Natural History Reservation, 2 km W of site L2, in analyses requiring daily summaries. Monthly summaries tabulated by the U.S. Environmental Data Service for the weather station on the main campus, about 15 km SW of the study sites, were used for geographic and year comparisons. Temperatures there average about 3°C higher than those at the Natural History Reservation (Rose 1974:10). I obtained daily photoperiod estimates for both localities from tables published by the Nautical Almanac Office (1945).

FIELD ROUTINES

In the 1974-1975 winter, I placed 10-30 nest boxes of the "bluebird" design (McElroy 1961:104) at each study site. The number at each site and the number of sites depended on the availability of suitable places for the boxes; a total of 150 boxes were put up at each geographic locality. Boxes were

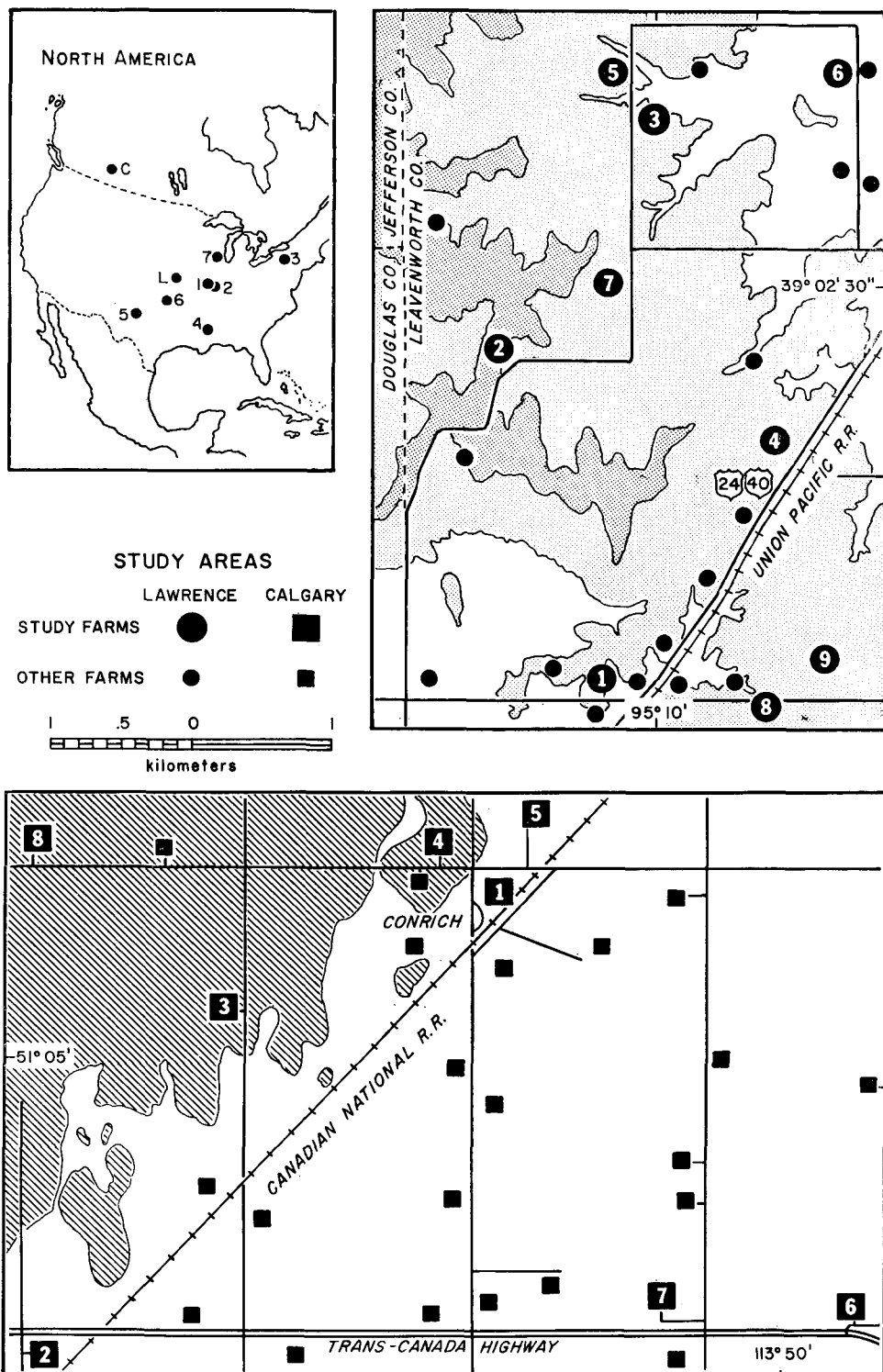


FIGURE 1. Breeding ecology of House Sparrows: Study areas. Upper left: North American study localities. L—Lawrence KS and C—Calgary AB (present study), 1—Portage des Sioux IL (Anderson 1973), 2—McLeansboro IL (Will 1969, 1973), 3—Ithaca NY (Weaver 1939, 1942, 1943), 4—Mississippi State MS (Sappington 1975), 5—Hale Co. TX (Mitchell et al. 1973), 6—Stillwater OK (North 1968), 7—Whitewater WI (North 1973). Upper right: Lawrence study area. Heavy stippling—1050–1080 ft, light stippling—900–1050 ft, unshaded—850–900 ft above mean sea level. Bottom: Calgary study area. Shaded—3500–3550 ft, unshaded—3425–3500 ft above mean sea level. Study sites at both localities are numbered (see text).

placed on east- and south-facing outside walls of farm buildings, on fences, or on crossbeams and rafters inside buildings. Height above the ground ranged from 2 to 8 m. P. E. Lowther and I collected breeding data in both 1975 and 1976 at seven Calgary sites and six Lawrence sites. One Calgary site and two Lawrence sites were studied one season only. I have omitted two sites, L1 and L6, from the analyses because few House Sparrows bred there (see Murphy 1977).

At Lawrence, Lowther and I began examining nest boxes in late winter, returning at several day intervals until the first egg of the season was found. Nests were checked every third or fourth day throughout the breeding season. I arrived in Calgary in late April in both years, shortly after the breeding season had begun there. Dates of clutch initiation for already active nests were estimated from knowledge of clutch size, average incubation period and weight of nestlings. I did not estimate initiation dates of clutches which were complete when first found but failed to hatch at least one egg. Field routines in Calgary were similar to those in Lawrence.

We marked eggs individually and at first finding we weighed them to the nearest 0.05 g with a 5 g Pesola scale. Nestlings were counted and then weighed to the nearest 0.25 g with a 50 g Pesola scale on each visit. Using vernier calipers we measured length of the longest remex, once in sheath, to the nearest 0.1 mm. Nestlings four days or older successfully retained a numbered U.S. Fish and Wildlife Service aluminum leg band. Early banding permitted individual identification on later visits. We placed two plastic, colored, leg bands on each nestling when last handling it in the nest. After the nestlings were older than 12 days they were no longer handled. This prevented premature fledging due to our disturbance. Nests with young about to fledge could be examined, and nestling counts continued until the brood had left the nest. Frequently we partially cleaned out nest boxes after completion of a nesting attempt to insure continued use by the same nesting pair.

DATA ANALYSIS

Parents often removed unhatched eggs and/or dead nestlings from the nest before our first examination of the nest after hatching. Consequently, I did not know hatching status of missing individuals and made two estimates of the number of eggs hatching from each clutch. The first (HMAX) assumes that all missing individuals hatched, and the second (HMIN) assumes that no missing individuals successfully hatched. Both show similar trends and only HMIN will be used in the analyses.

Because we did not check nests every day, it was necessary to estimate age of nestlings when first found, so that the 10th day or fledgling weight and wing length (see Dawson 1972) could be estimated. The procedure is outlined in detail elsewhere (Murphy 1977:6-7). No wing lengths were measured at Lawrence in 1975, consequently annual replication of Lawrence data for fledgling wing length is lacking.

BMDP2D (Dixon 1975) computes skewness and kurtosis and associated *t* values (also see Sokal and Rohlf 1969), as well as other basic statistics, permitting evaluation of the null hypothesis that a variable is normally distributed. As the distributions of several variables—numbers of eggs, numbers hatching, and numbers fledging per season and aver-

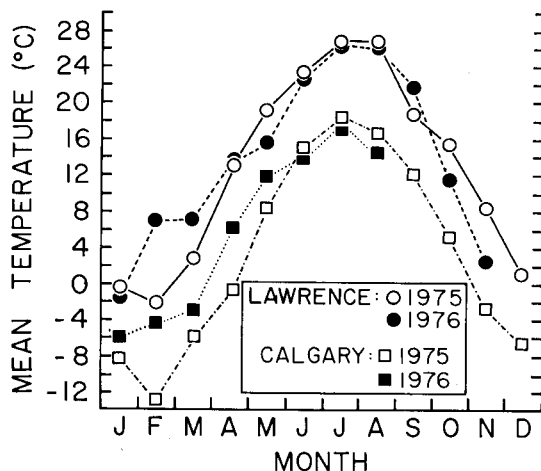


FIGURE 2. Monthly temperatures in Lawrence and Calgary during the study period.

age egg weight per clutch—did not deviate significantly from normality in any of the four locality-year samples, I used analyses of variance (ANOVA) for these variables. I grouped data by site, year, nest box, and, if applicable, by clutch attempt. Year and locality were considered fixed effects; farm, box and clutch attempt, being nested factors, were random effects. ANOVA computations were made using BMDP2V (Dixon 1975), except for significance testing which followed the procedure outlined by Winer (1956:190), and Sokal and Rohlf's (1969:712-715) ANOVA program for hierarchical designs and unequal sample sizes.

The distributions of all other variables deviated significantly from normality. As samples were large but the number of distinct values small for most such variables, I generally applied either the χ^2 test for differences in probabilities (Conover 1971:150-154) or the median test (Conover 1971:167-172) to the data, rather than the Kruskal-Wallis test, the non-parametric equivalent of ANOVA. The Kruskal-Wallis test was used only for testing of locality-year variation in temperature thresholds (see below). Locality-year comparisons of variables characterized by few distinct values, e.g. clutch size, were based on contingency tables. Each sample defined a column and each value of the variable a row. If the expected value for a cell was less than five, frequencies in that row were pooled with those of an adjacent row before calculation of the χ^2 test statistic. I used the median test to assess locality-year variation in breeding phenology and tenth day size, as well as variation among study sites for all variables except egg weight. Unless otherwise stated, all reported χ^2 values are median test statistics. The null hypothesis usually stated for the median test is that all samples have the same median (e.g. Conover 1971:168). Yet if a variable is characterized by few values and the median value is shared by a large number of cases (or is the modal value), e.g. clutch size in the present study, the appropriate null hypothesis is that all samples contain the same proportion of cases above the median.

I computed a product-moment correlation coefficient, pairing the 1975 and 1976 mean values for each farm (see Sokal and Rohlf 1969:130 on normality of distributions of means). A positive and sig-

nificant correlation would indicate that farms were stable from year to year relative to other sites in their suitability for breeding.

Kendeigh (1963:421) calculated temperature "thresholds" for clutch initiation. I calculated these for Lawrence and Calgary House Sparrows with two modifications of Kendeigh's procedures: (1) temperatures for the third day before the laying of the first egg of a clutch were used, and (2) clutches started after the median date of initiation of first clutches were eliminated from the analysis. I have assumed that such clutches are not limited by a temperature threshold. The sample thus corresponds to Seel's (1968a) "early nesting" sample.

I obtained data on reproduction from other North American studies (Weaver 1939, 1942, 1943, North 1968, 1973a, Will 1969, 1973, Anderson 1973, Mitchell et al. 1973, Sappington 1975) and regressed North American values on latitude for assessment of geographic trends. I also compared values found in the present study with those recorded in England (Summers-Smith 1963, Seel 1968a, b, 1970, Dawson 1972). If data on sample size and variance were reported, differences between ancestral and descendant populations were assessed using the *t*-test (e.g. Sokal and Rohlf 1969:220). If the frequency distribution was reported, I computed the more conservative median test statistic.

RESULTS AND DISCUSSION

BREEDING PHENOLOGY: ANNUAL AND BETWEEN-LOCALITY VARIATION

Figure 2 summarizes the annual temperature regimes during the study period. At both localities temperatures in late winter were below normal in 1975 and above normal in 1976. The exceptional warm trend did not continue in 1976 in Lawrence: late spring temperatures were below normal. Temperatures at other times in both years were close to normal at both localities.

Table 1 summarizes the events marking the beginning and end of the breeding season (lines 1-2 and 5-6, respectively) for both localities. The breeding season started earlier in 1976 than in 1975 at both localities (Calgary: $\chi^2 = 28.62$, $df = 1$, $P < 0.005$; Lawrence: $\chi^2 = 75.14$, $df = 1$, $P < 0.005$) and began sooner in Lawrence than in Calgary ($\chi^2 = 81.99$, $df = 1$, $P < 0.005$). The two-year means for the date the first egg of the season was laid were 9 April in Calgary and 23 March in Lawrence.

Several investigators (e.g. Farner 1964, Immelmann 1973) have documented the importance of photoperiod as a proximate cue for initiation of breeding by temperate bird species, but others (e.g. Jones and Ward 1976) have questioned its precise influence. Certainly photoperiod alone is not a sufficient Zeitgeber for initiation of breeding because variation between years is significant in both Calgary and Lawrence.

Nice (1937) and Kendeigh (1963) suggested that temperature may be superimposed on photoperiod to provide optimal entrainment to suitable breeding conditions. Alternatively, temperature may simply be correlated with suitability of conditions and consequent ability of adults to breed (see Jones and Ward 1976). Temperature "thresholds" (Kendeigh 1963:421) are shown in Table 1 (rows 3 and 4). At both localities the minimum temperature thresholds were lower in 1976 than in 1975 (Calgary: Mann-Whitney $U = 1790$, $n_1 = 81$, $n_2 = 65$, $P < 0.005$; Lawrence: $U = 1735$, $n_1 = 62$, $n_2 = 44$, $P < 0.01$). Only in Lawrence was the maximum temperature threshold significantly lower in 1976 (Lawrence: $U = 2233$, $n_1 = 62$, $n_2 = 44$, $P < 0.005$). Thus, in both localities House Sparrows began laying earlier and in cooler temperatures in 1976. Temperature at the time of egg formation likewise does not fully account for intralocality variation in the start of the breeding seasons. Pinowska (1975) found that females ate more insects during egg laying than at any other stage of the nesting cycle. Perhaps availability of insects is implicated in initiation of breeding.

The differences between Calgary and Lawrence in temperature thresholds (see Table 1, lines 3 and 4) are highly significant (maximum temperature: $U = 4994$, $n_1 = 146$, $n_2 = 106$, $P < 0.001$; minimum temperature: $U = 5239$, $n_1 = 146$, $n_2 = 106$, $P < 0.001$). House Sparrows begin breeding at cooler temperatures in Calgary than in Lawrence.

In both years nesting activities ceased about the same time within a locality (Table 1, lines 5 and 6), but significantly earlier in Lawrence than in Calgary ($\chi^2 = 21.950$, $df = 1$, $P < 0.005$). Work capacity of House Sparrows decreases at temperatures above 22°C (Kendeigh 1973: 33-36). In both years Lawrence experienced mid-summer droughts as well as typically high temperatures, and one or both of these factors apparently curtailed breeding. In contrast, in Calgary, few clutches were begun after temperatures started to decline in mid-summer. In both localities breeding ceased as the weather changed but was signalled by opposite temperature trends.

The duration of the breeding season (the period from the date when the first egg of the season is laid until the date when the first egg of the last clutch of the season is laid; Moreau 1950, Anderson 1973) averaged 135 days in Lawrence and 119 days in Calgary. The duration of the breeding season of the average nesting pair could likewise be defined as the mean initiation date of last

TABLE 1. Summary of nesting phenology of House Sparrows at Calgary, Alberta and Lawrence, Kansas.

	Calgary		Lawrence		Test statistic ¹
	1975	1976	1975	1976	
1. First egg of season	19 Apr	31 Mar	9 Apr	7 Mar	—
2. First clutch: median initiation date	15 May	1 May	28 Apr	5 Apr	109.586**
3. Min. temp. threshold (°C) ²	0.0 ± 3.1(65) ³	-0.2 ± 2.9(64)	8.3 ± 5.7(44)	3.0 ± 4.6(62)	35.967**
4. Max. temp. threshold (°C)	13.4 ± 4.3(65)	14.5 ± 5.3(64)	20.9 ± 6.0(44)	17.7 ± 6.2(62)	41.633**
5. First egg of last clutch of season	4 Aug	8 Aug	7 Aug	3 Aug	—
6. Last clutch: median initiation date ⁴	17 Jul	18 Jul	4 Jul	8 Jul	27.098**
7. Duration of breeding season (days) ⁵	107	130	120	149	—
8. Average duration of breeding season ⁶	62	77	67	95	—
9. Incubation period ⁷	10.7 ± 1.1(227)	10.6 ± 0.9(385)	10.7 ± 1.3(117)	10.7 ± 1.2(258)	4.593
10. Duration of successful attempt ⁸	36.3 ± 3.3(142)	37.1 ± 3.6(213)	35.9 ± 4.1(72)	37.7 ± 4.3(153)	17.368**

** $P < 0.005$.

¹ Median tests were used for all variables except temperature thresholds, for which the Kruskal-Wallis test statistics are reported. For all tests $df = 3$.

² See text, Methods and Materials section.

³ Mean ± standard deviation (sample size).

⁴ Nest boxes with only one clutch omitted in analyses.

⁵ Date of first egg, last clutch of season minus that of first egg of the season.

⁶ Median initiation date of last clutches minus that of first clutches.

⁷ Period in days between dates clutch completed and hatching initiated.

⁸ Period in days between initiation of an attempt which fledged one or more young and the next attempt in the same nest box. Values greater than 60 were omitted.

clutches minus that of first clutches (Table 1, line 8). The two-year mean durations were 70 days in Calgary and 81 days in Lawrence. Differences between localities were less than between-year variation within a locality.

Locality differences were also quantified for two aspects of phenology of attempts: incubation period and duration of the attempt if successful, i.e. if at least one young fledged. I defined the duration of the incubation period as the period between laying of the last egg and hatching of the first young. If hatching of the clutch spans more than one day this definition is not equivalent to that normally used (e.g. Drent 1975:334-335), i.e. the in-

terval between laying and hatching of the last egg. The latter definition cannot be applied either to clutches in which the last egg laid fails to hatch or if hatching is asynchronous and brood reduction occurs between nest observations, as occasionally happened in this study. As true incubation in House Sparrows probably begins before the clutch is complete, generally once the penultimate egg is laid (Seel 1968b:279), both definitions are only approximate and the former is better suited to this study. The incubation period was similar in both years and in both localities (Table 1, line 9).

The duration of a successful attempt was

TABLE 2. Nesting phenology: intralocality differences, median test statistics.

	Calgary			Lawrence		
	1975	1976	r	1975	1976	r
First clutch: initiation date	15.812(5)* ¹	30.544(5)**	.30	0.586(3)	17.164(5)**	.33
Last clutch: initiation date ²	7.425(4)	10.228(5)	.21	8.576(2)*	24.567(5)**	0.58
Incubation period	3.037(5)	6.231(5)	.68	12.498(4)*	5.967(5)	.30
Duration of successful attempt	8.503(5)	1.098(5)	-.17	15.571(2)**	11.629(5)*	-.09

* $P < 0.05$, ** $P < 0.005$.

¹ χ^2 test statistic (degrees of freedom).

² Nest boxes with only one attempt/season omitted.

defined as the period from the date the first egg of a clutch fledging at least one young was laid until the date the next attempt was started (see Seel 1968a:135). Successful attempts required approximately the same time in both localities, but the attempt duration varied between years, particularly in Lawrence (Table 1, line 10).

NESTING PHENOLOGY: VARIATION WITHIN LOCALITIES

Within-locality (among-farm) variance in initiation of breeding activities was significant for three of the four locality-year samples (Table 2, line 1). Thus, in those three samples conditions peculiar to each farm influenced the start of egg laying. Farm differences in termination of egg laying (Table 2, line 2) were significant only in both Lawrence samples. The coefficients comparing the year-to-year correlation in farm means, although positive, were insignificant.

Significant farm effects in incubation period occurred only in one sample, Lawrence, 1975 (Table 2, line 3). Duration of successful attempts exhibited significant farm influences in Lawrence but not in Calgary samples (Table 2, line 4). Yet the correlation coefficient between years for Lawrence was low, indicating that individual farm effects were not temporally consistent. Therefore, particular conditions on a farm apparently dictated phenological aspects of breeding, but the controlling factors varied annually relative to those on other farms.

Environmental differences among farms were not quantified. Therefore, factors that may have affected intralocality variance in nesting phenology can only be examined qualitatively. At site C2 breeding began earlier in the spring and ceased later in the summer than at any other Calgary site in both years. This farm had greater diversity of livestock and more heated outbuildings than others. Possibly House Sparrows roosted in the heated buildings and attained a positive energy balance sooner in the spring there and thus could breed earlier. Greater livestock diversity may be correlated with availability and diversity of both grain and insect foods for nesting sparrows, thus permitting breeding to continue well into summer.

Insect abundance was not quantified but seemed to decline markedly in early summer at all Lawrence farms except L2. There, the runoff from the troughs of pigpens and wallows provided moist, organically rich, areas throughout the summer. Mean initiation dates of last clutches were later by 23 days in 1975

and 10 days in 1976 at L2 than any other Lawrence farm in both years. Continued successful breeding at L2 indicates that high temperatures and consequent reduced work capacity of House Sparrows alone were insufficient to curtail breeding activities. Maintained abundance and high quality of food may have been overriding factors.

REPRODUCTIVE OUTPUT PER ATTEMPT: ANNUAL AND BETWEEN-LOCALITY VARIATION

Average weight of eggs in a clutch was higher in Calgary than in Lawrence and higher in 1976 than in 1975 at both localities (Table 3, line 1). Clutches were larger in Lawrence in 1976 than in the other samples (Table 3, line 2).

Between-locality variation in hatching success was not statistically significant ($\chi^2 = 1.809$, $df = 1$, n.s.) although in both years success was higher in Calgary than in Lawrence (Table 3, line 3). Clutch records can be divided into two subsamples: (1) those which failed to hatch any eggs, and (2) those hatching at least one egg. Seventeen percent of Calgary clutches and 33% of Lawrence clutches failed to hatch a single egg. Differences based on actual sample sizes are highly significant ($\chi^2 = 12.24$, $df = 1$, $P < 0.005$). Table 4 summarizes the fates of these clutches. House Sparrows failed to incubate clutches and/or deserted clutches more frequently in Lawrence ($\chi^2 = 4.884$, $df = 1$, $P < 0.05$). Clutches disappeared completely, either during laying or incubation, far more frequently in Lawrence than in Calgary ($\chi^2 = 51.13$, $df = 1$, $P < 0.005$).

Nest predation was often the probable cause of complete clutch disappearance (see Ricklefs 1973:373). Black rat snakes (*Elaphe obsoleta*) accounted for complete loss of at least seven clutches in Lawrence. We witnessed no other egg predation at either locality. A Norway rat (*Rattus norvegicus*) temporarily inhabited a previously active Lawrence nest box in summer, 1975. However, few other boxes were accessible to rats, and rat predation was probably infrequent at both localities. Much of the difference between Calgary and Lawrence in rates of clutch disappearance could be due to differential predation rates by snakes during the egg phase of the nesting cycle.

For only those clutches hatching at least one egg ("successfully incubated"), locality-year sample means of hatching success were comparable (Table 3, line 7), i.e. there were

TABLE 3. Summary of reproductive output/attempt.

	Calgary		Lawrence		Test statistic ¹
	1975	1976	1975	1976	
1. Egg weight (g)	2.85 ± 0.22(272) ²	2.92 ± 0.26(464)	2.73 ± 0.25(205)	2.80 ± 0.24(387)	F _x = 19.67*; F _y = 8.42*
2. Clutch size	5.02 ± 0.80(291)	5.04 ± 0.83(443)	5.07 ± 0.83(166)	5.20 ± 0.92(350)	χ ² _{12df} = 32.357**
3a. Number hatching	3.43 ± 1.90(312)	3.28 ± 1.87(483)	2.52 ± 2.23(207)	2.92 ± 2.25(393)	χ ² _{18df} = 76.402**
b. Hatching success (%)	68	65	50	56	—
4a. Number fledging	2.62 ± 2.01(310)	2.00 ± 1.87(473)	1.66 ± 1.96(207)	1.80 ± 2.01(393)	χ ² _{18df} = 82.413**
b. Fledging success	76	61	66	62	—
5. Breeding success (%)	52	40	33	35	—
6. Clutches hatching no eggs (%)	16	17	38	31	χ ² _{3df} = 42.896**
7a. Number hatching ³	4.07 ± 1.29(263)	3.96 ± 1.23(400)	4.04 ± 1.34(129)	4.24 ± 1.32(271)	χ ² _{15df} = 20.485
b. Hatching success	81	79	80	82	—
8a. Number fledging ³	3.11 ± 1.80(261)	2.45 ± 1.78(387)	2.66 ± 1.88(129)	2.61 ± 1.93(271)	χ ² _{18df} = 46.091**
b. Fledging success	76	62	66	62	—
9. Breeding success ³	62	49	52	50	—
10. Broods fledging no young (%)	16	24	26	27	χ ² _{3df} = 6.790
11. Fledging tenth day weight (g)	23.5 ± 3.6(606)	23.9 ± 3.5(802)	24.3 ± 2.7(196)	22.6 ± 3.5(518)	χ ² _{3df} = 45.637**
12. Fledging tenth day primary length (mm)	26.3 ± 4.3(375)	25.4 ± 4.6(800)	—	27.1 ± 4.7(443)	χ ² _{2df} = 24.850**

¹F_x and F_y are the F values for geographic and year components of variation, respectively. Complete ANOVA tables are listed in Murphy (1977:130). The χ² test statistic is reported for variables with highly skewed and/or kurtotic distributions (see text).

²Mean ± standard deviation (sample size).

³"Successfully incubated" clutches only (see text).

no differences in the number of young hatching from a successfully incubated clutch.

Fledging success was higher in Calgary than in Lawrence ($\chi^2 = 13.288$, $df = 1$, $P < 0.005$; Table 3, line 4). Considering successfully incubated clutches only, fledging success in Calgary and Lawrence was comparable ($\chi^2 = 0.064$, $df = 1$, $P > 0.5$). Fledging success varied annually, particularly in Calgary (all clutches: $\chi^2 = 14.172$, $df = 1$, $P < 0.005$; successfully incubated clutches: $\chi^2 = 15.371$, $df = 1$, $P < 0.005$).

Probability of complete brood loss was similar for all locality-year samples (Table 3, line 10). Loss of an entire brood, unlike disappearance of an entire clutch, cannot be directly linked to predation. Water damage to nests during storms (e.g. Mitchell et al. 1973: 52) or lack of nestling food (e.g. Seel 1970: 10) may result in the death of all nestlings in a brood and their removal by parents.

The rate of clutch disappearance was much higher in Lawrence than in Calgary but the rate of brood disappearance was not (Table 3, lines 6, 10). Snakes were clearly implicated in disappearance of entire clutches in Lawrence, but it is unlikely that snakes were predators of eggs in Calgary nest boxes. Other predators common to both localities, such as domestic cats (*Felis domestica*) and small mustelids, probably detected nestlings more easily than eggs, simply because the calls made by young nestlings allow them to be easily located. It is likely that predation rates were much higher in Lawrence than in Calgary during the egg stage but were similar at both localities during the nestling stage.

Overall breeding success, the proportion of eggs which became fledged young, was much higher in Calgary (46%) than in Lawrence (34%, Table 3, line 5). Tenth-day weight of fledglings varied considerably among the locality-year samples (Table 3, line 11); the Lawrence means bracketed those for Calgary. Tenth-day primary length also varied, averaging about 1 mm longer in Lawrence than in Calgary. Adult House Sparrows are larger in Calgary than those of the same sex in Lawrence (Murphy, unpubl. data). The data on tenth day-size suggest that such size differentiation does not begin until after the nestling stage.

REPRODUCTIVE OUTPUT PER ATTEMPT: VARIATION WITHIN LOCALITIES

At both localities and in both years, the number of young fledged per clutch varied among farms (Table 5, line 4). Among-farm variation was significant for several other variables

TABLE 4. Known clutch failures: frequency (%) of clutches initiated.

	Calgary		Lawrence	
	1975	1976	1975	1976
Entire clutch missing	3.2	6.2	23.2	16.3
Part of clutch missing	2.6	1.0	4.8	2.8
Clutch deserted or not fully incubated	5.1	5.6	8.2	6.1

in at least one year at both localities. Generally the study sites can be considered distinct microenvironments influencing reproductive output.

Correlation coefficients assessing the temporal stability of farm differences were usually statistically insignificant. In each locality correlation coefficients were high for the number fledging per clutch and significant in Calgary, i.e. if fledging success was relatively high on a Calgary farm in 1975 it was also likely to be relatively high in 1976. Because farms differed more markedly in fledging success than in hatching success, much of the difference was due to variation in nestling survivorship.

VARIATION WITHIN FARMS

Nest effects (Table 5B) were consistently significant for egg weight (Table 5B, line 1). Elsewhere (Murphy 1977:117-118) I have shown that the weight of the female parent and egg weight were positively correlated. Thus among-nest variance in egg weight was largely due to maternal effects. For other variables the nest effect was generally small. Therefore, among box nesters factors associated with the nest site itself did not strongly influence reproductive success.

The last egg laid in a clutch was generally less pigmented than other eggs in the clutch (also see Seel 1968b:270, Dawson 1964:187), allowing it to be identified in most clutches. At both localities, last eggs were generally heavier than all other eggs and significantly so in 1976 (Calgary 1976: $t = 2.722$, $df = 2055$, $P < 0.01$; Lawrence 1976: $t = 2.036$, $df = 1707$, $P < 0.05$). Conversely, first eggs were generally lighter than all other eggs. These differences in weights were significant at both localities in 1976 (Calgary 1976: $t = 3.907$, $df = 2055$, $P < 0.001$; Lawrence 1976: $t = 2.734$, $df = 1707$, $P < 0.01$). Thus weight of eggs is positively related to position in the laying sequence.

Hatchability of eggs was unrelated to egg weight except in the Lawrence 1975 sample.

TABLE 5. Intralocality variation in reproductive output per attempt.

	Calgary			Lawrence		
	1975	1976	r	1975	1976	r
A. Farm differences¹						
1. Egg weight	1.0	2.49*	-.34	0.38	1.12	.25
2. Clutch size	10.323(6)	11.684(5)*	.70	12.371(3)*	14.511(5)*	.37
3. Number hatching	13.955(7)	9.405(5)	.40	14.887(4)**	13.647(5)*	.57
4. Number hatching ²	10.666(7)	8.534(5)	.48	2.520(3)	9.086(5)	.40
5. Number fledging	27.069(7)**	18.531(6)*	.85*	11.782(4)*	30.339(5)**	.80
6. Number fledging ²	23.718(7)**	19.231(5)**	.75	6.414(3)	25.162(5)**	.29
7. Fledgling weight	9.653(7)	27.886(6)**	-.32	14.099(4)*	57.063(6)**	.74
8. Fledgling wing length	15.422(7)*	19.284(6)**	.45	—	33.024(6)**	na
B. Nest differences³						
1. Egg weight	2.74**	2.73**		2.47**	1.56*	
2. Clutch size	1.26	1.37		0.94	1.17	
3. Number hatching	0.85	1.05		1.31	1.75	
4. Number hatching ²	0.81	0.94		0.97	0.94	
5. Number fledging	0.85	0.95		1.08	1.58	
6. Number fledging ²	0.73	0.84		0.97	1.04	
7. Fledgling weight	0.89	0.99		0.93	0.95	
8. Fledgling wing length	0.55	0.63		—	1.09	

* $P < 0.05$; ** $P < 0.005$; na = not applicable.

¹ All variables except egg weight: values reported are the χ^2 median test statistic (degrees of freedom). If sample size was less than ten for a particular farm, it was deleted from the calculation. Egg weight: values reported are $F_{farm} = MS_{farm} / MS_{nest}$ (complete ANOVA tables are in Murphy 1977:133-134).

² "Successfully incubated" clutches only (see text).

³ $F_{nest} = MS_{nest}/error$, nests were grouped within farms in hierarchical ANOVA's (see Murphy 1977). The statistical significance of the F_{nest} value is reported only for egg weight. As the distributions of other variables violated assumptions of ANOVA, the F value is simply an approximation of the magnitude of variance among nests in relation to that both within and among nests.

In that sample, eggs which hatched were heavier than those which did not ($t = 3.15$, $df = 1836$, $P < 0.005$). Hatchability of eggs did vary with position in the laying sequence. Significantly fewer first eggs hatched than would be expected if hatchability of eggs were independent of position in the laying sequence in two samples: Calgary 1975 ($\chi^2 = 4.15$, $df = 1$, $P < 0.05$) and Lawrence 1976 ($\chi^2 = 2.79$, $df = 1$, $P < 0.10$). Hatchability of last eggs was similar to eggs other than the first in the laying sequence. Because, as a rule, the last egg is laid after incubation has begun, it hatches last. For example, in the Lawrence 1976 sample the last egg laid was known to be the last to hatch in 26 cases; no exceptions were found (also Seel 1968b:279). Relatively heavy weight may compensate for the initial disadvantage of late hatching (see Howe

1976). Alternatively, the last eggs may be of different composition (e.g. see Ricklefs 1977:167), enabling relatively rapid development before hatching.

REPRODUCTIVE OUTPUT PER SEASON

No locality differences were found for season reproduction totals (Table 6). Greater numbers of clutches were attempted and more young hatched during the longer 1976 breeding season at both localities. Reduced fledging success per clutch in 1976 equalized total number fledging in both years.

Intralocality variance was generally significant in both localities (Table 7). The temporal stability of farm differences was quite low, as in other aspects of reproduction. In Lawrence relative differences were maintained for the number of eggs hatching. Site

TABLE 6. Reproductive output: season totals.

	Calgary		Lawrence		Test statistics
	1975	1976	1975	1976	
Number of clutches	2.7 ± 0.9(115)	3.5 ± 0.8(143)	2.6 ± 1.2(80)	3.4 ± 1.3(116)	$\chi^2 = 46.50^{**}$
					F_{geog}^1 F_{year}
Number of eggs	12.8 ± 4.1(114)	15.6 ± 4.4(143)	11.7 ± 6.0(72)	16.0 ± 6.5(114)	0.0 26.19**
Number hatching	9.6 ± 3.1(111)	11.3 ± 3.7(140)	8.1 ± 4.4(64)	10.7 ± 5.4(107)	0.61 10.15*
Number fledging	7.5 ± 2.9(109)	7.0 ± 3.0(136)	6.6 ± 3.5(52)	7.6 ± 4.5(93)	0.16 0.26
Juvenile/adult ratio	3.7	3.0	3.3	3.8	— —

* $P < 0.05$; ** $P < 0.005$.

¹ Complete ANOVA tables listed in Murphy 1977:144-145.

TABLE 7. Reproductive output: Intralocality variation in season totals.

	Calgary			Lawrence		
	1975	1976	r	1975	1976	r
χ^2 test statistics						
Number of clutches ¹	28.96(5)**	17.66(5)**	.59	21.60(3)*	8.23(5)*	.37
<i>F</i> farm values ²						
Number of eggs	7.86**	2.48*	.51	9.24**	3.16*	.82
Number hatching	4.65**	1.36	-.04	5.01*	4.71**	.95*
Number fledging	4.38**	2.02	.32	3.56*	4.52**	.86

* $P < 0.05$; ** $P < 0.005$.¹ 1975 samples: Nest boxes with one or two attempts vs. those with more than two attempts. 1976 samples: Nest boxes with one to three attempts vs. those with more than three attempts.² Complete ANOVA summary tables are listed in Murphy 1977:146-147.

L2 was clearly distinct: about 21 young fledged from each L2 nest box over the two seasons. Comparable values for other Lawrence farms ranged from 11 at L3 to 13 at L7. High total reproductive output at L2 reflected a relatively long breeding season, short incubation periods, short duration of successful clutch attempts, high clutch size, hatching success and fledging success relative to other farms.

GEOGRAPHIC PATTERNS: BREEDING PHENOLOGY

Table 8 summarizes data on breeding phenology of House Sparrows in North America and England. Geographic trends in initiation of breeding activities and duration of the breeding season are evident. The breeding season starts earlier ($r = 0.667$, $df = 7$, $P < 0.05$) and appears longer ($r = -0.675$, $df = 6$, $0.1 < P < 0.05$) at lower latitudes.

Calgary and Oxford are at the same latitude and breeding phenology is almost identical at these two localities. Yet elsewhere (Murphy 1977:105) I have shown that annual temperature range is more tightly associated with these breeding events (initiation of breeding activities: $r = 0.811$, $df = 7$, $P < 0.05$; duration: $r = -0.783$, $df = 6$, $P < 0.05$) than is

latitude, and the annual temperature ranges, i.e. mean June temperature minus mean January temperature, are markedly different (13.4°C at Oxford, 27.4°C at Calgary).

The use of only extreme values may obscure genuine differences. For example, as noted earlier, the breeding season ends earlier in Lawrence than in Calgary, but Table 8 shows that the very last clutches were started only one day apart. Seel (1968a:132) reported the period in which 95% of the clutches were initiated at Oxford. On the average this period began in 17 April, ended on 24 July, and lasted 98 days. The corresponding period in Calgary started on 19 April, ended on 30 July, and lasted 102 days. Therefore, deleting the extreme values still fails to produce any substantial difference between Calgary and Oxford in either the start of breeding activities or duration of egg laying.

Seel (1968a:139) also tabulated the start of the breeding season relative to ambient temperature. Following his procedure and determining the overall mean for each locality, I calculated values of 6.3°C at Calgary, 10.0°C at Oxford and 9.9°C at Lawrence. Breeding begins at similar ambient temperatures in Lawrence and Oxford. Earlier I showed that breeding begins at lower tem-

TABLE 8. Summary of studies of breeding phenology of House Sparrows.

	Latitude (°N)	Start of first clutch	Start of last clutch	Duration of breeding season ¹	Incuba- tion period	Duration of attempt	Source
Ithaca NY	42	≈7 Apr	25 Aug	140	12	—	Weaver 1939, 1943
Stillwater OK	36	7 Apr	—	—	9.4	(29.4) ³	North 1968
McLeansboro IL	38	26 Mar	6 Aug	125	—	36.1	Will 1969
Whitewater WI	43	9 Apr	10 Jul	92	11.7	(26.5)	North 1973a
Hale Co. TX	34	18 Mar	16 Aug	152	—	—	Mitchell et al. 1973
Portage des Sioux IL	39	9 Apr	9 Aug	124	(14.2) ²	(28.9)	Anderson 1973
Mississippi State MS	33	24 Feb	28 Jul	154	12.2	—	Sappington 1975
Lawrence KS	39	19 Mar	5 Aug	139	10.7	36.9	Present study
Calgary AB	51	10 Apr	6 Aug	115	10.7	36.7	Present study
Oxford, England	51	9 Apr	4 Aug	116	10.8	40.0	Seel 1968a, b

¹ Number of days between date first egg of season laid and first egg of last clutch of season laid.² Period from clutch initiation until at least one egg hatched.³ Numbers in parentheses are from first egg to fledging.

TABLE 9. Summary of studies of reproductive output of House Sparrows.

	Latitude	Number of nests	Clutch size	Initial brood size	Number fledged	Number of clutches	Total fledging	Source ¹
Ithaca NY	42	26	4.73	—	3.34	1.68	5.61	Weaver 1942, 1943
Stillwater OK	36	97	4.50	2.2	1.5	1.54	3.15	North 1968
McLeansboro IL	38	168	4.46	2.93	1.37	2.29	3.14	Will 1973
Whitewater WI	43	52	4.96	2.5	1.5	2.2	1.46	North 1973
Hale Co. TX	34	73	4.21	2.5	1.3	3.9	3.0	Mitchell et al. 1973
Portage des Sioux IL	39	229	4.63	2.81	1.81	2.14	3.87	Anderson 1973
Mississippi State MS	33	79	4.2	3.7	2.85	2.84	8.09	Sappington 1975
Lawrence KS	39	192	5.16	2.74	1.70	3.00	7.11	Present study
Calgary AB	51	230	5.05	3.36	2.31	3.09	7.22	Present study
Oxford, England	51	399	3.98	3.46	1.57	2.13	2.9	Seel 1968b, 1970
Oxford, England	51	314	4.19	3.42	2.19	2.01	4.54	Dawson 1972
Oxford, England	51	713	4.13	3.44	1.88	2.07	3.7	Average

¹ If particular values were not reported in original source, they were calculated when possible for inclusion in this table.

peratures in Calgary than in Lawrence. Although the published data do not permit similar statistical evaluation of differences between Calgary and Oxford, these are probably comparable to those between Calgary and Lawrence. Thus, House Sparrows begin to breed under cooler conditions in Calgary than those in Lawrence or in England. Summarizing breeding activities by date therefore obscures a marked difference between Calgary and Oxford populations in the onset of breeding relative to temperature.

Geographic patterns of breeding phenology of House Sparrows in North America and differences between Calgary and Oxford do not simply reflect differences in environmental restraints. The differences are consonant with geographic patterns of thermal tolerances (Hudson and Kimzey 1966), and bioenergetics (Blem 1973, Kendeigh 1976; also see Blem 1974). These physiological differences among House Sparrows inhabiting different North American localities were noted while the birds were maintained in captivity in the same environmental conditions. Consequently, Hudson and Kimzey (1966:214) concluded that the differences have a genetic basis. Initiation of breeding activities at relatively low ambient temperatures in Calgary probably shares the same physiological basis and therefore presumably represents genetic divergence from ancestral populations in England.

North American data on incubation periods and duration of successful attempts are fragmentary and incubation period has not been consistently defined (Table 8). Consequently, I attempted no analyses of geographic trends. Nevertheless, comparison of Oxford values (Seel 1968b:276) for duration of successful attempts with those calculated for Lawrence and Calgary is possible. Successful attempts lasted about three days longer in Ox-

ford (Seel 1968a:135) than at either of these localities (Oxford vs. Calgary: $\chi^2 = 87.897$, $df = 1$, $P < 0.005$; Oxford vs. Lawrence: $\chi^2 = 27.789$, $df = 1$, $P < 0.005$).

GEOGRAPHIC PATTERNS: REPRODUCTIVE OUTPUT

Table 9 summarizes data on reproductive output from several studies. Anderson (1973:44) found a positive and significant correlation between clutch size and latitude. Adding the grand means for Lawrence and Calgary found in this study and those reported by Sappington (1975) and North (1968) at two other localities to the data set still shows a significant, positive relationship (Figure 3). Clutch size is clearly higher at mid-latitudinal localities than at more southern localities in North America. No other measures of reproductive performance were correlated with latitude.

Comparison of North American values with those at Oxford shows that clutch size in Oxford is relatively small. Differences between Oxford (see Seel 1968b) and both localities included in the present study are highly significant (Lawrence: $\chi^2 = 316.631$, $df = 1$, $P < 0.005$; Calgary: $\chi^2 = 440.247$, $df = 1$, $P < 0.005$). Differences are also highly significant for the number of clutches at a nest per year (Lawrence: $\chi^2 = 65.144$, $df = 1$, $P < 0.005$; Calgary: $\chi^2 = 90.296$, $df = 1$, $P < 0.005$). The number of young fledged per year is also much higher in Lawrence and Calgary than in Oxford. As neither Seel (1970) nor Dawson (1972) reported variance, these differences could not be tested statistically.

Dawson (1972) reported an average egg weight per clutch of 2.77 g and average tenth-day weight of fledglings of 22.9 g in Oxford, but again I could find no measures of variance for statistical tests. Egg weights in Lawrence, which are significantly lighter than those in

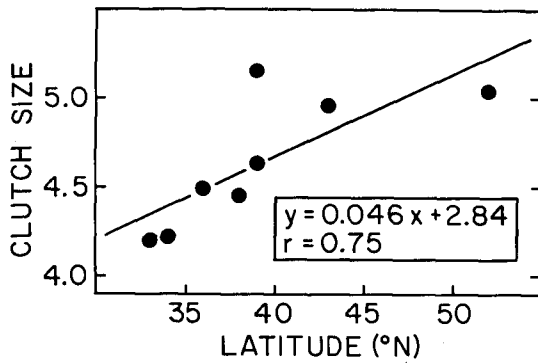


FIGURE 3. Clutch size of House Sparrows and latitude, North America.

Calgary, are comparable (see Table 3, line 1) to those at Oxford. Calgary and Lawrence values for tenth-day weights of fledglings were about 0.5 g higher than the Oxford values. Summarizing, eggs and young are slightly heavier in Calgary than in Oxford; clutch size, the number of clutches per year and the number of young fledged per year are higher in both Lawrence and Calgary than in Oxford.

In contrast to patterns in breeding phenology, geographic patterns in clutch size and divergence in reproductive output of Lawrence and Calgary populations from that of English populations may simply reflect differences in environmental suitability for breeding. Juvenile dispersal and adult movement patterns (e.g. Will 1969, North 1973b) are sufficient to preclude any genetic substructuring on a local scale. I have shown that intralocality variation was quite high in both Lawrence and Calgary (Table 5) and interlocality variance low (Table 3) in most aspects of reproductive output. Therefore, nutritional or other locally and geographically variable proximate factors should provide an adequate and parsimonious explanation of variation in reproductive output after such factors are quantified. No evolutionary mechanisms for divergence in reproductive output in North America from that found in ancestral populations need be invoked (e.g. see Williams 1966, Stearns 1976).

SUMMARY

Geographic differentiation in breeding ecology of House Sparrows between Calgary, Alberta and Lawrence, Kansas is limited primarily to differences in nesting phenology and probability that clutches will be successfully incubated. Breeding begins later but at cooler temperatures in Calgary than in Lawrence. Annual variation in initiation of breed-

ing activities indicates that breeding is not strictly cued to photoperiod or temperature. Breeding continues later in summer in Calgary, ceasing when temperatures start to decline. Cessation of egg laying in Lawrence appears to be associated with high temperatures and dry conditions of mid-summer.

General aspects of most study sites, particularly in Calgary, were similar. Yet variation within localities (among farms) was high. These productivity differences probably reflect microenvironmental variation in diversity and abundance of insect prey since variation among farms was particularly high for fledging success. Nest site effects were high only for egg weight. Thus variation in reproductive output among box-nesting House Sparrows could not be attributed to the micro-environment of the nest itself.

Geographic patterns in onset and duration of the breeding season and clutch size have been rapidly established since House Sparrows were introduced to North America a little over a century ago.

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