

The Auk 111(3):714-716, 1994

## Supplementary Food in the Nestling Phase Affects Reproductive Success in Pied Flycatchers (*Ficedula hypoleuca*)

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Many studies have tested the hypothesis that food availability plays a role as a proximate factor affecting the timing of breeding (for review, see Daan et al. 1988). However, few studies have experimentally investigated the role of food availability in the nestling phase (Martin 1987). Eden et al. (1989) provided supplemental food to Moorhens (*Gallinula chloropus*), and this reduced the interclutch interval. Simons and Martin (1990) provided supplemental food to Cactus Wrens (*Campylorhynchus brunneicapillus*), and this enhanced fledgling production and the proportion of pairs that started a second clutch. Ens et al. (1992) provided supplemental food to Eurasian Oystercatchers (*Haematopus ostralegus*), and this enhanced growth rate of the young.

To test the hypothesis that food availability during the nestling phase affects reproductive success, Pied Flycatchers (*Ficedula hypoleuca*) were provided with extra food. The effect of the experiment on reproductive success, including fledgling recruitment and parental survival, was evaluated.

The Pied Flycatcher is a small single-brooded migratory insectivorous passerine that breeds in cavities and readily uses nest boxes. There is biparental care. Data presented in this paper were collected in 1987 in De Hoge Veluwe study area, a mixed forest in The Netherlands (for details, see Van Balen 1973). In the Pied Flycatcher polygyny occurs (Lundberg and Alatalo 1991), but its frequency varies between populations; polygyny was not common in our study area (J. Visser pers. comm.).

**Methods.**—Pairs of control and experimental clutches were selected with approximately equal laying dates, clutch sizes, hatching dates, and numbers of hatched young. In a few cases there was more than one control clutch per experimental clutch. Experimental pairs were supplied with mealworms *ad libitum* in a cup inside the nest box. Food supplementation started two days after hatching. Mealworms were provided each day between 1500 and 1800 CET. Each day, the mealworms provided were weighed to the nearest 0.1 g, as were the remaining mealworms. In many cases, at the time of food provisioning, the whole brood was weighed to estimate growth rate, and some of the control nests were checked and weighed at the same time. Not all broods were weighed every day; therefore, sample sizes differ between ages.

The young were banded when they were nine days

old (hatching date designated day 0). At the same time, mass (to nearest 0.1 g) and tarsus length of the young (to nearest 0.1 mm) were measured. When their nestlings were approximately seven days old, the parents were caught with a spring trap, weighed, and measured. Breeding birds were caught in later years to estimate local survival and juvenile recruitment. Thus, recruitment rate is defined as the proportion of fledglings recaptured as breeding birds in the study area. I only have data on local survival and, if the experiment affected site tenacity, this will bias the results.

**Results.**—There was no significant difference in laying date, clutch size, hatching date, or number of hatched young between control and experimental clutches (*t*-test, all  $P > 0.6$ ; Table 1). Tarsus length of parents of both sexes did not differ between control and experimental pairs (*t*-test, both  $P > 0.7$ ; Table 1).

One control pair and one experimental pair failed to fledge any young for unknown reasons. The experimental pair that failed did not consume any mealworms, as could be judged from the weighings of the mealworms. Both pairs were omitted from the analysis.

Nonsystematic observations confirmed that the flycatchers used the food to feed the nestlings. Over the nestling period,  $265 \pm \text{SD of } 39 \text{ g}$  of mealworms were consumed per nest box (on average 49 g per nestling). The parents may have consumed part of the supplemented food. However, that would still give the parents the opportunity to feed nestlings the food they would otherwise have needed for self-feeding.

The energy content of mealworms is 8.9 kJ per gram fresh mass (J. A. L. Mertens pers. comm.). Assuming an assimilation efficiency of 80%, nestlings received 350 kJ per nestling. To scale this to the energy budget of the nestlings, the maximum energy expenditure was calculated using the allometric equation developed by Kirkwood (1983). The maximum energy expenditure summed over the period from 3 to 15 days old was 960 kJ. Assuming that the nestlings consumed the mealworms, this accounted for a substantial proportion (one-third) of their energy budget.

Nestling survival, nestling mass, tarsus length, and age at fledging were not significantly affected by the additional food (*t*-test, all  $P > 0.2$ ; Table 1). Growth curves of young of control and experimental clutches did not differ at any age (Fig. 1;  $P \geq 0.2$  at all ages).

TABLE 1. Reproductive parameters ( $\bar{x} \pm SD$  with  $n$  in parentheses<sup>a</sup>) of control broods and experimental broods that received supplemental food.

Variable	Control	Experimental
Laying date <sup>b</sup>	139.1 $\pm$ 2.0 (16)	138.9 $\pm$ 1.7 (13)
Clutch size	6.2 $\pm$ 0.9 (16)	6.3 $\pm$ 0.9 (13)
Hatching date <sup>b</sup>	157.3 $\pm$ 1.5 (16)	157.2 $\pm$ 1.4 (13)
Number hatchlings	5.4 $\pm$ 1.4 (16)	5.5 $\pm$ 1.3 (13)
Number fledged	5.5 $\pm$ 1.4 (15)	5.5 $\pm$ 1.3 (12)
Nestling mass	13.8 $\pm$ 0.7 (15)	13.9 $\pm$ 0.4 (12)
Nestling tarsus	17.2 $\pm$ 0.4 (15)	17.4 $\pm$ 0.5 (12)
Fledging age	15.9 $\pm$ 0.8 (14)	15.4 $\pm$ 1.0 (12)
Female tarsus	17.5 $\pm$ 0.6 (14)	17.5 $\pm$ 0.6 (12)
Female mass	12.5 $\pm$ 0.8 (14)	12.5 $\pm$ 0.5 (12)
Male tarsus	17.6 $\pm$ 0.5 (13)	17.5 $\pm$ 0.3 (11)
Male mass	12.2 $\pm$ 0.3 (13)	12.1 $\pm$ 0.3 (11)
Survival of females	0.33 (15)	0.58 (12)
Enlarged sample	0.27 (60)	
Survival of males	0.54 (13)	0.55 (11)
Enlarged sample	0.33 (51)	

<sup>a</sup> Sample sizes differ between variables because fledging age of one brood was not recorded, one control female was identified but not measured, and two control males and one experimental male were not identified.

<sup>b</sup> Dates are Julian dates (counting on from 1 January).

Apparently, nestling growth, as estimated using body mass and tarsus length, was not limited by food availability during this year of study.

The effect of the experiment on fledgling recruitment was analyzed with logistic regression (McCullagh and Nelder 1983), using each brood as one degree of freedom. Food supplementation significantly enhanced fledgling recruitment ( $P < 0.05$ ). Mean recruitment rate was  $0.011 \pm SE$  of  $0.011$  ( $n = 15$ ) for control broods and  $0.079 \pm 0.029$  ( $n = 12$ ) for broods that received supplemental food. Consequently, additional feeding affected the proportion of nests that produced a local recruit (chi-square-test,  $X^2 = 4.8$ ,  $df = 1$ ,  $P < 0.03$ ). This was surprising considering the absence of any effect on parameters of pre fledging reproductive success.

Males and females did not differ in mass ( $t$ -test, both  $P > 0.4$ ; Table 1). Local survival of males was not affected by the experiment (chi-square test,  $P > 0.9$ ; Table 1). Local survival of experimental females was much higher than local survival of control females (Table 1), but the effect was not significant (chi-square test,  $P > 0.1$ ). However, when survival of experimental females was compared with the survival of all females with unmanipulated first clutches ("enlarged sample" in Table 1), the difference was just significant (chi-square test,  $P < 0.04$ ). For males a comparison with the enlarged sample did not change the results (chi-square test,  $P > 0.1$ ).

As the experiment was carried out at the end of the season, the additional control females on average bred earlier than the experimental females and this could have biased the results. However, hatching date of the clutch was not correlated with female survival in

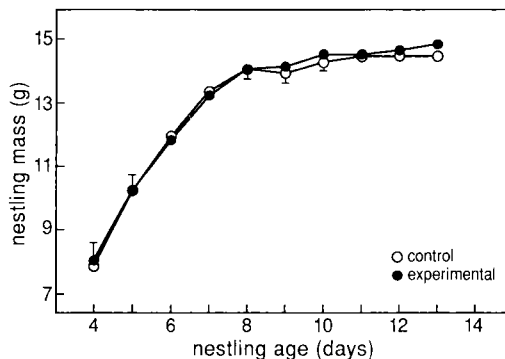


Fig. 1. Mean nestling mass ( $\pm SE$ ) in control broods, and broods that received supplemental food. Standard errors that are not shown are smaller than symbols. Sample sizes: 5 for control nests and 7 for experimental nests at all ages, except at 4 days ( $n = 4$  and 6, respectively) and at 13 days ( $n = 3$  and 4, respectively).

1987 ( $P > 0.4$ ), and the experimental effect is still significant when hatching date is controlled for (logistic regression,  $P < 0.03$ ).

*Discussion.*—The feeding experiment enhanced the contribution to fitness of the clutch. There also was an indication that the experiment affected female survival, which is an important component of the residual reproductive value (Williams 1966). However, sample sizes were small, and the experiment was carried out in only one year. To my knowledge, there are no other studies in which long-term effects of food supplementation were investigated. More experimental work is needed to evaluate the effect of food availability on reproductive success.

Note that the absence of a difference in reproductive success between (experimental) categories of birds cannot be inferred from data on number and mass of fledglings. Data on subsequent success of the fledglings and adults are required to assess the effect of a variable on fitness.

Although fledgling recruitment increased sevenfold, no effect of additional food was found on the nestlings before fledging. A possible explanation is that aspects of nestling quality other than nestling mass and size were affected, such as plumage development or behavioral traits. An alternative explanation is that parents receiving the additional food were in better condition at the time of fledging. This may have resulted in better postfledging care, which in turn could explain the increase in local recruitment. The enhanced survival of experimental females supports this hypothesis.

*Acknowledgments.*—D. Westra, J. Visser and J. Graveland collected a large part of the data under the guidance of J. H. van Balen. The manuscript benefited from discussions with Joost Tinbergen. Dick Visser

prepared the figure. I was supported by BION-grant 436-911 P during preparation of this paper.

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Received 22 October 1992, accepted 15 March 1993.

*The Auk* 111(3):716-720, 1994

### Allozyme Phylogeny of *Spheniscus* Penguins

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There are four species of *Spheniscus* penguins, all with distributions limited to the Southern Hemisphere. The Humboldt (Peruvian) Penguin (*S. humboldti*) is found on the west coast of South America in the cold, upwelled waters of the Humboldt Current (Stonehouse 1975). The Magellanic Penguin (*S. magellanicus*) occurs to the south of the Humboldt Penguin on the west coast and on the south-eastern coast of South America. The Jackass Penguin (*S. demersus*) occurs on the west and south coasts of southern Africa in the cold Benguela Current, while the Galapagos Penguin (*S. mendiculus*) is restricted to the tropical Galapagos Archipelago.

The phylogenetic relations among these birds are uncertain. Murphy (1936) suggested that the Humboldt and Galapagos penguins were sister taxa and that the Magellanic and Jackass penguins were sister taxa, basing this conclusion on several morphological features and geographic distributions. However, a recent analysis of measurements of external and skeletal

structures showed that the Humboldt and the Magellanic penguins were phenetically more similar to each other and to the Jackass Penguin than to the Galapagos Penguin (Livezey 1989). The larger skeletal analysis in the latter study revealed that of the four congeners, *S. magellanicus* and *S. humboldti* were most similar (Livezey 1989). These similarities, however, may not reflect phylogenetic relations because of convergence.

In this study, we estimated a phylogenetic tree from allozyme frequencies for three of these taxa (the Humboldt, Magellanic, and Jackass penguins) and used the closely related Rockhopper (*Eudyptes chrysocome*) and Macaroni (*E. chrysolophus*) penguins from the Southern Ocean as outgroups. We also examined tissue expressions of loci to search for changes in expression during speciation (Mindell and Sites 1987) and compared the average heterozygosities among taxa to search for historical population bottlenecks.

*Methods.*—We collected tissues from 45 Jackass Penguins on 19 December 1986 at Stony Point (34°20'S, 18°53'E), Cape Province, South Africa about six hours after a leopard (*Pantherus pardus*) killed the birds. Samples of cardiac and breast muscle, liver, and vitreous fluid were removed for electrophoretic analysis. Four

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