

Feeding time and brood rearing capacity in the Pied Flycatcher *Ficedula hypoleuca*

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Lack (1947) suggested that one factor affecting clutch size in birds is the latitude at which the clutch is laid. He proposed that this geographical variation is partly influenced by latitudinal differences in day length. We studied the effect of reduced daily feeding time (day length) on the breeding success of the Pied Flycatcher, *Ficedula hypoleuca*, and whether parents were able to compensate for the lost feeding time. We kept both adults captive for 2–5 hours each day when the nestlings were from 8 to 13 days old and recorded the effects on the development of the offspring. The nestlings with reduced feeding time were lighter when fledging and had a lower expected survival rate than those of the control nests. The results indicate that the adults were unable to compensate for the lost feeding time, since the feeding rate did not differ between the experimental and control nests. Since some bird species feed the oldest nestling of the brood more frequently than the younger ones when they cannot find enough food for all the nestlings, we calculated the coefficient of variation (CV) for nestling weights for each brood. The results from this analysis suggested that all the nestlings within each brood developed in an almost identical manner. Our results suggest that day length may be critical for the ability of the parents to feed their nestlings, supporting Lack's findings that day length may influence geographical variation in brood size.

1. Introduction

Optimisation of clutch size and the cost of reproduction have been widely studied in birds because they are very suitable for studying reproductive behaviour at the individual level. Lack (1954, 1966, 1968) suggested that an individual bird sets its clutch size at the level that maximises the number of recruits that will reach reproductive age. After that there have been many examples to propose that the modal clutch size is smaller than the most productive one (e.g. Murphy & Haukioja

1986) and it has been shown in many instances that adults optimise their clutch size relative to the ambient environmental conditions and resources (e.g. Högstedt 1980, Tinbergen & Boerlijst 1990). Alternatively, it has been proposed that this kind of optimisation does not occur because of genetic flow between habitats of different quality and hence different optimal clutch sizes (e.g. Pettifor et al. 1988, Dhondt et al. 1990, Dias & Blondel 1996).

The influences of environmental factors on clutch size have been investigated in numerous

species by examining the effects of such factors on breeding performance (e.g. the supply of extra food, e.g. Davies & Lundberg 1985, Arcese & Smith 1988) or brood size (e.g. Askenmo 1977, Lessells 1986, Gustafsson & Sutherland 1988, Pettifor et al. 1988, Orell & Koivula 1988). Many male removal experiments have also been performed (e.g. Gowaty 1983, Sasvari 1986, Bart & Tornes 1989, Wolf et al. 1990, Duckworth 1992, Johnson et al. 1992, Aho et al. 1997) that focused on the role of the male in parental care or on the relationship between the fitness components and the female's ability to use the resources for the benefit of the nestlings.

Lack (1947) suggested that one factor affecting clutch size is the latitudinal location of the breeding pair. He proposed that this variation in clutch size is partly influenced by the latitudinal differences in day length. Because adults forage by means of visual perception, they can feed their offspring for longer periods when daylight is longer and can therefore rear larger broods than their counterparts living nearer to the equator. Lack's idea has been explored on only a few occasions (Murphy 1978, Yom-Tov & Hilborn 1981, Lundberg 1985a, b), and only Lundberg found weak evidence to support it. It is difficult to separate the effects of one factor from another, e.g.

day length, or food supply without experiments. Few experiments have been carried out to study the effects of daylight length on clutch size (e.g. Kuitunen & Suhonen 1991).

In this experiment, we changed the length of the feeding time of the Pied Flycatcher (*Ficedula hypoleuca*), a species which forages by means of visual perception. The nestlings are fed mainly with flying insects and insects captured from foliage and the ground (e.g. von Haartman 1954). We assessed whether the shorter feeding time reduces the growth and survival of the nestlings.

2. Area and methods

The field experiments were performed in June and early July 1988, in Central Finland (62°37'N, 26°20'E) in plots located in an area of mixed forests that contained all together about 100 nest boxes. Nests were randomly assigned to the treatment and control groups and did not differ in hatch time or brood size (Table 1). Polygynous males were able to divide their feeding between their primary and secondary nests. The mating status of the males was confirmed by observing their feeding behaviour. Males attending primary nests were chosen for the experiment.

The experiment was started when the nestlings were 8 days old and was completed 6 days later. The parents were captured, banded and weighed to the nearest 0.1 g with a spring balance (50 g). We then caught them daily at the same time, roughly at noon, and kept them in empty nest boxes for 2–5 hours. This time period is equivalent to the natural daylight length variation between Northern and Southern Finland. The distance between Lapland and Southern Finland is ca. 1 000 km and daylight length varies from 24 hours in Lapland to ca. 18 hours in Southern Finland during the Pied Flycatcher breeding season.

The nestlings (both treatment and control) were weighed with a spring balance and wing lengths were measured with a ruler to the nearest 1.0 mm daily. Since the adult birds became more cautious and difficult to catch during the experiment, the resulting data were too limited to enable any differences in adults' weights to be detected between the treatment and control broods. When we were unable to catch the adult birds, we

Table 1. Characteristics of treatment and control broods. T = Treatment (A, B, C = group of the experiment; c = control; 2, 3, 4, 5 = reduction of the feeding time per day, hours), E = date of the beginning of the experiment, S = clutch size, H = number of hours, that adults were in captivity, t = ambient mean temperature during the treatment (°C) and P = mean precipitation during the experiment period (mm).

T	E	S	H	t	P
Ac	27.6	7	0	22.2	0.4
A2	26.6	7	2	22.4	0.4
A3	26.6	7	3	22.4	0.4
A4	26.6	7	4	22.4	0.4
Bc	25.6	6	0	22.1	30.7
B2	25.6	6	2	22.1	30.7
B3	25.6	5	3	22.1	30.7
B4	25.6	7	4	22.1	30.7
Cc	5.7	5	0	18.3	0.0
C3	6.7	5	3	18.1	0.0
C4	5.7	6	4	18.3	0.0
C5	5.7	6	5	18.3	0.0

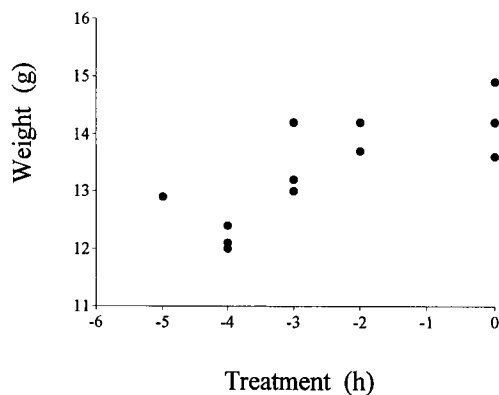


Fig. 1. The mean nestling weight of the brood in relation to treatment. The nestlings were weighed at the end of the experimental period when they were 13 days old. The treatment is the length of the time (hours) per day that parents were removed to empty nest boxes (reduction time) during the experimental period ($r_s = 0.815$, $n = 12$, $P < 0.01$).

closed the entrance to the box to prevent the adults from feeding their nestlings. We only used nests which had originally been attended to by the male bird and his primary female. The nest boxes were equipped with photocell devices and automatic recorders (for details, see Kuitunen & Suhonen 1989) to determine the feeding rate of the adult birds over the whole nestling period.

3. Results

There were no differences in the weights between broods at the beginning of the experiment (8 days old; Kruskal-Wallis one-way test, $n = 12$, $H = 3.82$, $P > 0.05$) at which time the Pied Flycatcher chicks weighed 13.1 g (SD = 0.6, $n = 74$) on average. The final weights of the fledglings (13 days old) ranged from 11.8–14.9 g. However, the shorter the feeding time, the lighter the fledglings (Fig. 1). If the reduction time lasted over three hours, the average fledgling weight decreased to below 13.0 g.

The mean wing lengths of the nestlings at the beginning of the experiment were 33.8 mm (SD = 3.0, $n = 74$) and between 51.2 and 53.8 mm at the end. There was no correlation between the nestlings' wing lengths and the daily feeding length of time ($r_s = -0.14$, $n = 12$, $P > 0.05$).

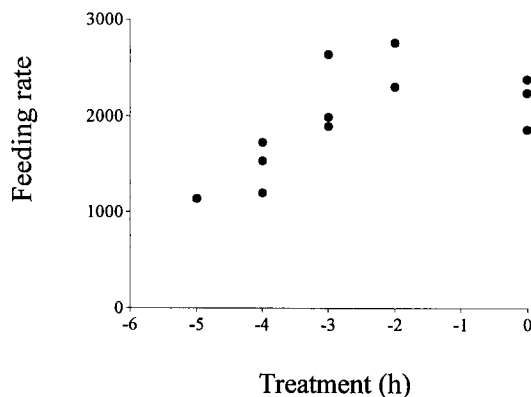


Fig. 2. Feeding rate per brood during the whole experimental period in relation to treatment ($r_s = 0.691$, $n = 12$, $P < 0.05$).

Feeding visits per hour per nest, as calculated by the automatic recorders, did not differ between the nests (treatment or control nests). The shorter the feeding time, the lower the total number of visits to nests (Fig. 2). Birds may attempt to compensate for the lost feeding time by feeding their offspring disproportionately, but the coefficient of variation (CV) for nestling weights calculated for every brood on the last day of the experiment suggested that the adults fed their nestlings equally (Fig. 3).

4. Discussion

Berndt et al. (1981) reported a tendency for the clutch size of Pied Flycatchers to increase northwards and eastwards in Europe (see also Berndt & Winkel 1967, von Haartman 1967), but Järvinen (1989) found no clear pattern with respect to latitude or longitude in a multivariate analysis of 103 study sites in Europe. Instead there was a clear effect of altitude on clutch size. The size of the area covered by his study may not have been large enough to detect the intraspecific differences between clutch sizes at northern and southern latitudes. Different populations face different local conditions, e.g. with respect to habitat or altitude, and these may easily mask any general changes in the environment due to latitude (Lundberg & Alatalo 1992).

Our results support the idea that day length may be an important factor for the evolution of

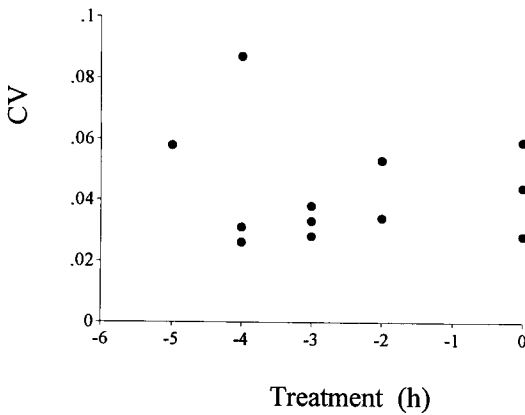


Fig. 3. Coefficient of variation (CV) for nestling weights of all broods calculated on the last experimental day in relation to treatment ($r_s = 0.036$, $n = 12$, $P > 0.05$).

clutch size, since a reduction in daylength for Pied Flycatcher parents reduced their breeding success. By preventing parents from feeding their young for certain time periods, feeding time and the amount of food delivered to their nestlings was reduced, because feeding rate per hour during this time did not increase. Thus, the nestlings in the treatment brood were lighter than those in the control broods, supporting Lack's suggestions (1947, 1948, 1954, 1966, 1968) that increased daylight gives the adults more time to forage and feed their offspring and therefore enables them to rear larger broods than their southern counterparts. When Lundberg and Alatalo (1992) compared the numbers of recruited and unrecruited fledglings in Cumbria, Northwest England, they found a threshold weight of 13.0 g for local recruitment because no offspring lighter than that were observed to return, while the recruit rate of heavier fledglings was from 9% to 13% and was independent of the fledgling weight when compared between the four higher weight classes in 1.0-g units. This observation suggests that also our experimental fledglings have a lower predicted value to be found as breeding adult birds next year. That means a significant difference in their fitness. As a consequence this may partially explain the major geographical variation in avian clutch size, in which species in the tropics have small clutch sizes, and clutch size tends to increase towards the subtropical and temperate zones.

A similar experiment with Eurasian Treecreepers (*Certhia familiaris*) showed that the total feeding rate of parents decreases and the treatment nestlings grow at a slower rate than control nestlings (Kuitunen & Suhonen 1991) for first clutches. The females were able to care for their offspring from their second clutches alone (see also Kuitunen et al. 1996), probably because of the increase in the food supply during the course of the breeding season (Kuitunen 1989, Kuitunen et al. 1996). The second brood of the Eurasian Treecreeper is the same size as the first (Kuitunen 1987).

The importance of territorial resources (e.g. food) as factors limiting reproductive success in the evolution of clutch size seems to include trade-off consequences if daylength variation is taken into account. The effects of variation in territorial resources has been studied directly or indirectly a great deal. It has been studied directly by augmenting the food supply (e.g. Davies & Lundberg 1985, Arcese & Smith 1988), which caused earlier laying dates, but in general had no effect on clutch size. Indirectly, the importance of territorial resources has been ascertained in brood enlargement experiments, in which extra nestlings have been shown to have detrimental fitness effects in terms of nestling body mass (Askenmo 1977, Nur 1984a, Slagsvold 1984, Hegner & Wingfield 1987, Tinbergen 1987, Lindén 1988, Orell & Koivula 1988), adult body mass (Askenmo 1977, Nur 1984b, Lessells 1986, Hegner & Wingfield 1987, Reid 1987), nestling survival (Askenmo 1977, Slagsvold 1984, Lindén 1988, Orell & Koivula 1988, Smith et al. 1989, Pettifor 1993), number of recruits produced (Gustafsson & Sutherland 1988), adult survival (Askenmo 1977, Nur 1984a, Reid 1987), future reproductive success, including a reduced tendency to lay a second clutch (Smith et al. 1987, 1989, Tinbergen 1987, Lindén 1988), reproductive success in the next breeding season (Røskoft 1985, Gustafsson & Sutherland 1988, Gustafsson & Pärt 1990), and the reproductive success of the young (Gustafsson & Sutherland 1988). The mechanism for these effects has been presumed to be food depletion in the territory during the nestling period.

Male removal experiments with biparental bird species are methodologically very similar to our experiment. In many altricial birds, male removal

reduces the growth of the chicks and the survival of the nestlings or juveniles (e.g. Wolf et al. 1988, Mock & Fujioka 1990). In some species, a decrease in the male parental contribution did not detectably affect offspring development or female feeding rate. This is in contrast to Lack's hypothesis (1968) that the clutch size of nidicolous species is adapted to the largest number of young that the parents can normally raise (Sasvari 1986, Dittami et al. 1991). Male activities have been proven to be important to altricial species for raising the young in some reproductive periods but of little or no help in others. That may be of benefit to the nestlings at times of unfavourable conditions in particular (Bart & Tornes 1989, see also Lyon et al. 1987 for indirect evidence). We found that Pied Flycatcher parents can compensate to some extent for the time lost by increasing their daily feeding activity, although they cannot entirely do so. Actually, it seems that individual birds of many species show great flexibility in their patterns of parental investment in response to both natural and experimental changes in resources and conditions in their territory (Partridge & Harvey 1988, and references therein).

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Selostus: Ruokinta-ajan pituuden vaikutus kirjiosiepon kelpoisuuteen

David Lack esitti jo vuonna 1947, että lintujen pesyekoossa havaittuun maantieteelliseen vaihteluun on saattanut vaikuttaa leveyspiiri, jolla pesye on munittu. Koska pesyekokojen oli yleisesti todettu kasvavan etelästä pohjoiseen, Lack päätteli, että ilmiö saattaisi selittyä päivän pituuden samansuuntaisella kasvulla lintujen pesintäkaudella. Pohjoisempana pesivillä lintuemoilla olisi tällöin enemmän valoisaa aikaa per vuorokausi käytettä-

vissään ravinnon etsintään ja poikastensa ruokkimiseen kuin eteläisemmällä pareilla. Tässä tapauksessa ne kykenisivät myös tuottamaan isompia pesyeitä lentoon. Päivän pituuden vaikutuksia on kuitenkin ollut vaikeata erottaa mahdollisesta samanaikaisesta ravinnon tarjonnan vaihtelusta. Lisäksi päivän pituuden merkitystä on hankalaa selvittää kokeellisesti. Tässä tutkimuksessa toteutimme kuitenkin kokeen, jossa ikään kuin lyhensimme päivän pituutta keski-suomalaisilla kirjiosiepoilla (*Ficedula hypoleuca*). Koska päivän pituutta ei voi lyhentää, lyhensimme emojen ruokinta-aikaa vangitsemalla ne päivittäin 2–5 tunnin ajaksi. Tämän teimme, kun poikaset olivat 8–13 vrk:n ikäisiä. Säilytimme emolintuja suljetussa erillisessä pöntössä ajan, joka oli arvottu kullekin pesälle. Punnitsimme poikaset kaikista pesistä päivittäin ja mittasimme niiden siiven pituuden. Kaikilla pesillä oli myös toiminnassa ruokintatiheyden mittaavat automaattiset laskurit. Verratesamme poikasten kasvunopeutta koe- ja kontrollipesien välillä huomasimme, että poikasten painokehitys oli merkittävästi hitaampaa koepesillä. Siivenpituuksissa emme havainneet eroja. Liioin ei eroa havaittu emolintujen kokonaisruokintamäärissä per vuorokausi. Koepesien poikasten alhaisemmasta painosta saatoimme ennustaa, että näillä poikasilla oli sitä huonompi ennuste selviytyä seuraavan kevään pesiviksi emoiksi mitä enemmän niiden emojen ruokinta-aikaa oli vähennetty. Näin ollen sekä koepesien poikasten että emojen kelpoisuus laskivat. Halusimme myös nähdä pystyvätkö emolinnut korvaamaan menettämänsä ruokinta-ajan lisäämällä ruokintatiheyttään. Emolinnut pystyivätkin lisäämään ruokintatiheyttään tuntia kohden, mutta eivät luultavasti kyenneet kantamaan pesälle joko riittävästi ravintoa tai riittävän energiapitoista ravintoa, koska poikasten painokehitys ei vastannut kontrollipoikkeitten painokehitystä. Koska joillakin linnuilla on havaittu, että emolinnut vaikeassa ravintotilanteessa kohdistavat ravinnontarjonnan vain tietyille poikasilleen, testasimme tämän mahdollisuuden vertaamalla poikasten painon vaihtelukertoimia (CV) pesyeiden sisällä. Emme kuitenkaan havainneet niissä eroja, joten emolinnut ruokkivat myös koetilanteissa tasapuolisesti kaikkia poikasiaan. Kaikkiaan tuloksemme tukevat mahdollisuutta, että rajallisten ravintovarojen tilanteessa päivän pituudella saattaa olla oletettua suurempi merkitys

emolintujen kyvyllä ruokkia isompia pesyeitä. Näin ollen tulos tukee myös David Lackin esittämää selitysmallia lintujen pesyekoossa havaittavalle yleisilmiolle, jonka mukaan lintujen keskimääräinen pesyekoko kasvaa maantieteellisesti etelästä pohjoiseen.

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