Body-mass Changes in Female Collared Flycatchers:
State-dependent Strategy

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ABSTRACT.—Collared Flycatcher (*Ficedula albicollis*) females experimentally were forced to prolong their incubation to address the question whether mass constancy during incubation and subsequent mass loss after hatching is actually related to breeding stage. Compared to unmanipulated control females a week after expected hatching, experimental females did not show any significant mass loss during prolonged incubation, whereas control females that successfully hatched their eggs dropped their mass significantly. Results show that body mass in females is associated with the reproductive stage and may reflect an adaptive strategy. High and stable incubation mass can be a fasting endurance in case of adverse weather conditions when females stay on the nest instead of foraging.

Body mass of fully grown vertebrates usually fluctuates over time as a result of changes in organ size and energetic reserves (Piersma and Lindström 1997). That flexibility may result from adaptive response to changes in environmental conditions, physiological status, and behavioral goals. Alternatively, body mass loss may reflect "nonadaptive" energetic stress in face of resource-demanding activities. Birds show remarkable mass changes over their life cycle connected with migration, wintering, and reproduction (see Piersma and Lindström 1997). Female birds are known to experience dramatic changes in mass during reproduction (Moreno 1989). However, in species showing incubation mass constancy, there is still a controversy about why a considerable mass loss occurs between incubation and feeding young. Mass loss during breeding has often been considered as an indicator of short-term reproductive costs and has been thought to be a simple reflection of reproductive stress (e.g. Askenmo 1977, Bryant 1988). However, patterns of mass change are not necessarily an inevitable and harmful consequence of reproductive stress, but may represent an adaptive response to reproductive stress and a compromise between different selective factors (Moreno 1989, Norberg 1995). For example, birds can be expected to benefit from mass loss due to decreased

flight costs (Freed 1981, Norberg 1981, Jones 1987, Moreno 1989, Cavitt and Thompson 1997).

Adaptive and nonadaptive explanations of the significance of mass loss in females between incubation and nestling feeding give similar predictions, so it is extremely difficult to design a proper experiment that would distinguish between those two alternatives. For example, both predict females will lose weight in face of elevated reproductive effort, either because of high reproductive stress and resulting resource depletion (nonadaptive explanation), or adaptive adjusting of body mass to allow higher mobility and loading ability during feeding travels (adaptive explanation). However, instead of looking at mass loss during feeding, one can think of a significance of mass constancy during incubation. Cost of incubation is not negligible (e.g. Cichoń 2000, and references therein), so if mass loss reflects energetical stress one should also predict resource depletion during that stage of breeding. Cavitt and Thompson (1997) proposed that by manipulating the length of each period of that nesting cycle, one could assess whether mass loss reflects energy deficit or adaptive decision. Experimental extension of the incubation stage allows testing specific predictions of those two alternatives. If mass loss is due to energetic stress, prolonged incubation should lead to a significant decrease in body mass caused by incubation costs. In contrast, mass constancy during prolonged incubation will indicate adaptive maintenance of body reserves. In the present experiment, some females of Collared Flycatcher (*Ficedula albicollis*) were experimentally forced to prolong their incubation time while control females were left unaffected. That allows testing of the above predictions by comparing mass dynamic between experimental and control females.

Methods.—This study was conducted in 1993 and 1994 on the island of Gotland, off the Swedish east cost in the Baltic Sea, where a population of Collared Flycatchers has been studied since 1981 (see Gustafsson 1989 for relevant information on study species and area). The Collared Flycatcher is a small (~13 g) migratory passerine species breeding mainly in eastern and central Europe, with wintering quarters in southern and central Africa. It nests in natural tree cavities, but readily occupy nest boxes when provided.

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In the present study, nest boxes were inspected once every five days to look for new nests. Nests were randomly assigned to experimental ($n = 77$) or control ($n = 67$) groups. To prolong incubation of experimental females, all eggs from the experimental nests were replaced with the same number of artificial eggs from the day when the clutch was completed until the seventh day of incubation. The eggs removed from experimental nests were never returned back and were used in the hormonal and immunological studies. In Collared Flycatchers, females incubate exclusively and incubation usually starts on the day of laying of the last egg of the clutch and lasts 14 days. Experimental females had incubation prolonged by approximately one week beyond their normal incubation time, and the majority of females deserted their nests shortly thereafter.

Females were captured at the nest while incubating. They were measured for tarsus and wing length, and weighed with a Pesola spring balance to the nearest 0.1 g. Their body mass was recorded three times during their reproductive cycle. The first time was seven days (plus or minus one day) after clutch completion, and the second time just before hatching, or in a very few cases on the day of hatching (14 days after clutch completion). Females were also weighed (third time) a week after expected hatching (plus or minus two days for control females), that is, when experimental birds were still incubating and control females were feeding young. I failed to weigh some females at the breeding stages specified above, therefore sample size differs between weighings.

Results and discussion.—This study provides evidence that in breeding Collared Flycatchers, female body mass was related to the breeding stage, indicating adaptive mass adjustment. That conclusion can be drawn because experimental females, which were forced to prolong their incubation, were not significantly lighter after expected hatching time, whereas control (unmanipulated) females lost weight after hathing. Two-way ANOVA showed a significant difference in body mass between experimental and control females ($F = 4.28$, df = 1 and 334, $P = 0.04$, Fig. 1) and highly significant differences between breeding stages ($F = 91.05$, df = 2 and 334, $P < 0.001$, Fig. 1). The significant interaction between experimental treatment and breeding stage (two-way ANOVA; $F = 23.58$, df = 2 and 334, $P < 0.0001$; Fig. 1) indicate that the pattern of mass loss differed between experimental groups. *A posteriori* Tukey test showed no significant difference between any breeding stages among experimental females ($P > 0.10$ in all cases), whereas among control females, there was a significant drop in mass between the end of incubation (day 14) and midperiod of feeding young (day 21 from the start of incubation; $P < 0.0001$). There was a very slight drop in mass between day 7 and day 14 in both groups, but it was nonsignificant ($P > 0.70$). On day 21 after clutch completion, control fe-
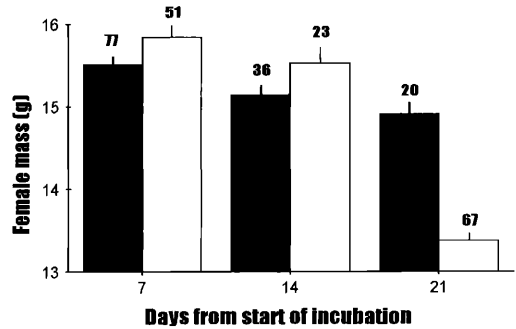

FIG. 1. Body mass of Collared Flycatcher females in relation to the stage of breeding cycle for experimental and control birds (black and white bars, respectively, represent means, and vertical lines represent standard errors). Numbers above the bars indicate sample sizes. Experimental females were forced into prolonged incubation until the day 21 after clutch completion, whereas in control nests, eggs hatched at day 14.

males were feeding young and weighed 13.4 g on average, which is 10% lower than experimental females (14.9 g), who were still incubating ($t = 9.62$, df = 85, $P < 0.0001$). Experimental females lost only 0.6 g (4%) between days 7 and 21 after clutch completion, whereas control females lost 2.6 g (16%) during the same period ($t = -8.76$, df = 60, $P < 0.0001$), but that large drop in mass of control females was observed only after hatching.

The present results are in accordance with the predictions of Cavitt and Thompson (1997) for adaptive mass dynamics that assume the constancy of body mass during incubation (compare figs. 1 and 5c in Cavitt and Thompson 1997). Because prolonged incubation was not associated with mass loss after expected hatching, the present data indicate that mass loss in Collared Flycatchers may be considered as an adaptive adjustment to the current reproductive needs. That is corroborated by a previous study on Collared Flycatchers that showed experimental enlargement of clutch size did not affect female body mass, whereas the costs of incubation of extra eggs were evident during later stages of breeding (Cichoń 2000). High and stable incubation mass can be a fasting endurance in case of adverse weather conditions when females are expected to stay in the nest instead of foraging (Moreno 1989). The slight but nonsignificant decrease in mass observed during incubation may in fact reflect improvement of food availability or an increase in ambient temperature later in the season. Possibly under more favorable conditions females can afford to have lower reserves if environment is more predictable. So, with respect to the present results, a depletion of resources due to incubation costs is not likely to account for the ob-

served body-mass dynamic. Furthermore, mass loss has also been interpreted as a simple reflection of the regression of female reproductive tissues (Ricklefs 1974, Ricklefs and Hussell 1984). The present data allows rejecting such a possibility, and the atrophy of reproductive organs must be simultaneously compensated through reserve storing (Moreno 1989).

The patterns of body-mass dynamics should be considered in a cost–benefit context: mass loss may decrease flight costs, but at the same time, losing too much mass may make individuals more susceptible to starvation if feeding conditions suddenly become less favorable (Nur 1984, Hillström 1995, Merilä and Wiggins 1997). Thus, body-mass changes should be state dependent, which was actually found in the present paper. Sanz and Moreno (1995) in their study of Pied Flycatchers (*Ficedula hypoleuca*) showed also that body-mass changes were related to nestling age. They performed an experiment in which nestlings of different age were swapped temporally between nests, demonstrating that females flexibly adjusted their body mass to nestling age, reaching the lowest level when their flight activity, as a consequence of high food provisioning rate presumably was at a maximum. Cavitt and Thompson's (1997) feeding experiment also indicate state-dependent mass changes because additional food provided during reproductive cycle of House Wrens (*Troglodytes aedon*) had no significant effect on mass dynamics.

In conclusion, the mass dynamic observed during reproductive cycle in Collared Flycatcher females is stage-dependent, and incubation, even if prolonged, is associated with relatively high body mass. Thus, body-mass changes may represent an adaptive compromise among an array of selective pressures.

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