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## **Climatic factors, activity budgets and breeding success of the Spanish Sparrow [*Passer hispaniolensis* (Temm.)]**

### ABSTRACT

This study examines the influence of environmental factors and time budget on reproductive success of Spanish Sparrows [*Passer hispaniolensis* (Temm.)]. Work was conducted in 1983 in a large cerealiculture zone in Western Algeria.

Nest construction was carried out primarily by males. The males also spent more time in nest defense than females. Nest construction was more frequent in the morning, but display was more frequent in the afternoon. Both sexes shared incubation. When left alone, or not regularly relieved, females extended their contribution to incubation. Males incubated less during windy conditions. Time spent brooding depended on age of nestlings and weather conditions. Females spent more time in these activities than males. Initially, the contribution by males to feeding young was comparable to that of females, though at the end of the brooding period it often diminished. When wind was strong or temperature high nestling feeding rates decreased.

The wind appears to be the climate factor that most influenced the activities and reproductive success of the sparrows in this study.

### 1. INTRODUCTION

Studies of granivorous birds have examined the effects of Man-modified areas on reproductive success (INDYKIEWICZ and PINOWSKI 1985). Species in the genus *Passer* have been valuable in this work because of their close association with human habitation (DYER et al. 1977, PINOWSKA and PINOWSKI 1977, MURPHY 1978a, ALONSO 1983 (1984), METZMACHER 1986). Reproductive success has also been analysed in relation to habitat (ESCOBAR and GIL-DELGADO 1984), climatic conditions, and nest environment (MC GILLIVRAY 1981). Complementary to these

field studies, laboratory studies have examined body composition of females in relation to the number of clutches and total number of eggs produced per season (PINOWSKA 1979).

During reproduction, the interaction of environmental factors and parental behaviour also can influence reproductive success (INDYKIEWICZ and PINOWSKI 1985). Certain aspects of this problem have been studied in the House Sparrow. MURPHY (1978b), for example, studied variation in clutch size and fledging success in relation to changes in day length and temperature. The feeding rate also varies according to age, number of offspring, time of day, sex of the parent (SUMMERS-SMITH 1963, SEEL 1969), the presence of helpers (SAPPINGTON 1977), climatic conditions and the body-size of the parents (MC GILLIVRAY 1984). This latter author also pointed out that only adult females increase their feeding rates in cloudy and rainy weather.

In this paper, I describe and compare activity patterns of the Spanish Sparrow [*Passer hispaniolensis* (Temm.)] during one reproductive cycle and characterize the reproductive ecology of the population. I also evaluate the relationships between environmental factors and incubation, brooding and care of the young. Finally, I relate reproductive success to the climatic context and behavioural patterns of the adults.

## 2. LOCATION OF THE STUDY

The study was conducted on the plain of Es Sénia (35°36' N, 0°40' W, altitude 100 m), 8 km to the south of Oran, Western Algeria, beginning on 15 April 1983. The nests were generally spread throughout three acacia hedges, and incidentally in jujube trees, *Zizyphus lotus* Lam. and certain olive trees *Olea europaea* L. (Fig. 1). Near these hedges were sown fields of oats, corn and barley. To drink, the sparrows flew to the irrigated market-garden plantations; the waters of the big lake, to the south of the colony, were salty.

The climatic data were obtained from the meteorological station of Es Sénia airport, about 5 km from the colony. In this weather station, air temperature and wind velocity were noted every three hours. During the reproductive period in 1983, rainfall was exceptionally slight: 1.3 mm for the month of April compared with an average 40 mm and 5.0 mm in May compared with average 21 mm (BALDY 1974). During the first fortnight of May there were several windy days. The average temperature, however, was normal: 15.3°C for April and 17.7°C for May.

## 3. MATERIALS AND METHODS

### 3.1. THE ADULTS

The size of the adult population was estimated by counting nests in the colony (METZMACHER 1986). During the construction of nests and incubation, adult activity was followed at four nests. The state of construction of these nests at the

beginning of the observation period suggested that these pairs were all at the same stage of reproduction. During the nestling period, five nests were observed. All were chosen in different points of Sector 1 (see Fig. 1). When a nest was abandoned, one of the neighbouring nests was taken as a replacement. As a general rule, from 16 April to 15 May, observations were carried out every other day, with two sessions per day (8 a.m. to 12 midday, 1.45 p.m. to 5 p.m.). During each session, and always following the same order, each observation period lasted 30 consecutive minutes. In the course of and between these periods, notes were also made on the behaviour of sparrows at other nests. Activity was monitored with binoculars and a telescope, and noted every 30 s.

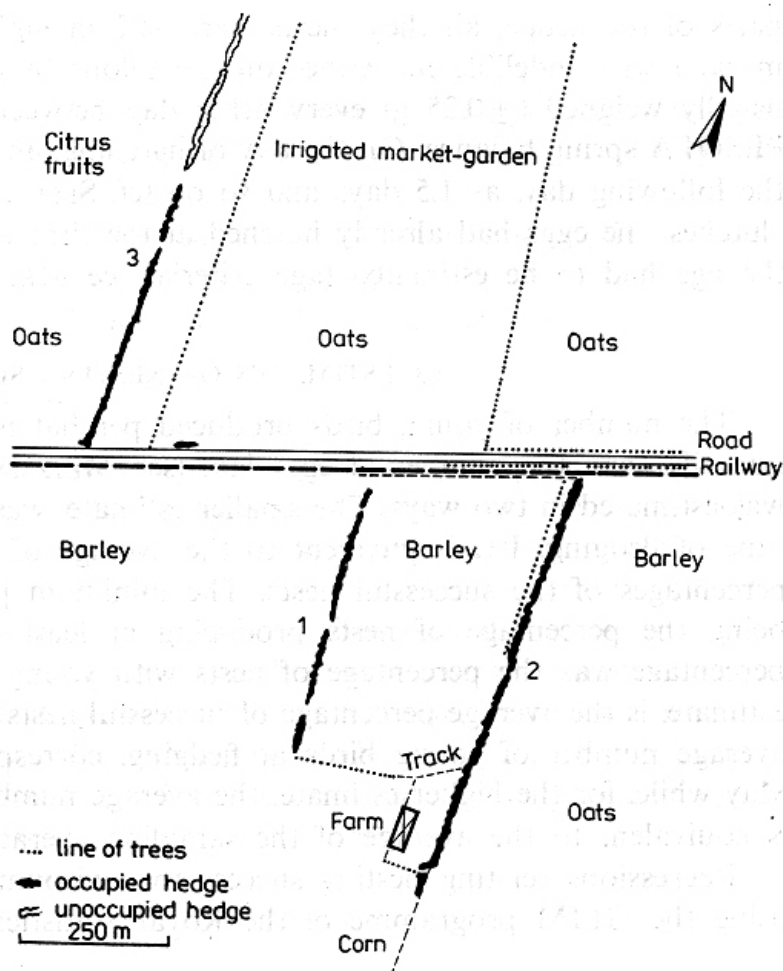


Fig. 1. Map of the study area

I recognized the following activities: (1) flight; (2) short flight consisting of a change of perch; (3) building activity, including transport and fitting together of nest materials; (4) aggressive pursuit; (5) display; (6) copulation; (7) defence of territory consisting of aggressive display; (8) cheeping; (9) preening; (10) "rest", on the perch or in the nest. With the exception of territorial defence, cheeping,

preening (all of which could be done while at "rest") the other activities were mutually exclusive. When cheeping and preening alternated rapidly, half of the time was attributed to each activity.

### 3.2. THE EGGS AND YOUNG

Clutch-size and brood-size was established through systematic sampling (see METZMACHER 1986). For eggs, 40 nests were visited on 28 April. For nestlings, 28 nests (in sectors 2 and 3) and 39 nests (from all three sectors) were examined on 11 and 15 May, respectively.

Growth of young was followed in 7 broods of Sector 1. Chosen in different parts of the hedge, all these nests were < 2 m high. Nestlings were individually marked with indelible ink either on the talons or on the tarsus. Nestlings were usually weighed ( $\pm 0.25$  g) every other day between 5.00 and 6.00 p.m. using a PESOLA spring balance. On the day of hatching, an age of 0.5 days was assigned; the following day, as 1.5 days and so on (cf. SEEL 1970). In five out of the seven clutches, the eggs had already hatched at the time of the first visit; consequently, the age had to be estimated (age criteria, see METZMACHER 1986).

### 3.3. ESTIMATES OF NESTING SUCCESS

The number of young birds produced per hatched clutch is more difficult to quantify than the number of eggs laid (see METZMACHER 1986). Fledging success was estimated in two ways. The smaller estimate, was calculated on 15 May at the time of fledging. It is equivalent to the average of the minimum and maximum percentages of the successful nests. The minimum percentage was considered as being the percentage of nests producing at least one fledgling; the maximum percentage was the percentage of nests with young bird(s) or faeces. The higher estimate, is the average percentage of successful nests on 11 May. Furthermore, the average number of young birds at fledging, corresponds to the sampling on 15 May while, for the higher estimate, the average number of young birds at fledging is equivalent to the average of the sampling averages on 11 and 15 May.

Regressions relating nesting success to environmental factors were calculated using the GLIM programme of the Royal Statistical Society, London.

## 4. RESULTS

### 4.1. REPRODUCTIVE SUCCESS

#### 4.1.1. SIZE OF THE NESTING COLONY

In 1983, 4678 nests were counted, 33.8, 28.8 and 37.4% of these were situated in Sectors 1, 2, 3, respectively (Fig. 1). I estimated 4023 females in the colony. This

was based on the absence of the nest lining in 14<sup>0</sup>/<sub>0</sub> of the nests. The lining is closely associated with the presence of a female. Finally, since polygamy is unknown in this species, the adult population was estimated to be a minimum of 8046 birds.

#### 4.1.2. CLUTCH-SIZE

The clutch-size ranged between 3 and 6 eggs; in 87.9<sup>0</sup>/<sub>0</sub>, the clutch was of 4 or 5 eggs. The average was 4.79 eggs per nest ( $SD = 0.65$ ,  $n = 33$ ) and the mode was 5.

#### 4.1.3. FLEDGING SUCCESS

95.6<sup>0</sup>/<sub>0</sub> of the eggs hatched. 2.9<sup>0</sup>/<sub>0</sub> of the lost clutches were due to nest abandonment (117 clutches of 4023). The number of broods producing at least one fledgling was estimated at 50<sup>0</sup>/<sub>0</sub> (smaller estimate) and at 53.4<sup>0</sup>/<sub>0</sub> (higher estimate). The number of fledglings produced per successful brood was estimated at 1.85 and at 2.09 respectively.

Differences in estimates between the smaller estimate and the higher estimate amounted to 20.9<sup>0</sup>/<sub>0</sub>. From 3906 hatched clutches (4023 - 117), the higher estimate amounted to 4359 fledglings, while for the smaller there were only 3605.

#### 4.1.4. NESTLING AND ADULT MORTALITY

In the sample of 7 clutches observed for growth, 19 young birds out of 32 (59.4<sup>0</sup>/<sub>0</sub>) did not fledge. Four were found dead in the nest after very windy days. Twelve other nestlings that were smaller than average also later disappeared from their nests. This suggests that death was caused by hunger or sickness. On the other hand, 3 nest mates showing normal growth disappeared together a day or two after their last weighing, suggesting that they were lost to predation.

Some predators did, indeed, frequent the colony, occasionally a snake, probably *Elaphe scalaris* (Schinz), and regularly at the end of the nestling period, the cattle egret, *Bubulcus ibis* L., (a maximum of 14 were observed). The egrets apparently preferred to search for nests in the upper part of the hedges.

TABLE I

*The numbers of Spanish Sparrows killed by car on 1 km of road*

| Dates    | Females | Males | Total |
|----------|---------|-------|-------|
| April 16 | 2       | 15    | 17    |
| April 28 | 4       | 1     | 5     |
| May 20   | 2       | 0     | 2     |
| Total    | 8       | 16    | 24    |

Road traffic was an important cause of mortality for adults. A count was made on three occasions over distance of approximately 1 km (Table I). The victims were mainly male birds which were killed during the nest building period.

#### 4.1.5. CHRONOLOGY OF THE REPRODUCTIVE CYCLE

The timing of major events in the reproductive cycle are shown in Figure 2. For a nine-day period, from 14–22 April, the birds built nests. Then, at the beginning of incubation, this activity decreased markedly and came to a complete stop at the end of incubation and during the nestling periods.

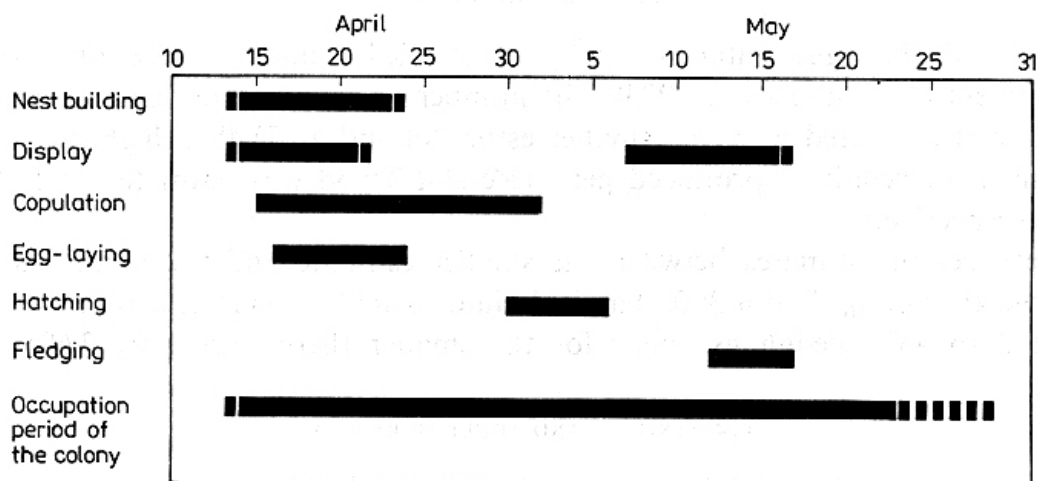


Fig. 2. Chronology of reproduction

Displays not followed by copulation were noted during the nest building period, and then, from 7 May onwards, during the second week of the nestling period. Copulation together with display apparently only took place from 15 April–1 May, only just preceding the beginning of egg-laying and ending at the beginning of hatching. These last two stages, which are highly synchronized, lasted about 8 and 6 days, respectively. The fledging period was staggered from 12 to 16 May. Finally, the abandonment of the colony took place between 22 and 29 May.

## 4.2. REPRODUCTIVE BEHAVIOUR

### 4.2.1. NEST BUILDING

The patterns of nest building activity varied over the day; both sexes were more active in the morning than in the afternoon (Figs. 3a and 3b). The pattern also varied in relation to the sex; males spent more time than the females in building activities (Figs. 3a and 3b). The females co-operated more, especially with addition of nest lining, towards the end of nest building.

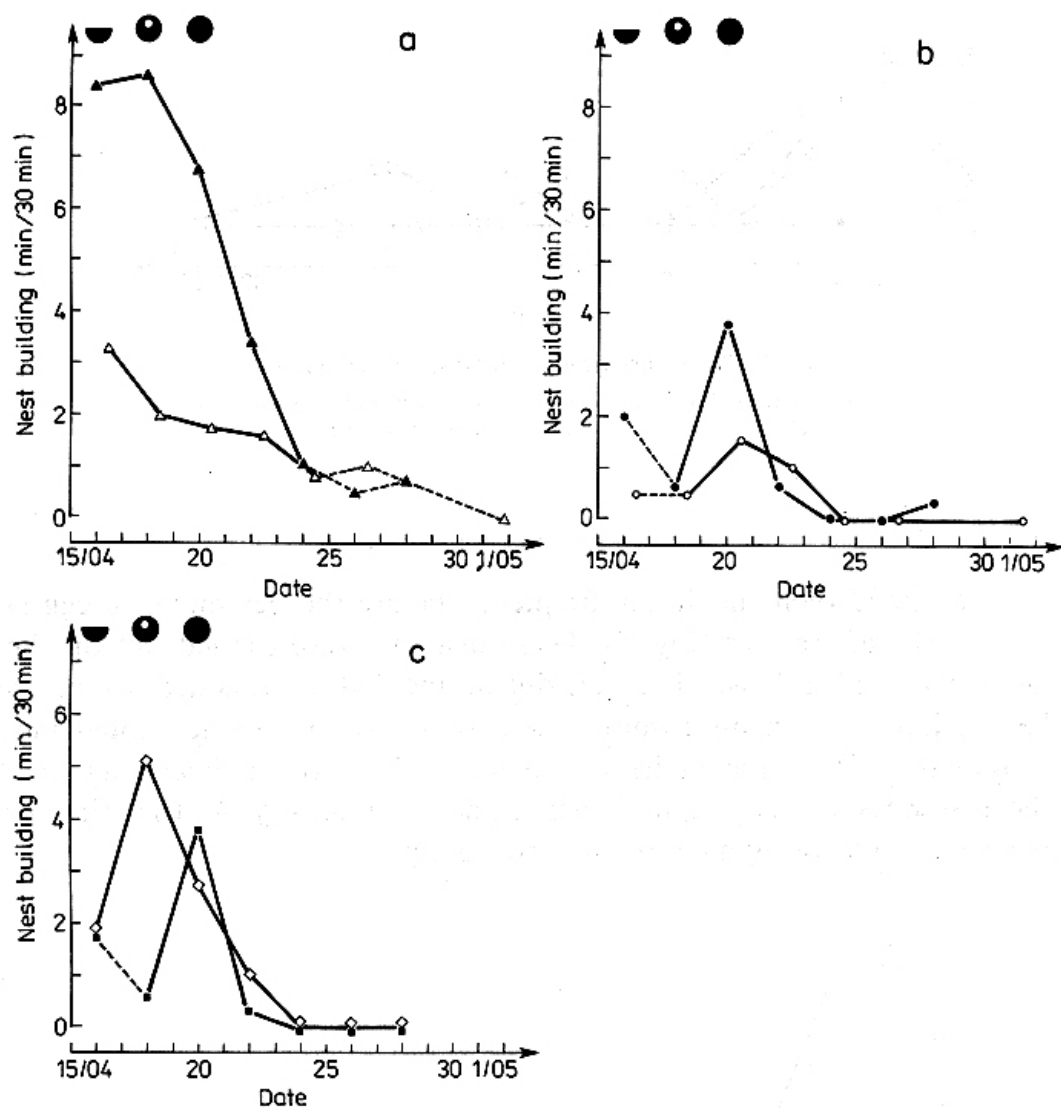


Fig. 3. Time variations among nest building activities (4 nests observed)

Symbols at the top of each chart represent schema of the nest construction; full symbols — morning activity, hollow symbols — afternoon activity; males — diamond shapes and triangles; females — squares and circles; transport and arranging of materials — circles and triangles; arranging only — squares and diamond shapes; dotted lines — sampling of two individuals; a, b — building activity for males and females; c — arranging of materials (males and females, in the morning)

#### 4.2.2. AGONISTIC BEHAVIOUR

The sparrows gave little time to aggressive activity (Fig. 4). However, such activities were, in general, more frequent among the males than females. Furthermore, the frequency of aggression tended to decrease as time went on, and, at the end of incubation, it was no longer noted. During the nest building period, defence of territory was assured by threatening postures comparable to those described for the House Sparrow (SUMMERS-SMITH 1963). These postures were as infrequent as aggressive activity. But, as we shall see later, the sparrows frequently had recourse to vocal jousts in order to mark their nests.

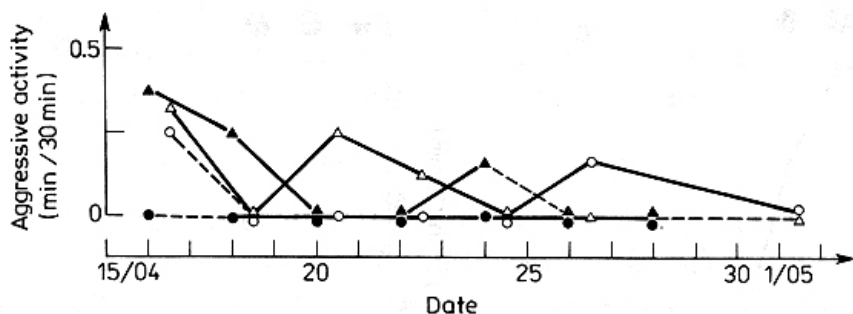


Fig. 4. Time variation in aggressive behaviour

Full symbols—morning activity, hollow symbols—afternoon activity; males—triangles; females—circles; dotted lines—sampling of two individuals

#### 4.2.3. DISPLAY AND COPULATION

Displays attained their maximum frequency before the beginning of egg-laying, particularly in the afternoons (Fig. 5). These displays were carried out on the nest even while it was still unfinished. Later, during incubation, this activity noticeably diminished in intensity. In my sample, the activity was no longer noted independent of copulation. With the males in particular, however, it began again at the end of the first week of fledging and then gained in intensity. At that time certain birds displayed while bringing food to the young.

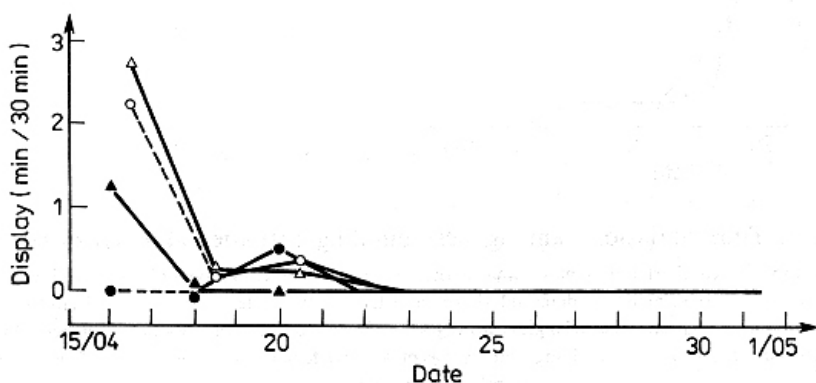


Fig. 5. Time variation in displaying behaviour not associated with copulation

For symbols see Fig. 4

The sexual display (BORTOLI 1969, ALONSO 1984), was accompanied by vocal utterances seemingly disyllabic. Copulation performed near the nest began with these noisy displays. It was noted at different times of the day, and occurred until the eggs hatched (Fig. 6). After egg-laying, copulation likely functions to maintain the pair bond.



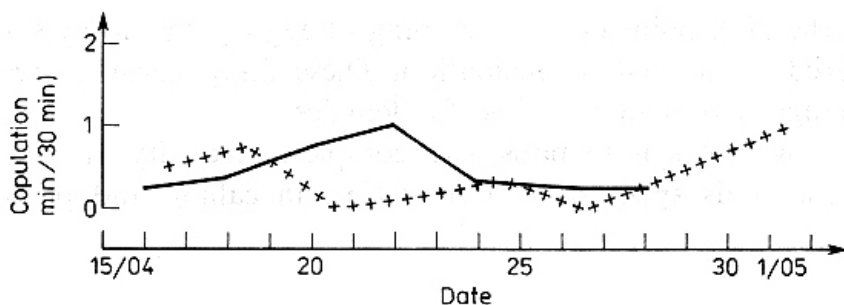


Fig. 6. Time variation in copulatory behaviour

Full line - morning; crosses - afternoon

#### 4.2.4. "REST" AND INCUBATION

Before the eggs hatched, both sexes spent from 33–66% of their time in "rest" and incubation.

The curves of Figures 7a and b show two maxima; the first, during the period of nest construction and the second, during incubation. Between these there is a minimum, particularly noticeable for the males. Since this is connected with a maximum number of absences, it is not possible to affirm that, ipso facto, it reflects maximum activity; the birds could rest away from the nest. Furthermore, minimum rest of the females appeared before that of the males and apparently

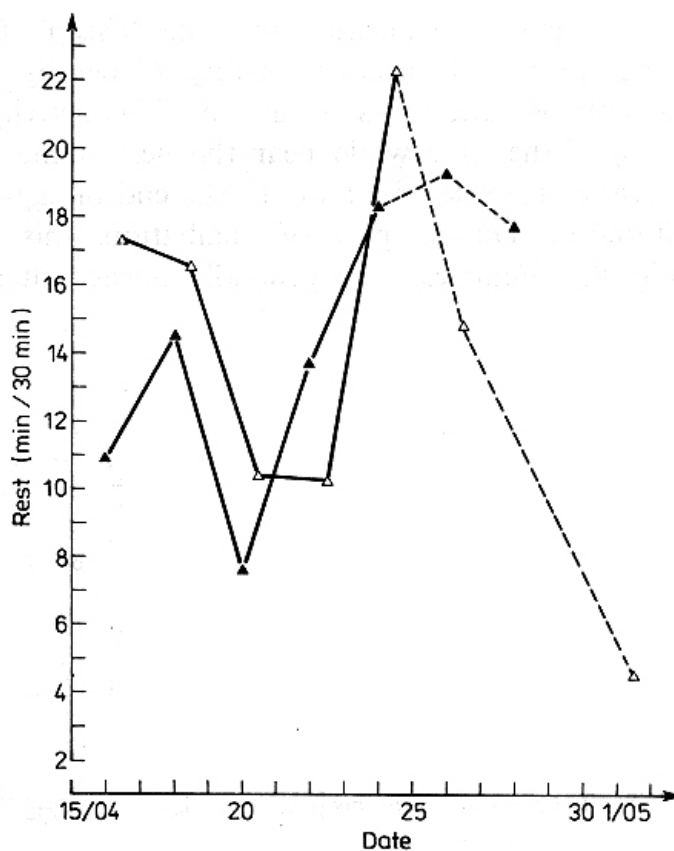


Fig. 7a. Time variation in resting behaviour by males

For symbols see Fig. 4

coincided with the high point of the beginning of egg-laying. In my sample, 2 of 4 males disappeared at the end of incubation. These disappearances resulted in an increase in average length of rest-time for females.

Rest is not, however, synonymous with complete inactivity. Indeed, when they were perched, the birds spent part of their time in calling and preening.

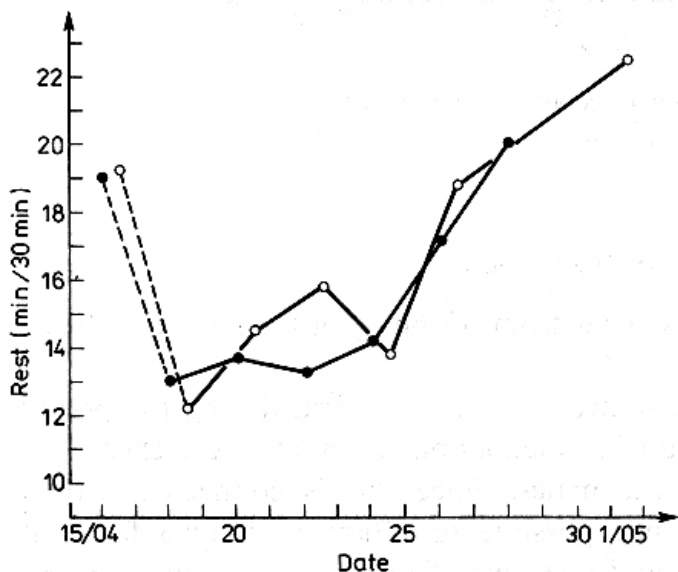


Fig. 7b. Time variation in resting behaviour by females

For symbols see Fig. 4

#### 4.2.5. VOCALIZATIONS

The main vocalization was the "cheep". Cheeping appeared to be of simple structure but of variable tonality. Generally, the males cheeped more frequently than the females (Figs. 8a and b). This activity could take, on the average, up to 30% of the time while near the nest. Time spent by males cheeping tended to decrease from nest building to the end of egg-laying, both in the morning and the afternoon. During part of incubation, this activity could, however, redevelop (Fig. 8a). Females were generally noisier after the end of egg-laying (Fig. 8b).

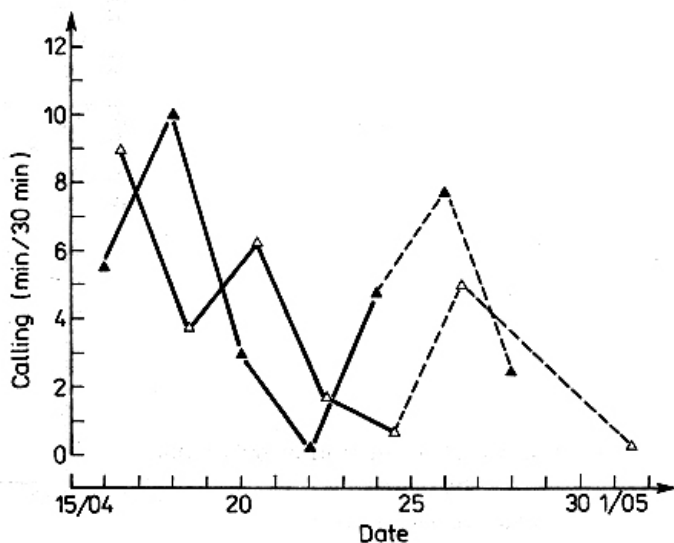
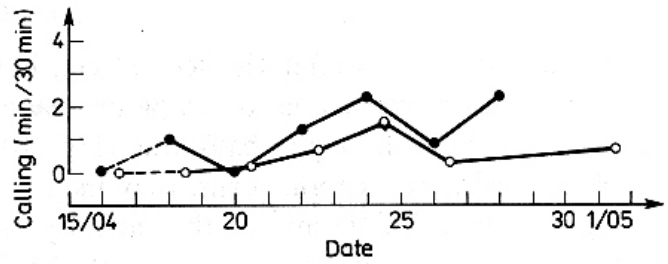


Fig. 8a. Time variation in cheeping by males

For symbols see Fig. 4

Fig. 8b. Time variation in cheeping by females

For symbols see Fig. 4



#### 4.2.6. PREENING

Preening frequently alternated with bouts of cheeping. For males, the length of this activity did not appear to fluctuate in a very defined sense (Fig. 9a). For females, however, preening decreased during incubation (Fig. 9b).

Fig. 9a. Time variation in preening by males

For symbols see Fig. 4

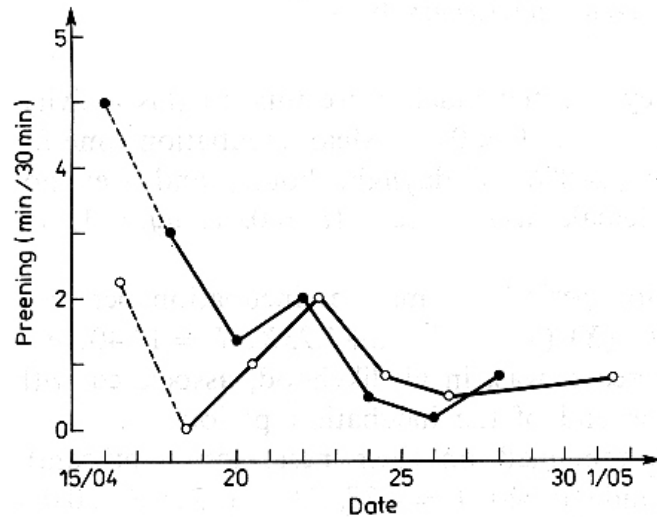
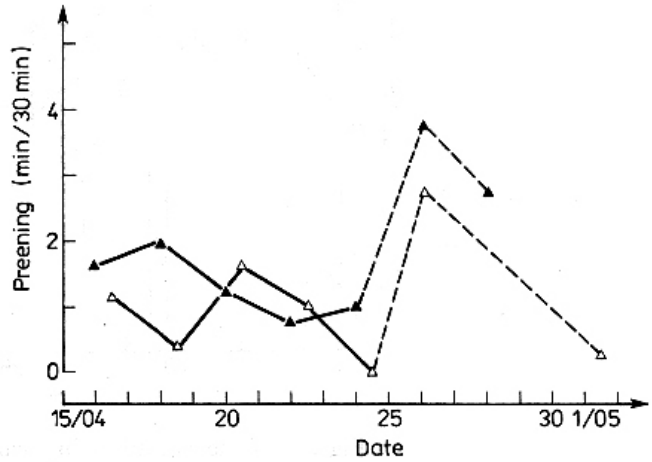


Fig. 9b. Time variation in preening by females

For symbols see Fig. 4

## 4.2.7. INCUBATION

Incubation begins after the second egg is laid (GAVRILOV 1963). In my sample, the time spent in incubation rapidly reached an average maximum value of approximately 19 min per half-hour (Fig. 10).

When the parents took turns, they incubated the eggs, on average, 72% of the daylight hours. Furthermore, this activity was equally shared; the female was responsible for an average of 48% of the incubation time (34.4% of daylight hours), the male 52% (37.5% of daylight hours).

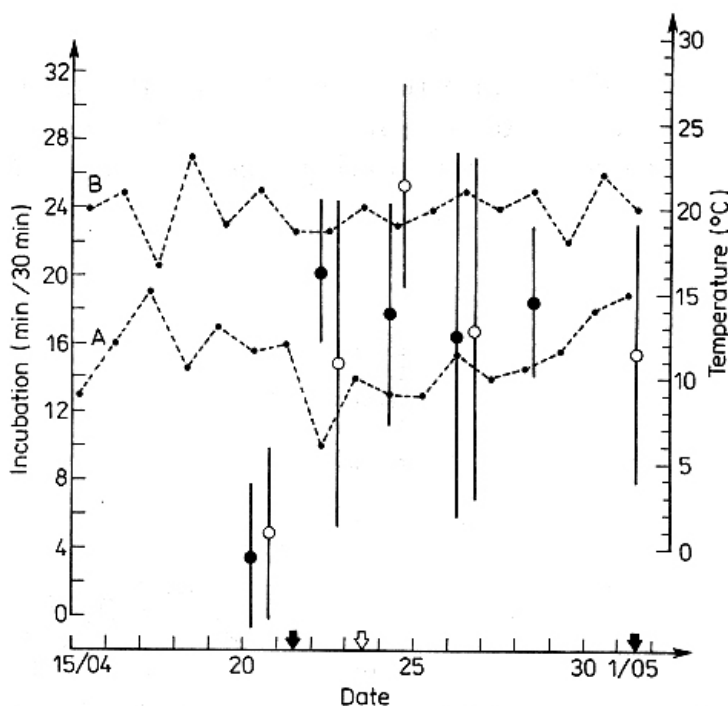


Fig. 10. Time variation in incubation of the eggs

Full circles - morning average; hollow circles - afternoon average; average  $\pm$  one standard deviation;  $n$  - number of nests = 4; A - temperature at 6.00 a.m.; B - temperature at 12 o'clock midday; full arrows - windy days; hollow arrows - half-day windy (see METZMACHER 1985)

When females incubated alone, they devoted much more time to this activity, on the average 61.5% ( $F = 4.18$ ;  $d.f. = 1, 30$ ;  $P < 0.05$ ). Mean incubation time for males increased far less when alone (44.8% of daylight hours) and was not significantly greater than when the female was present ( $F = 0.41$ ;  $d.f. = 1, 19$ ,  $P > 0.05$ ).

For females the length of incubation periods ( $Y$ , minutes incubation per half-hour) increased significantly with date ( $X$ ) ( $Y = -16.92 + 1.23X$ ,  $F = 13.40$ ;  $d.f. = 1, 21$ ;  $P < 0.01$ ,  $r^2 = 0.39$ ). This increase, was, in all likelihood, associated with the disappearance of two males at the end of the incubation period.

Following a disturbance, females remained on their nests for significantly shorter periods than when they were undisturbed ( $F = 4.37$ ,  $d.f. = 1, 21$ ;  $P < 0.05$ ).

They remained perturbed up to several hours after a predator approached the nest, and after hesitated to return to the nest when an observer was nearby.

For females I found no relation between wind and incubation time, but for males incubation time ( $Y$ , minutes per half-hour) decreased significantly with increasing wind velocity ( $X$  m/sec) ( $Y = 27.42 - 2.55 X$ ,  $F = 7.43$ ;  $df. = 1, 19$ ;  $P < 0.05$ ,  $r^2 = 0.28$ ).

During the period of maximum incubation, there were on average 2.3 interruptions of incubation per half-hour. These breaks lasted about two minutes when the two adults alternated on the eggs, and about six minutes when the incubating bird was alone or irregularly relieved. Females, as well as males, left the nest for periods averaging 6 to 7 minutes (females, 0.5 to 16 minutes; males, 1 to 19 minutes). Female absences were asymmetrical having a modal value of 8 to 9 minutes. This asymmetry was the result of disturbances; each time the male brought material to the nest, the female had to suspend incubation. She also sometimes interrupted incubation to chase away a congener from near the nest.

#### 4.2.8. BROODING AND NESTLING CARE

##### 4.2.8.1. BROODING

For the first few days after hatching, the young birds were still brooded almost half time (Fig. 11). Afterwards brooding decreased considerably. However, on 9 May, a very windy and cold day, brooding activity abruptly increased. I found a significant relation between length of brooding ( $Y$ , minutes per half-hour) and wind velocity ( $X$ , m/sec) ( $Y = 4.84 + 0.52 X$ ,  $F = 8.12$ ;  $df. = 1, 29$ ;  $P < 0.01$ ,  $r^2 = 0.22$ ).

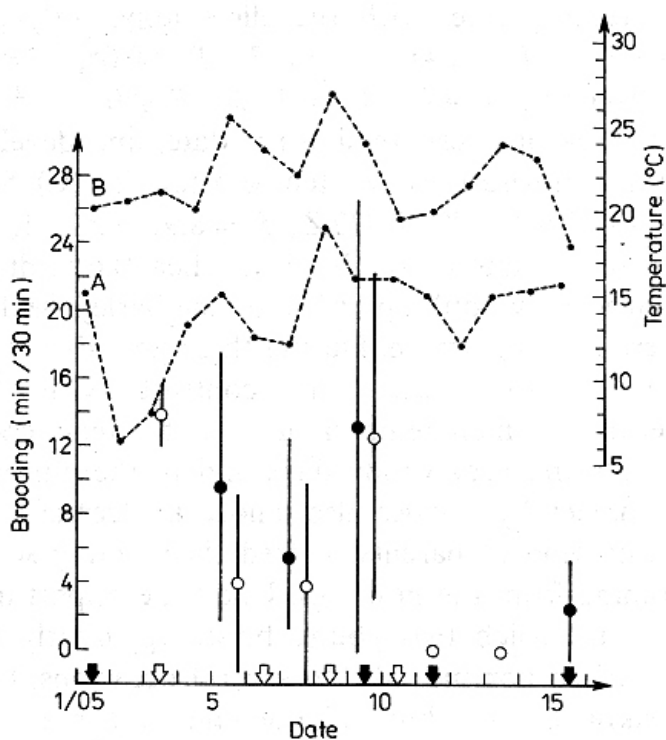


Fig. 11. Time variation in brooding of the nestlings

For symbols see Fig. 10

While both parents were concerned with brooding the young, the role of the female was nevertheless preponderant. For 6 nests (23 half-hours of observation) females brooded on average 8.5 min/half-hour, while males (18 half-hours) spent on average 3.6 min/half-hour. I did, however, find significant differences for females in incubation time among nests ( $F = 8.11$ ;  $d.f. = 4, 20$ ;  $P < 0.05$ ).

During the second week, the nestlings no longer required brooding as their feathers had broken out of the sheaths (METZMACHER 1986). In the daytime, in dry weather, the parents no longer occupied the nest even when the wind was very strong (for example, on 11 May).

#### 4.8.2.2. NESTLING CARE

When males fed the young, their average feeding frequency (4.6/half-hour) was not significantly different from that of females (3.0/half-hour/14 half-hours of observation) ( $F = 1.42$ ;  $d.f. = 1, 26$ ). During the same period, for females who did the feeding alone, this frequency (3.4/half-hour; over 15 half-hours' observation) was similar to that of paired females and not significantly different.

By the end of the fledging periods, 13 and 15 May, males no longer fed the young in any of the five nests observed. For the females, the feeding frequency averaged 5.5/half-hour (over 9 half-hours' observation). This is similar to results for the House Sparrow (MC GILLIVRAY 1981). The other values, however, are notably lower.

I found that feeding rate ( $Y$ , feedings per half-hour) was related to several other factors. It was significantly higher when both parents participated in providing for the young ( $F = 14.0$ ;  $d.f. = 1, 40$ ;  $P < 0.01$ ). Wind ( $X$ , m/sec) was inversely related to feeding rate, with the effect apparently greater in the afternoon ( $Y = 15.37 - 1.21 X$ ;  $F = 4.41$ ,  $d.f. = 1, 38$ ,  $P < 0.05$ ,  $r^2 = 0.17$ ), than in the morning ( $Y = 4.25 - 0.05 X$ ;  $F = 4.41$ ,  $d.f. = 1, 38$ ,  $P < 0.05$ ,  $r^2 = 0.17$ ). Feeding rate also increased with seasonal progression ( $X$ , date) and development of the nestlings, however, at high temperatures ( $Z$ , temperature in °C) feeding rates tended to decrease ( $Y = 13.97 + 0.68 X - 0.832 Z$ ;  $F = 8.92$ ,  $d.f. = 1, 40$ ,  $P < 0.01$ ,  $r^2 = 0.28$ ).

In the middle of the day, when the temperature was normally at its highest, journeys by adult sparrows to the barley fields and the irrigated zones (see Fig. 1) were at a maximum. During these periods the adult birds perhaps spent more time on their own needs. This contrasts with the incubation period when, during periods of high temperatures, nest attentiveness increased (METZMACHER 1985).

During very windy days and in the afternoons especially, the average feeding frequency by females also tended to decrease ( $F = 6.93$ ,  $d.f. = 1, 29$ ,  $P < 0.05$ ). The motivation of parents to feed their young seemed also to depend on stimulation coming from the nestlings. I had the opportunity of noting this while observing a nest in which two young birds, apparently ill, (they were later to die), neither vocalized nor moved. On several occasions, the female landed on the nest with a beakful of prey but did not enter the nest.

## 5. DISCUSSION AND CONCLUSIONS

Reproductive success of Spanish Sparrows was low in the Es Sénia colony, in 1983. Clutch-size and hatching success were not, however, lower than those of the other colonies in the Oran district (see METZMACHER 1986). In contrast, the percentage of successful broods and fledging success were rather low. In order to explain these effects, I will examine the climatic and behavioural factors likely to have influenced them (for other aspects concerning the variation of reproductive success, see also METZMACHER 1986).

### 5.1. CLIMATIC FACTORS

The wind appears to be the climatic factor that most influenced the activities and reproductive success of the sparrows. Hatching success was very high, thus the influence of wind during incubation would seem to be secondary. Nevertheless, wind could have an indirect effect. On windy days, the males were less assiduous in assuming incubation duties. The females, because they were relieved by males less frequently, had less time for feeding themselves. As a result, they had greater difficulty in restoring the reserves of fat which they had used up during egg-laying (PINOWSKA 1979). Females who were in poor condition could thus be less effective in rearing their nestlings and less able to lay additional clutches.

In the nestling period, increases in wind speed are related to decreases in feeding frequency. The pattern of this activity (Fig. 12) thus presents fluctuations that are both very marked and very specific. Normally, the feeding frequency increases during the first week of the brooding period, then levels off and remains constant until the young are near fledging (SUMMERS-SMITH 1963, SEEL 1969). In contrast, in my colony the frequency of feeding decreased as the young developed. The reduction in feeding frequency did not appear to have been compensated for with larger prey. This frequency reduction is analogous to that noted in windy weather for female House Sparrows (Mc GILLIVRAY 1984).

Flight in a strong wind undoubtedly requires additional energy that the birds may not be able to supply. Or they may need to compensate for the added energy demand by an increase in feeding time. Thus, the physical capacities of the parents to gather food might limit fledging success.

This hypothesis has received some support from work on the House Sparrow. Results of SEEL (1969, 1970) suggest an energy limitation based on the parents ability to gather food. SEEL found that the frequency of feeding does not increase in broods of more than three young birds. However, limits on adult feeding rates may have alone not been responsible. Rather it may be an adaptation to avoid attracting the neighbours' attention by too frequent feeding trips (*ibidem*).

An energy limitation could, however, account for the higher rate of adult mortality during the reproduction period (GRAMET 1973). For the Willow Tit

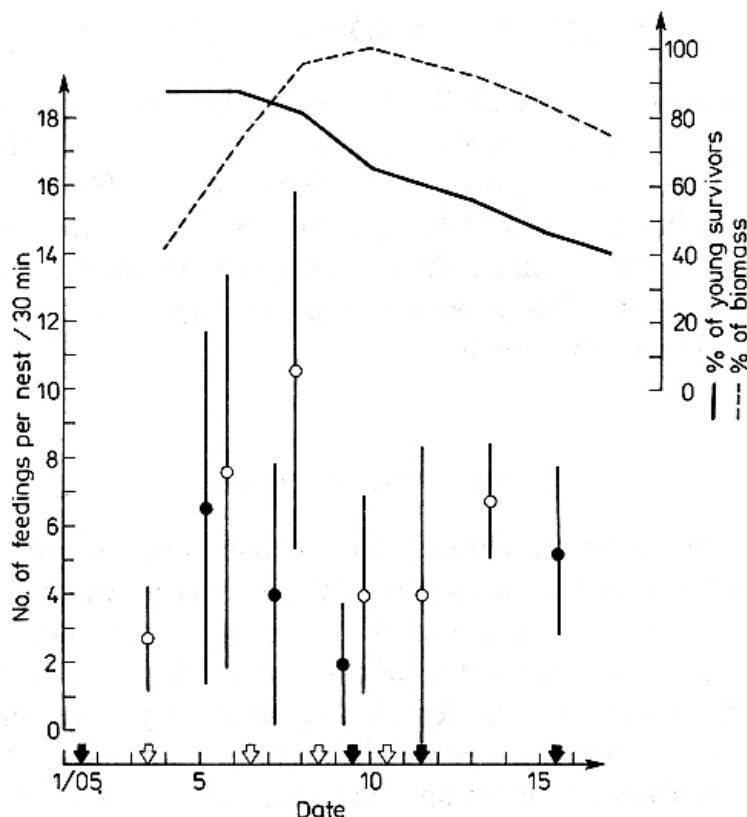


Fig. 12. Top — survival curve of nestlings and variation in their biomass (sampling of 7 broods). Bottom — variation in average feeding rate (5 nests observed)

For symbols see Fig. 10

(*Parus montanus* Conv.), for example, parental survival is negatively linked to the average number of young birds produced per adult (EKMAN and ASKEMNO 1986) and for the House Martin [*Delichon urbica* (L.)], the survival rate is less for females having two broods (BRYANT 1979).

On the other hand, the wind acts also on the activity of the arthropod prey. If it slows down their activity as does temperature, it may well render them less vulnerable to their predators. This effect has been noted for the Coal Tit (*Parus ater* L.) chasing spiders (AVERY and KREBS 1984).

## 5.2. BEHAVIOURAL FACTORS

Behaviour of nestlings can influence parental behaviour. For example, the silent and unmoving young birds did not incite their parents to feed them. As with the nestlings of other species, (see, for example, HALLET-LIBOIS 1985), activity of the young sparrows seems to influence the rate of feeding. Changes in the level of activity could, in consequence, modulate reproductive success.

During the course of one reproductive cycle, changes in male behaviour may



also effect reproductive success. As with the House Sparrow, (SELL 1969, pers. obs.), male Spanish Sparrows begin to display again during the second half of the brooding period. The re-appearance of this behaviour and its growth in intensity result in a decrease in visits to the nest. At the end of the brooding period, the five females observed were alone in feeding the young. It is unlikely that all the males who had disappeared were dead because at the same period many males were displaying in different parts of the hedge. According to SEEL (1969), such behaviour would stimulate females to reproduce again. This behaviour would thus encourage a maximum of clutches per reproduction season. But this behaviour can also have negative effects, especially on the production of the young. It is quite probable that nestlings fed by the female alone have a lower success rate than nestlings fed by both adults, especially when the climatic conditions are unfavourable. This is the case, for example, with the Savannah Sparrow [*Passerculus sandwichensis* (Gmel.)] (WEATHERHEAD 1979), the Marsh Warbler [*Acrocephalus palustris* (Bechst.)] (DOWSETT-LEMAIRE 1981) and the Kingfisher (*Alcedo atthis* L.) (HALLET-LIBOIS 1985).

At the end of the brooding period, the behaviour of the Spanish Sparrow (this study) is similar to the House Sparrow (SUMMERS-SMITH 1963, SEEL 1969, SAPPINGTON 1975, NORTH 1981); the male takes proportionally less responsibility than the female for feeding the young. For the House Sparrow, the contrast between sexes is even greater in northerly latitudes where MC GILLIVARY (1984) found that the simultaneous loss of weight for the large males is likely a result of stress. However, it seems that this interpretation is insufficient as it does not explain the re-activation of display behaviour noted for the males of both species immediately after the first week of brooding. The tendency to display could thus suppress the tendency to feed, which might enhance the opportunity for reproduction.

Given that re-activation of sexual display can signify an increase in the influence of internal factors, the endocrine changes in male sparrows merit closer study. This would provide an understanding of the way these factors interact with the external environment. Such an approach, placed in its ecological and behavioural context, would provide a better understanding of the role of the sexes in the reproductive cycle in general, and in the raising of the young in particular.

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