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CLIMATIC INFLUENCES ON PRODUCTIVITY IN THE HOUSE SPARROW

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The selection of a poor nesting site could drastically lower the breeding success of a pair of birds. Given particular habitat requirements, selection should constrain nest structure and nest-site to characteristic types. This conclusion has been tacitly assumed by biologists and field naturalists who were aware that nest-sites were not randomly scattered but associated with species specific habitat and structural configurations. However, several studies have demonstrated intraspecific variation in nest-site choice and subsequent differences in productivity among sites (Orians 1961, Robertson 1973, Will 1973, Caccamise 1977, Murphy 1977, Anderson 1978).

Cody (1971) suggested that predation is the single greatest cause of reproductive failure in most species of birds. Predation was also considered to be an important factor in the distribution of nests (Horn 1968, Lack 1968), with higher productivity in the best concealed or least accessible nests. Climate is accorded a role in nesting success but usually only indirectly as a determinant of food abundance. Severe weather can have a major effect on reproductive output at a site (Mitchell et al. 1973) by damaging or destroying nests. Birds thus could be expected to construct nests to reduce the detrimental influence of weather (Collias 1964, Austin 1974, Inouye 1976, Schaeffer 1976, Mertens 1977); this tendency would be strong if weather was the major cause of reproductive failure. This situation obtains for a population of House Sparrows (*Passer domesticus*) on a ranch near Calgary, Alberta. Human activity, plus thick blue spruce (*Picea pungens*) foliage combine to reduce egg and nestling loss to predators (Black-billed Magpies [*Pica pica*] and cats) to negligible levels (Murphy 1977, McGillivray 1978). The large population of House Sparrows provided an opportunity to assess variation in reproductive performance associated with nest-site differences. This study was undertaken to determine if weather-related factors could influence the nest placement and reproductive performance of House Sparrows.

MATERIALS AND METHODS

Study site.—The study area was on a ranch located 8 km east of Calgary, Alberta (51°05′N, 113°50′W). The 146 nests found were in 2 rows of blue spruce originally grown as windbreaks. Generally, several thousand bushels of grain were stored on the ranch and high protein feed was always available. Two heated barns supplied shelter for the sparrows in inclement weather and throughout the winter. Twenty-four nest boxes were installed on the sides of farm buildings at this site in late 1974 (Murphy 1977).

Data collection.—Nests were inspected at 3–5-day intervals from 2 May–15 August 1977. Usually 4-day intervals were maintained, but if weather conditions were severe, the inspections were curtailed to avoid affecting nestling survival. Eggs were numbered and weighed to the nearest 0.1 g on a 5 g capacity Pesola scale and nestlings were weighed to the nearest 0.5 g on a 50 g capacity Pesola scale. Nestlings 5–6 days old were banded with a U.S. Fish and Wildlife Service aluminum band and also color leg bands after their weight reached 20 g. Nest height, tree height, tree basal diameter and distance between trees were measured directly with a tape measure. Tree volume was calculated assuming a conical shape for the trees [$V = {}^{1}/_{12}\pi$ (basal diameter)^2(height)]. Nest orientation was measured as the direction of a line from the center of the entrance to the back of the nest. Standard compass orientation was used; N = 0°, E = 90°, S = 180°, W = 270°.

Breeding success.—Estimates were sometimes needed to determine nestling age when first found, date of clutch initiation and 10-day nestling weight. The estimation procedures used were those of Murphy (1978a). As nests were not checked each day, it was not always possible to know the fate of some eggs and nestlings. Therefore, maximum and minimum estimates of success were used. The estimate of maximum hatching success was based on the assumption that eggs disappearing between successive nest checks hatched and the young subsequently died. The estimate of minimum hatching success was based on known hatch. The estimate of the minimum number of fledged nestlings was the number reaching a weight of 24.8 g or more (mean 10-day weight) before leaving the nest. The number of nestlings with a weight of 20.0 g before leaving the nest was the estimate of the maximum number fledged.

Data analysis.—Counts of the number of young fledged and eggs hatched were bimodally distributed due to a high frequency of nest failures. For this reason, the Mann-Whitney *U*-test was used for paired and the Kruskal-Wallis test was used for grouped comparisons of reproductive performance. Substantial variation existed in the reproductive output from the nests; both seasonal and per clutch output were investigated. Multiple regression analysis (BMDP2R, Dixon 1975) was used to determine the extent to which reproductive performance could be accounted for by variation in the continuous variables describing nest-site position. Where the data were normally distributed, *t*-tests were used for paired comparisons and correlation analysis used to investigate temporal variation.

RESULTS

The 2 spruce rows studied were oriented in a north-south direction on either side of the main ranch house. The average distance between the rows was 82 m. Both rows were bordered on 1 side by a honeysuckle hedge (*Lonicera* sp.). A plowed field, house, garage and driveway lay between the 2 rows (Fig. 1). Deciduous hedges and trees on the ranch were not used as nest-sites by the sparrows. The west tree row was more densely vegetated and more varied in tree size and number of nests per tree than the east tree row (Table 1). A significant positive regression was found when the frequency of nests was plotted against tree volume ($Y = 0.2014X + 0.0107$; $r = 0.562$, $P \leq 0.01$, N = 60). This was not a simple consequence of overpopulation as some box nests and former nest-sites in unoccupied trees remained vacant while large trees contained up to 14 nests. Almost all (97%, N = 146) nests were built adjoining the main trunk of a tree.

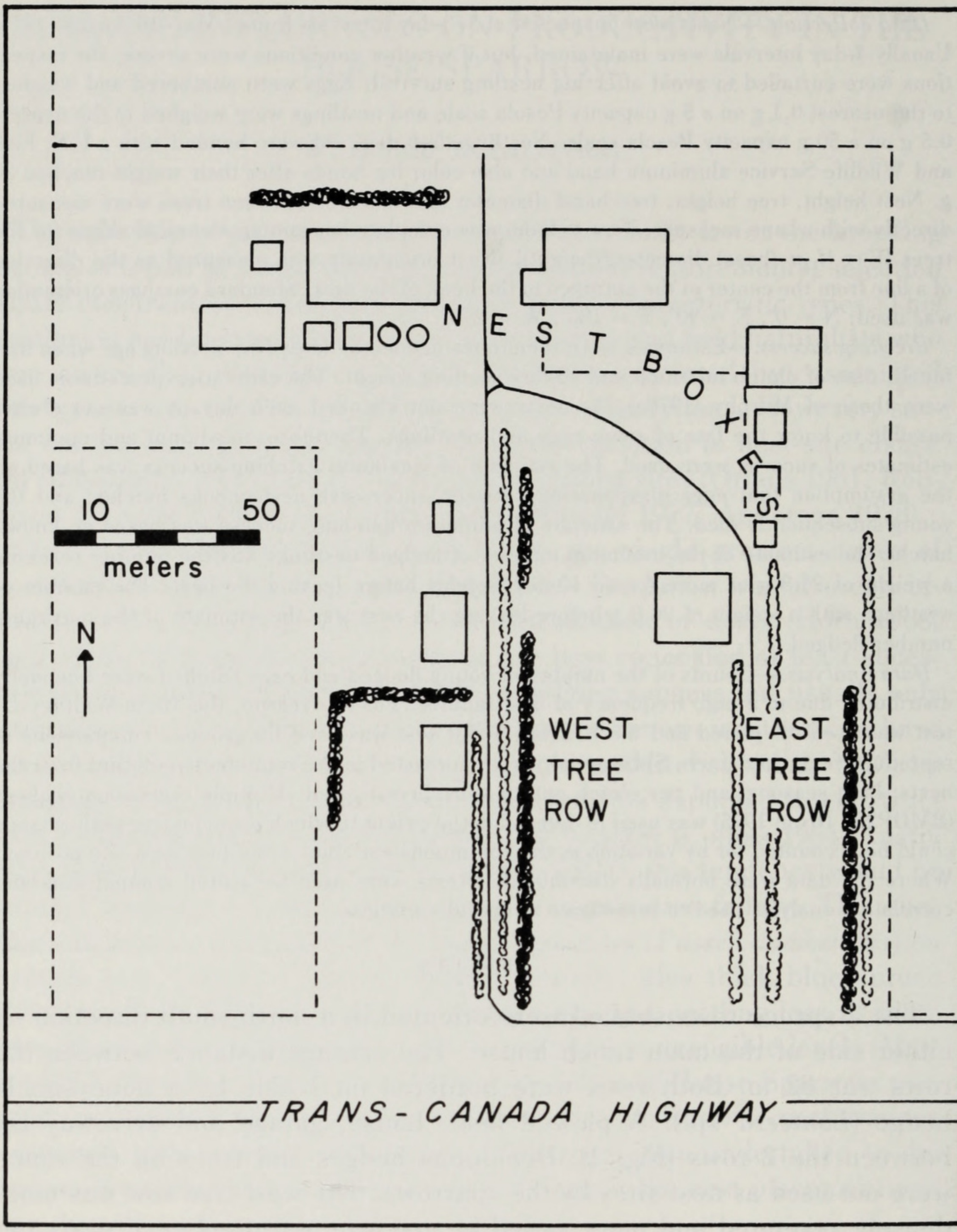

FIG. 1. Map of the study area. Major House Sparrow nesting occurred in rows of spruce windbreaks as well as in nest boxes attached to buildings on the ranch. Buildings are outlined, fence rows shown by dashed lines, roads by solid lines, hedgerows by irregular outlines and spruce rows by solid outlines. Only nests along the east tree row, west tree row and in the nest boxes provided the data for this study.

TABLE 1

SOME CHARACTERISTICS OF NEST-SITES IN THE EAST AND WEST ROWS

Variable	West row	East row	*U*-value
Total length (m)	94	81	NA
Total number of trees	34	24	NA
Total number of nests	110	36	NA
Mean tree height (m)	5.61**	4.50**	678
Mean inter-tree distance (m)	2.77**	3.58**	249
Mean tree volume (m^3)	13.42**	10.09**	692
Mean nest height (m)	3.87**	3.27**	1167
Mean distance to nearest neighbor (m)	0.66**	1.52**	439
Mean number of nests within 1 m	3.43**	0.76**	1345
Mean nest height/tree height ratio	0.69*	0.73*	610

* $P < 0.05$, Mann-Whitney *U*-test.
** $P < 0.01$ Mann-Whitney *U*-test.

Nest position.—Univariate inter-row comparison of means describing reproductive success show few differences (Table 2). No clear trends are apparent, but this is noteworthy since the average density of nests was much higher in the west row. Each row was then partitioned into 4 equal sections to determine whether position within a row affected reproductive performance. The west row displayed considerably more intra-row variation (Table 3). The nests were significantly more grouped in the southern half of the rows (west row: $t = 7.5$, df = 97, $P < 0.001$; east row: $t = 2.5$, df = 33, $P < 0.05$). In addition, the ratio of nest height to tree height increased from north to south along the west row.

TABLE 2

SEASONAL AVERAGES OF REPRODUCTIVE OUTPUT FROM BOX AND TREE NESTS

Variable	Box	West	East	H-stat.
Number of clutches[a]	2.71	2.12	2.06	8.86**
Total number of eggs	12.10	10.43	9.39	12.67**
Min. number hatching	7.50	5.43	4.89	12.24**
Max. number fledging	5.29	3.38	3.21	14.33**
Clutch-size	4.91	4.92	4.79	2.74
Min. hatch/clutch	2.86	2.70	2.57	1.86
Max. fledge/clutch	1.95	1.67	1.76	4.17
Egg weight	2.91	2.90	2.88	1.21
Nestling 10-day wt.	23.55	25.35	23.49	4.34

** $P < 0.01$ Kruskal-Wallis test.
[a] Lines connect groups not significantly different by comparison of rank sums (Dunn 1964).

TABLE 3

AVERAGE VALUES OF SEASONAL REPRODUCTIVE OUTPUT FOR NESTS ALONG BOTH TREE ROWS; EACH ROW WAS PARTITIONED INTO 4 EQUAL SECTIONS: NQ = NORTH QUARTER, NM = NORTH MIDDLE, SM = SOUTH MIDDLE, SQ = SOUTH QUARTER

	West tree row					East tree row				
Variable	NQ	NM	SM	SQ	*H*	NQ	NM	SM	SQ	*H*
Sample size	27	18	14	30		6	8	8	7	
Nest height (m)	3.83	3.76	3.83	3.97	1.1	3.67	3.23	3.14	3.09	3.9
Nest height/tree height	0.62	0.68	0.70	0.74	12.2**	0.74	0.74	0.70	0.73	1.2
Nests within 1 m	2.67	2.44	4.50	4.20	6.4	0.28	0.55	1.11	0.92	3.84
Total clutches per nest	2.29	2.50	1.85	1.86	9.3*	2.28	2.00	2.00	2.00	3.09
Total eggs per nest	11.04	12.22	9.07	9.43	8.3*	9.71	9.22	9.33	9.37	1.14
Total fledging per nest	2.70	5.40	3.57	2.67	20.1**	2.12	3.66	4.00	2.12	1.97
Fledging success	0.56	0.78	0.67	0.62	3.2	0.49	0.74	0.78	0.66	1.84
Clutch-size	4.80	4.90	4.95	5.01	0.6	4.31	4.83	4.80	5.17	4.60
Fledging per clutch	1.35	2.35	1.88	1.54	8.2*	0.93	1.94	2.12	1.89	3.86

[1] Maximum value.
[2] Fledging success = number of fledglings/number of nestlings.
* $P < 0.05$.
** $P < 0.01$ (Kruskal-Wallis test).

Table 4 gives the average weather conditions prevailing in the Calgary region during the House Sparrow breeding season. The relatively strong northerly winds and high incidence of storms suggests that southerly position in a row or low nest height could enhance nest-site security. The earliest breeders suffered the most rigorous weather conditions of the breeding season, including 6 days of snow, 13 of rain and an average daily

TABLE 4

CLIMATIC TABLE FOR CALGARY, ALBERTA[a]

Month	Temperature (C)	Wind (m/sec)	Precipitation (mm)	No. of days of rain	Thunderstorms
April	3.6	SE 5.0	35	10	0.2
May	9.8	NW 5.0	52	11	1.4
June	13.0	N, NW 4.6	88	14	5.8
July	16.7	NW 4.1	58	11	8.2
August	15.1	N 4.0	59	12	5.3

[a] Data from R. A. Bryson and E. K. Hare (1974). Figures given represent multi-year means.

TABLE 5
SEASONAL VARIATION OF NEST ORIENTATION IN THE WEST ROW[a]

Portion of row		Nest orientation NE	NW	SW	SE
Northern-most quarter	N =	5	7	8	8
		16 June	4 July	13 May	29 May
Middle half	N =	6	9	9	10
		9 June	14 June	16 May	11 May
Southern-most quarter	N =	5	8	10	8
		6 June	13 May	31 May	5 June
Whole row	N =	16	24	27	26
		4 June	10 June	17 May	21 May

[a] Dates are the average date of the initiation of first clutches for nests oriented in 1 of 4 directions: NE = 1°–90°, SE = 91°–180°, SW = 181°–270°, NW = 271°–360°.

minimum temperature of 3.5°C in May. Positive correlations between clutch initiation date and absolute and relative (to tree height) nest height indicated an early start for low nests. For means calculated over 10-day intervals, the correlation of clutch initiation date and absolute height was: $r = 0.809$, df = 9, $P < 0.01$, west row; and $r = 0.629$, df = 8, $P < 0.05$, east row; the correlation of clutch initiation date and relative nest height was $r = 0.630$, df = 9, $P < 0.05$, west row; and $r = 0.550$, df = 8, $P < 0.1$, east row.

Orientation.—Nests found in the spruce trees were bulky, ball-like structures composed of grasses, straw, small twigs and occasionally, paper, plastic and hair. The nest entrance was usually at the side of the structure, but it was frequently found on top or even underneath the main body of the nest. The direction in which the entrance faced was the measured orientation. When nests were grouped in 45° arcs, the nest entry directions were randomly distributed ($\chi^2 = 9.07$, df = 7, $P > 0.1$, NS). Nest entry direction depended on the date of first clutch initiation. North-facing nests (arc 270°–90°) were built by late nesters, particularly at the northern end of the west row (Table 5). The east tree row, perhaps due to restricted number of nest-sites showed little variation of nest orientation. Only 8 first clutches were initiated after 1 June along the east row; however, 5 of these were oriented either northeast or northwest. A trend for higher annual productivity from south-facing nests (arc 90°–270°) was noted. South-facing nests contained more successful clutches (2.26 vs 1.91) and correspondingly more fledglings (3.56 vs 3.11). In addition, the average number of fledglings per clutch was slightly higher for south-facing nests (1.74 vs 1.66).

TABLE 6

REGRESSIONS OF MEASURES OF REPRODUCTIVE SUCCESS ON NEST HEIGHT FOR BOTH ROWS AND THE WEST ROW ALONE[a]

Y	Both rows	West row alone
Total number of young fledging	$Y = -0.729X + 6.4$	$Y = -0.9575X + 6.6$
	$F = 6.1$, $P < 0.05$	$F = 12.76$, $P < 0.01$
	df = 1, 106	df = 1, 88
Total fledgling weight	$Y = -20.89X + 182.5$	$Y = -24.90X + 179.15$
	$F = 6.52$, $P < 0.05$	$F = 10.19$, $P < 0.01$
	df = 1, 106	df = 1, 88
Total nestling weight	$Y = -20.16X + 200.02$	$Y = -33.77X + 242.7$
	$F = 6.4$, $P < 0.05$	$F = 11.21$, $P < 0.01$
	df = 1, 106	df = 1, 88

[a] Residuals were checked for departures from normality (X = nest height in m).

Variation in productivity.—Significant relationships were found between measures of reproductive performance and simple parameters of nest-site position. Seasonal totals of number of young fledged, fledgling weight and nestling weight were negatively related to nest height (Table 6). There was a clear inverse relationship between the number and quality of fledged young and the height of the nests. This result is surprising because other factors known to influence House Sparrow breeding productivity, such as age and experience of the parents and the nutritional state of the female (Summers-Smith 1963, Dawson 1972, Pinowska 1979), did not mask the effect of nest height.

Many of the preceding analyses have assumed a relationship between nest-site exposure and security. Data from this study support this assumption. Eighteen nests were either destroyed or severely damaged after violent windstorms. All but 2 of the nests were oriented in a northerly direction and 61% (11 of 18) were in the northernmost quarter of each row. The ratio of nest height to tree height was slightly higher than average for the destroyed nests (west row: 0.72, east row: 0.77, see Table 1 for averages). All of the destroyed nests had at least one of the characteristics reducing nest-site security.

Box nests vs tree nests.—Seasonal totals of productivity were higher for birds nesting in boxes (Table 2). This probably occurred because more clutches were initiated at each box nest over the breeding season. First clutches were initiated earlier at box nests and the peak initiation of second clutches at box nests coincided with the peak of first clutch initiation at tree nests.

DISCUSSION

A unique aspect of this study site was the predominance of natural vs artificial nest-sites. The box nests were clearly the best nest-sites since clutches were initiated earlier in the box than tree nests. The observed increase in productivity at box nests is probably due to the protection afforded by the structure. They are impervious to wind damage, almost waterproof and probably provide a warmer micro-climate for the nest (Mertens 1977). The probability that an egg laid in a box nest resulted in a fledged young was 0.44; in contrast, for the tree nests, it was only 0.32 (west row) and 0.34 (east row). Differential productivity should also exist between differently positioned tree nests. The weather-related nest destruction supports the qualitative assessment that certain nest-sites and orientations are better suited to ambient conditions.

The attractiveness of large trees as nest-sites, the close proximity of the nests to the main trunks and the negative relationship between nest height and fledgling number all suggest the importance of nest-site security. Nests near the tops of spruce trees are exposed to rain and wind and wind-induced movements of the tree. Such movements may dislodge the nest more readily than the wind alone. The choice of spruce trees over deciduous trees for nest substrates is probably due to the thicker foliage and greater protection offered by the conifers.

Thunderstorms and strong winds are common in Calgary throughout the summer, but wind direction is predictable and a response to lower its effect would be anticipated (Austin 1974, Cink 1976). The decrease in the ratio of nest height to tree height towards the north end of both rows can be interpreted as a response to the usual wind direction.

The random distribution of nest entry direction is surprising considering the importance of nest orientation for other birds such as the Cactus Wren (*Campylorhynchus brunneicapillus*) and Verdin (*Auriparus flaviceps*) (Ricklefs and Hainsworth 1969, Austin 1974) and the demonstrated effect of weather on House Sparrow nests (Mitchell et al. 1973). Cactus Wrens orient their nest entrances into the wind to reduce heat stress on the nestlings. Kendeigh (1976) found that heat stress begins at 22°C in adult House Sparrows. Throughout July and August in Calgary, the maximum daily temperature often reaches or exceeds 22°C (23 days in 1977). This, combined with a long daylength and concomitant high level of incident radiation on the nests, could produce heat stress in nestlings. In Calgary, though, House Sparrows begin breeding in poor conditions relative to populations studied at lower latitudes (Murphy 1978a). Cool temperatures and rain early in the season combine to lower productivity compared to midsummer values (Murphy 1978b, McGillivray 1978).

The preponderance of south-facing nests early in the season is perhaps a response to protect the nests from the north wind. The increase in the number of north-facing nests later in the season for both rows would be expected if wind ventilation were used as a cooling agent in warm weather. The change in average nest entrance orientation (Table 5) from early to late nesters may serve to minimize the detrimental influence of weather on reproductive output. The overall randomness of nest entry direction can be accounted for by the long House Sparrow breeding season and the resultant variation in optimal orientation.

The apparent relationship between average weather conditions and the pattern of nest position and construction may explain the variation in nest entrance orientation, nest height and the date of first clutch initiation. The better protected box nests allow birds to breed earlier, thus increasing the number of clutches possible in a season. Birds nesting in low tree nests begin to breed earlier and fledge more young. Birds nesting in south-facing nests begin to breed earlier and show marginally higher fledgling production. Sometimes the adaptive significance of the pattern is not entirely evident. Despite the presence of unused nest-sites, there is a strong relationship between the number of nests in a tree and tree size, suggesting that large trees make good nest substrates. Yet, there is no relationship between the number of fledglings from a nest and the size of the tree containing that nest.

These data imply that some of the variation in reproductive performance could be predicted with a knowledge of local climate and the position of the House Sparrow nests. However, as noted earlier, other variables affect reproductive output and may prevent the determination of the importance of weather. Recent banding recaptures at my study site have shown a large turn-over of birds. It is likely that at least 50% of the birds nesting on the ranch are either first-year birds or immigrants from neighboring ranches. Summers-Smith (1963) has shown that first-year birds start breeding later in the season and are less skilled at nest building than older adults. It is interesting that at this site the best protected nests were built by pairs who began to breed early. This suggests that the older adults built the early, and hence, more productive nests; unfortunately, the ages of the breeding birds were not known. Weather is clearly a major force determining the productivity of House Sparrows. Many nests on the study area were positioned to minimize the severity of the weather. The observation that many poor nest-sites were also chosen could be the result of experiments by first-year birds or simply an inability of pairs to find and maintain better sites.

SUMMARY

The variation in reproductive performance observed in this study appears to be partly attributable to the influence of weather. Box nests are well protected against the elements

and usually birds nesting in boxes were more successful than those nesting elsewhere. Tree nests are exposed and, to be productive, must be constructed to withstand strong winds, storms and cold temperatures. South-facing nests, central position along a tree row and low nest height to tree height ratio were determined to be beneficial in reducing the impact of the cool north winds. South-facing nests fledged more young early in the season, while north-facing nests were more productive in mid-summer. Throughout both tree rows, the number and weight of fledglings was negatively correlated with nest height.

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WORKING GROUP ON GRANIVOROUS BIRDS—INTECOL

The Third International Congress of Ecology will take place in Warsaw, Poland, 5–11 September 1982. The Working Group on Granivorous Birds—INTECOL—is organizing a special symposium along the theme of "The role of granivorous birds, especially Corvidae and Columbidae, in ecosystems." Such problems as population dynamics, biomass and production rates, energetics, impact of granivorous birds on ecosystems and management of pest situations will be covered.

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