

Effect of Food Availability on Incubation Period in the Pied Flycatcher (*Ficedula hypoleuca*)

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Incubation may be stressful because it restricts time for foraging (Walsberg 1983, Murphy and Haukioja 1986). Many bird species in which the females incubate alone, females obtain part of their food from their mates (e.g. Lack 1968, Ricklefs 1974, Lyon and Montgomerie 1985, Lifjeld and Slagsvold 1986, Nilsson and Smith 1988). This behavior may function to supply the female with energy or essential nutrients, thereby increasing her nest attentiveness and shortening periods away from the nest (e.g. Lifjeld and Slagsvold 1986, Nilsson and Smith 1988, Smith et al. 1989).

This "female-nutrition hypothesis" (Royama 1966) mainly rests on two arguments. First, a reduction in male assistance, caused by experimental removal of males (Lyon and Montgomerie 1985) or by the male being polygynously mated (Lifjeld and Slagsvold 1986, Lifjeld et al. 1987), reduces female attentiveness. This decreases hatching success and increases the length of the incubation period (Lyon and Montgomerie 1985, Lifjeld and Slagsvold 1986, Lifjeld et al. 1987). Second, there is the negative correlation of the rate of feeding during incubation with: (1) the proportion of time the female spends off the nest (Lifjeld et al. 1987); and (2) the length of the incubation period (Nilsson and Smith 1988).

Female Wheatears (*Oenanthe oenanthe*) experimentally supplied with food during incubation had significantly shorter foraging recesses, but did not increase the length of time spent in the nest or hatching success compared to control females (Moreno 1989). Female Blue Tits (*Parus caeruleus*) supplied with food during incubation had a significantly shorter incubation period and a higher hatching success than control females (Nilsson and Smith 1988). In another similar experiment (Smith et al. 1989), female Pied Flycatchers (*Ficedula hypoleuca*) spent shorter periods away from the nest than control females.

Birds in poorer condition leave the nest more often to forage, thus increasing the variation in egg temperature, which may reduce hatching success (Martin 1987, Webb 1987) and prolong the incubation period (Martin 1987, Arcese and Smith 1988, Moreno and Carlson 1989, Smith et al. 1989). Prolonged incubation may increase predation on eggs and young (Ricklefs 1969, Martin 1987, Moreno and Carlson 1989, Weath-

ers and Sullivan 1989), and delayed hatching may reduce survival of young (Perrins 1965, Arcese and Smith 1985, Nilsson and Smith 1988, Tinbergen and Boerlijst 1990, Nilsson 1993, Nilsson and Svensson 1993).

In harsh environments, physiological constraints on a bird's incubation and feeding capacities are clearer than in more favorable conditions (Mertens 1987, Järvinen 1980, 1990). In the present study conducted in an unfavorable habitat (Sanz 1995), I experimentally increased the amount of food available to incubating females. The aim was to investigate whether food availability affect the duration of incubation and hatching success in an unfavorable habitat.

Methods.—The study was conducted in a montane forest of Scots pines (*Pinus sylvestris*) at an elevation of 1,900 m in the vicinity of Navacerrada Pass, Sierra de Guadarrama, central Spain (40°48'N, 4°01'W). The study plot was on steep northern slopes close to the tree limit, where snow can remain until well into May due to a severe climate (May temperature in 1970–1994, $\bar{x} = 5.9^\circ \pm \text{SD of } 2.2^\circ\text{C}$; Sanz 1995). In 1989, 250 nest boxes were erected in a grid with a 50-m spacing between adjacent boxes.

The feeding experiment was conducted during the breeding season of 1994. When two nest boxes were found with the same clutch size and laying date (± 1 day), one was assigned to the control group and the other to the experimental group. Incubating females were captured and weighed to the nearest 0.1 g with a spring balance on the first or second day after completion of laying, and then again on the tenth day (28 of 30 females could be weighed on second occasion).

Starting on day 12 of incubation, nest boxes were checked daily for signs of hatching. The incubation period was defined as the number of days between the completion of the clutch and the first signs of pipping. This is a minimum measure of incubation duration and differs from the usual measure (i.e. time from laying of last egg to hatching of last young; Drent 1975). In contrast to the usual measure, it is not biased by clutches where some eggs do not hatch. Nests were visited daily to check how many eggs hatched. Two measures of reproductive success were used, namely hatching success (percent of eggs hatched) and breeding success (percent of eggs laid that resulted in fledged young).

Experimental nests were provisioned with food from one day after the female had laid her last egg until hatching day. The food consisted of 10 g of live mealworms (larvae of *Tenebrio molitor*) in plastic cups placed

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TABLE 1. Mean (\pm SD) laying date (1 = 1 May), clutch size, incubation period (days), female initial mass (g), female final mass (g), and mass change (g) during incubation period with respect to experimental treatment. Sample sizes in parentheses.

	Control	Experimental	<i>t</i>
Laying date	32.30 \pm 1.15 (15)	32.53 \pm 1.30 (15)	0.74
Clutch size	4.80 \pm 0.41 (15)	4.80 \pm 0.41 (15)	0.00
Incubation period	14.33 \pm 0.72 (15)	13.73 \pm 0.70 (15)	2.30*
Initial mass	14.01 \pm 0.87 (15)	14.39 \pm 1.04 (15)	1.09
Final mass	14.12 \pm 0.67 (14)	14.67 \pm 0.82 (14)	1.94
Mass change	0.05 \pm 0.88 (14)	0.25 \pm 0.68 (14)	0.70

* $P < 0.05$; others not significant, $P > 0.05$.

daily on the front side and under the entrance of the nest boxes. Control nest boxes had empty plastic cups.

Results.—The mean food consumed daily was 9.7 \pm SD of 0.6 g (range 8–10 g, $n = 15$). The total food consumed per nest was on average 133.5 \pm 7.5 g (range 120–150 g, $n = 15$). Assuming that the assimilation efficiency of mealworms is 0.65 (Kacelnik 1984), the daily food consumption of 9.7 g would correspond to a daily metabolizable energy intake of 53.3 kJ (energy content of mealworms = 8.54 kJ \cdot g⁻¹; McCause and Widdowson 1960). Incubating Pied Flycatchers expend on average 60.7 kJ per day (Moreno and Sanz 1994). Assuming that males take one-half of the food, the food supplements represented 44.6% of the average energy requirements of females. Observations of the experimental nestboxes allowed me to verify that the Pied Flycatcher females made use of the feeders on their nest boxes. During some observations, the male took mealworms and fed them to his mate. No other birds were observed close to my experimental nest boxes.

The laying date and clutch size did not differ between experimental and control females while the duration of the incubation period differed significantly between control and experimental nests (Table 1). On average the experimental group had incubation periods 0.6 days shorter than the control group (Table 1).

The incubation period decreased significantly with laying date in the experimental group ($r = -0.54$, $df = 14$, $P = 0.04$), while it did not in the control group ($r = -0.09$, $df = 14$, $P = 0.76$). We used an ANCOVA (Sokal and Rohlf 1981) with experimental treatment as a factor and laying date as covariate to separate the effects of food availability and date on the duration of the incubation period. The incubation period differed significantly between experimental groups when the effect of date was removed (ANCOVA; model, $F = 4.40$, $df = 2$ and 29, $P = 0.022$; laying date, $F = 4.31$, $df = 1$ and 29, $P = 0.048$; experimental treatment, $F = 4.49$, $df = 1$ and 29, $P = 0.044$).

There was no significant effect of experimental treatment on initial female mass (Table 1). There was a nearly significant effect of experimental treatment on final female mass (Student *t*-test, $P = 0.06$; Table

1). There was no significant effect of experimental treatment on female body mass change during the incubation period (Table 1). However, female tarsus length differed significantly between experimental groups (control females, $\bar{x} = 17.39 \pm 0.72$ mm; experimental females, $\bar{x} = 17.91 \pm 0.49$ mm; $t = 2.32$, $df = 28$, $P = 0.03$). As final mass and mass change may depend on initial mass and female size, I performed ANCOVAs with experimental treatment as factor, and initial mass and tarsus length as covariates. There was no significant treatment effect on final mass when controlling for the effect of initial mass and tarsus length (ANCOVA; model, $F = 8.43$, $df = 3$ and 27, $P = 0.001$; factor, $F = 0.86$, $df = 1$ and 27, $P = 0.36$; covariate initial mass, $F = 12.30$, $df = 1$ and 27, $P = 0.002$; covariate tarsus length, $F = 4.96$, $df = 1$ and 27, $P = 0.036$). There was no significant effect of treatment on female mass change during incubation when controlling for the effect of initial mass and tarsus length (ANCOVA; model, $F = 8.07$, $df = 3$ and 27, $P = 0.001$; factor, $F = 0.86$, $df = 1$ and 27, $P = 0.36$; covariate initial mass, $F = 22.71$, $df = 1$ and 27, $P < 0.001$; covariate tarsus length, $F = 4.96$, $df = 1$ and 27, $P = 0.036$).

Pooling the experimental group, initial female mass during incubation did not correlate significantly with incubation period ($r = -0.11$, $df = 29$, $P = 0.57$). However, final mass and mass change during incubation showed negative correlations with incubation period (Fig. 1).

Hatching success did not differ significantly between experimental groups (Table 2). Breeding success, as well as the nestling body mass and tarsus length on the 13th day of nestling life, did not differ significantly between experimental groups (Table 2).

Discussion.—In this study, females that received extra food shortened their incubation period. In a previous experiment with Blue Tits, females experimentally supplied with food during incubation had a significantly shorter incubation period. Also, in a similar experiment with Wheatears, females that received extra food shortened the incubation period (Moreno 1989). A shorter incubation period may enhance the fitness of both parents, because it means a smaller probability of predation of eggs and an advance of

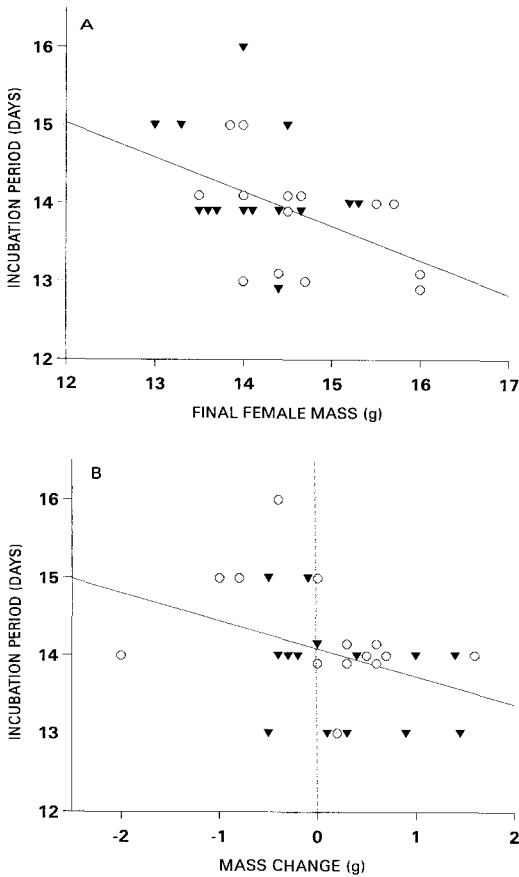


Fig. 1. Relationship of incubation period (Y; days) of control (circles) and experimental (triangles) females to: (A) final female mass (g); and (B) female mass change (g) during incubation period. Relative to final female mass: $Y = 20.31 - 0.44X$ ($F_{1,27} = 7.01$, $P = 0.014$, $r = -0.46$). Relative to female mass change: $Y = 14.09 - 0.36X$ ($F_{1,27} = 4.22$, $P = 0.05$, $r = -0.37$).

the hatching date (Ricklefs 1969, Martin 1987, Moreno and Carlson 1989, Weathers and Sullivan 1989).

Early hatching increases the survival prospects of young in several species (Perrins 1965, Kluyver et

al. 1977, Kikkawa 1980, Dhondt and Olaerts 1981, Hochachka 1990, Lundberg and Alatalo 1992). The shorter incubation period advances hatching date and, thus, may affect recruitment of fledglings (Lundberg and Alatalo 1992). Although experimental females received extra food at their nest boxes during the incubation period, they did not augment significantly their body reserves (Nilsson and Smith 1988). Experimental females probably spent more time on the nest (Smith et al. 1989), thus reducing the incubation period (Nilsson and Smith 1988). In my study, independently of the experimental group, heavier females at the end of their incubation period had significantly shorter incubation periods.

Hatching success did not differ between experimental groups. In this population of Pied Flycatchers, hatching success was positively correlated with female body mass during the first days of incubation period (Sanz 1995). Birds in poorer condition may leave the nest more often to forage; the resulting increase in variation in egg temperature may reduce hatching success (Aldrich and Raveling 1983, Morton and Pereyra 1985, Sibly and McCleery 1985, Jones 1987, Martin 1987). Hatching success decreases under adverse weather conditions (Sibly and McCleery 1985, Jones 1987, Martin 1987). During the spring of the experimental year (1994), the weather conditions were not especially harsh during the incubation phase, which may have reduced the effect of food availability on hatching success.

In conclusion, female Pied Flycatchers supplied with food at the nest box during incubation had significantly shorter incubation periods than control females. Clutches of experimental females did not hatch more successfully, and females did not differ in body condition during incubation period compared to control females. The extra food provided to females was not used by them to improve their own condition, the effect was only marginally nonsignificant; instead, females presumably used it to increase nest attendance and shorten their incubation periods.

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TABLE 2. Mean (\pm SD) hatching success (percent, arcsin transformation), breeding success (percent, arcsin transformation), nestling mass (g), and tarsus length (mm) on day 13 after hatching with respect to experimental treatment. Sample sizes in parentheses.

	Control	Experimental	t^*
Hatching success	94.67 \pm 11.87 (15)	91.33 \pm 11.09 (15)	0.99
Breeding success	89.33 \pm 18.31 (15)	76.78 \pm 20.34 (15)	1.75
Nestling mass	12.75 \pm 1.61 (15)	12.81 \pm 2.18 (14)	0.09
Nestling tarsus	16.80 \pm 0.75 (15)	16.80 \pm 0.56 (14)	0.00

* All $P > 0.05$.

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Absence of Blood-parasitization Effects on Lesser Kestrel Fitness

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Blood parasites were thought to be benign to their avian hosts, but recent reviews uncovered important alterations in birds infected with blood parasites (Atkinson and van Riper 1991, Bennett et al. 1993). Hamilton and Zuk (1982) proposed that secondary sexual traits evolved as signals of parasite resistance that are used in mate choice. This hypothesis has been the focus of recent research and reviews (Gibson 1990, Pruett-Jones et al. 1990, Weatherhead 1990, Clayton 1991, Weatherhead et al. 1991, Weatherhead and Bennett 1991, 1992, Lozano 1994, Seutin 1994). Recent studies also have focused on possible detrimental effects of haematozoan infection on reproductive effort (Apanius 1993, Norris et al. 1994), breeding success (Davidar and Morton 1993, Korpimäki et al. 1993, Allander and Bennett 1995), male spring arrival (Rätti et al. 1993), dominance (Weatherhead et al. 1995), and bird survival (Davidar and Morton 1993). Weatherhead (1990) failed to find any fitness cost caused by blood parasites.

The Lesser Kestrel (*Falco naumanni*) is a migratory colonial falcon with strong sexual dimorphism in plumage. Adult males are brightly colored, whereas females and juveniles of both sexes are dull (Cramp and Simmons 1980). We report on levels of parasitization by haematozoa in a Lesser Kestrel population and relate these to hosts' reproductive effort, clutch size, and survival.

Methods.—Our study was conducted in Los Monegros (northeastern Spain; 41°25'N, 0°11'E), where a large population of Lesser Kestrel breeds in abandoned farm houses (Tella et al. in press). Adult birds were caught while roosting or attending nests; cap-

tures occurred from spring arrival (March) to the end of the breeding season (July) in 1993 and 1994. Nestlings were sampled in 1993. We took 498 blood samples from the brachial vein of as many hosts. Thin blood smears were individually labelled, air dried, fixed with 100% methanol, and stained with Giemsa (Bennett 1970). A 100× oil-immersion lens was used to count blood parasites in 100 microscope fields on each smear. Fields were chosen in a line from one end of the slide to the other to compensate for differences in the thickness of the smear (Weatherhead and Bennett 1991). Haemoparasite prevalence was defined as the percentage of infected individuals in a sample, and intensity as the number of parasites per infected bird per 100 microscope fields. The identity of parasite species was determined at the International Reference Centre for Avian Haematozoa (Memorial University of Newfoundland, Canada).

We were able to age most of the birds as they were banded when young. Clutch size was determined in focal pairs, after successive visits to estimate egg losses due to predation (Tella et al. in press). A two-factor ANOVA showed no differences in clutch size between years ($F_{1,107} = 1.774, P = 0.18$), but significant differences between first-year and older females ($F_{2,107} = 4.257, P = 0.016$). Thus, we only analyzed clutches from after-first-year (AFY) females and pooled years. Laying and hatchling dates were estimated according to the length of the eighth primary feather of the largest chick in each brood (Negro et al. 1992). Based on these data, we grouped the known parents into the prelaying (March to beginning of May), incubation (most birds until beginning of June), and nest-