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## Feeding Time and Brood-rearing Capacity in the Common Treecreeper (*Certhia familiaris*)

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Lack (1954, 1966, see also Ricklefs 1980) proposed that seasonal and geographical changes in day length could be partially responsible for the seasonal and geographical variation in clutch sizes found in birds. This idea is based on the ability of the adult birds to forage longer and feed more offspring if more daylight hours are available. The idea has received little direct experimental testing (Murphy 1978; Yom-Tov and Hilborn 1981; Møller 1984; Lundberg 1985a, b), and only Lundberg found evidence—albeit weak—supportive of Lack's hypothesis. At least three problems complicate tests. First, clutch size does not always increase proportionately with latitude. Second, differences in clutch size with latitude are not consistent between species. Third, some trends between clutch size and latitude are contrary to the general pattern (e.g. in owls; Perrins and Birkhead 1983). Even where the results are consistent with Lack's explanation, it is difficult to assess causality without experiments to separate effects of day length from effects of food supply. Surprisingly, the effect of day length has not been studied experimentally. Resource availability during the breeding season in relation to clutch size has been studied experimentally a great deal. For example, researchers supplied extra food (see Davies and Lundberg 1985, Arcese and Smith 1988), or manipulated the brood size (see Lessells 1986, Gustafsson and Sutherland 1988, Pettifor et al. 1988, Orell and Koivula 1988).

The Common Treecreeper (*Certhia familiaris*, hereafter Treecreeper) is a suitable species with which to study this problem. Clutch size in Treecreepers first increases with time during the breeding season and then decreases (Kuitunen 1987) roughly in proportion to its food supply (Kuitunen 1989), the ambient temperature, and the length of the day (Kuitunen and Suhonen 1989). Treecreepers prefer mature forests, and nestlings are fed mainly on spiders (Kuitunen and Törmälä 1983, Suhonen and Kuitunen 1990) found in crevices on tree trunks. The variation of this type

of food supply between years (Huhta 1965) is less than that of passerine food supply, which is gleaned from the small foliage (e.g. Gibb 1960, Betts 1955, Perrins 1965). As a consequence, the resources and environments used by specialized species such as the Treecreeper may be more predictable from one year to the next than those of the more commonly studied avian species (e.g. *Parus* and *Ficedula*; but see Bryant 1975, 1988).

The Treecreeper forages only on tree trunk surfaces, where food density is low (Kuitunen 1989), and its home range is relatively large (Kuitunen and Helle 1988). In mature coniferous forests, the tree density is also low, and Treecreepers fly large distances during foraging. Thus one could assume that the Treecreeper may be greatly affected in its ability to forage by seasonal change in day length, which was also supported by Kuitunen and Suhonen (1989).

We examined experimentally the effects of day length on foraging ability and reproductive success of Treecreepers by preventing adult birds from feeding their young for certain periods. We attempted to determine (1) if nestlings in the "manipulated" broods developed more slowly and suffered from a higher mortality due to starvation than those in the control nests, and (2) if the adult birds had the capacity to compensate for the loss in foraging and feeding time. Positive answers for these questions would support the idea that the brood-rearing capacity of the adult birds would be better if the day is longer.

We performed field experiments from late May to mid-June, 1987 and 1988, in central Finland (62°37'N, 26°20'E). We studied five experimental and five control Treecreeper nests, all located in mature, spruce-dominated coniferous forests in an area that contained 50 Treecreeper nest boxes (Kuitunen 1985) that had been used by approximately 15 pairs a year since 1983. Two of the experiments were conducted in 1987 and three in 1988. Pairs were chosen for similarity in the timing of hatching and brood size (see Table 1) and assigned

TABLE 1. Characteristics of the experimental and control Treecreeper broods. Renewed nests were re-nested after desertion of first nest. The daily mean temperature (T) and total precipitation (P) during the manipulation period are reported. E = experiment; C = control.

Pair Group	Hatch date	Manipulation age (days)	Clutch size	No. hatched	No. fledged	Brood status	T (°C)	P (mm)
1 E	9 May 1987	7-13	6	6	3	First	9.8	12.9
1 C	13 May 1987	7-13	5	5	5	First	8.0	0.0
2 E	24 May 1987	6-12	6	5	5	First	11.4	37.7
2 C	24 May 1987	6-12	6	5	5	First	11.4	37.7
3 E	22 May 1988	7-13	5	5	0	First	11.2	51.3
3 C	22 May 1988	7-13	5	5	5	First	11.2	51.3
4 E	28 May 1988	7-13	5	5	5	Renewed	15.9	3.9
4 C	28 May 1988	7-13	6	6	5	Renewed	15.9	3.9
5 E	24 May 1988	10-16	5	5	5	Renewed	15.5	3.9
5 C	24 May 1988	10-16	6	6	5	Renewed	15.5	3.9

randomly to the experimental and control groups. Clutch size varied in the nests between 5 and 6, which is within normal variation ( $\bar{x} \pm SD = 5.65 \pm 0.9$ ; Kuitunen 1987).

In each of the five experimental nests, feeding of the nestlings was prevented for 3 h each day over 6 days by closing the entrances to the nest boxes when the nestlings were ca. 7 days old (Table 1). The nests were watched continuously to insure that feeding did not occur. No broods were deserted.

Nest boxes were equipped with photocell devices and automatic recorders (for details, see Kuitunen and Suhonen 1989) to determine the feeding rate of adult birds. We chose a period of 3 h (0800-1100) as the interruption in feeding so that the breeding conditions would resemble those prevailing in Central Eu-

rope ca. 1 June (ca. 47° latitude; see Kuitunen 1985, 1987).

Nestlings were weighed daily to the nearest 0.1 g on a spring balance, and their wing lengths were measured with a ruler to the nearest 1.0 mm. Weather data were obtained from the Tikkakoski meteorological station ca. 50 km west of the site.

The Treecreeper chicks averaged  $6.4 \pm 1.4$  g ( $n = 52$ ) at the beginning of the experiments, and the mean wing length was  $19.7 \pm 5.6$  mm ( $n = 52$ ). The high variance was caused by variations in nestling age between the five sets of experiments (Table 1). To test for possible differences in nestling weights and wing lengths between the experimental and control broods, we used nested designs separately for each day. Nestling weight before the first day did not vary signifi-

TABLE 2. Results of nested ANOVA for weights and wing lengths of nestling Treecreepers in experimental (E; adult feeding prevented) and control (C) broods. The first measurements (A) were taken before manipulation; the number of nestlings measured is in parentheses.

Day	Experiment ( $\bar{x} \pm SD$ [n])	Control ( $\bar{x} \pm SD$ [n])	Between groups E/C			Within groups E/C		
			F	P	df	F	P	df
<b>Weight (g)</b>								
A	6.3 ± 1.6 (26)	6.5 ± 1.3 (26)	1.6	0.17	5	22.8	0.002	
1	6.7 ± 1.6 (26)	7.1 ± 1.3 (26)	3.0	0.02	5	12.1	0.009	4
2	7.3 ± 1.3 (26)	7.7 ± 0.9 (25)	2.4	0.06	5	10.4	0.01	4
3	7.7 ± 1.1 (25)	8.2 ± 0.9 (25)	2.6	0.04	5	6.4	0.03	4
4	7.7 ± 1.2 (25)	8.5 ± 0.6 (25)	6.9	0.001	5	1.1	0.43	4
5	8.1 ± 1.0 (18)	8.7 ± 0.5 (25)	5.8	0.001	4	1.0	0.47	3
6	8.1 ± 1.1 (18)	8.7 ± 0.5 (25)	4.5	0.006	4	0.2	0.89	3
<b>Wing length (mm)</b>								
A	20.0 ± 5.5 (26)	19.4 ± 5.7 (26)	4.7	0.37	5	65.5	0.001	4
1	23.2 ± 6.2 (26)	22.9 ± 6.3 (26)	1.3	0.26	5	54.7	0.001	4
2	26.3 ± 6.6 (26)	26.3 ± 6.3 (25)	0.5	0.77	5	67.0	0.001	4
3	28.7 ± 6.8 (25)	29.5 ± 6.3 (25)	0.8	0.55	5	88.5	0.001	4
4	31.2 ± 7.3 (25)	32.5 ± 6.0 (25)	2.0	0.10	5	37.9	0.001	4
5	35.3 ± 7.9 (18)	35.8 ± 6.3 (25)	2.2	0.09	4	34.6	0.003	3
6	37.4 ± 7.7 (18)	38.3 ± 5.7 (25)	2.8	0.04	4	22.0	0.006	3

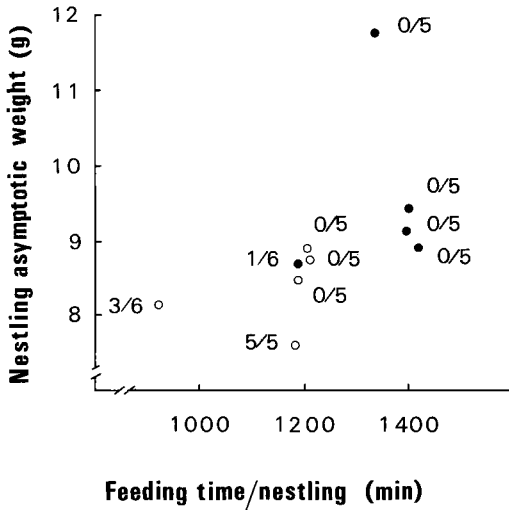


Fig. 1. Average values of the average asymptotic body weight (Crossner 1977; see details in the text) per brood in relation to day length per nestling (min). Numbers indicate the number of nestlings that died and the original brood size;  $\circ$  indicates experimental broods and  $\bullet$  control broods.

cantly between the experimental and control broods, but was significantly lower in experimental broods on all subsequent days. The difference also increased day by day (Table 2). Effect of food deprivation on wing length was only apparent on the last day of the manipulation period. A weak response of wing growth to the scarcity of resources is often found among nestlings that suffer a lack of food (e.g. Ricklefs 1973, Orell 1983). Significantly, the prevention of feeding eventually affected wing length.

Growth-rate indices were calculated according to Crossner (1977) for chicks, and used to predict asymptotic fledgling weights for each brood. Mean ( $\pm$ SD) predicted asymptotic brood weights were  $8.5 \pm 0.5$  g ( $n = 5$ ) for the experimental nests and  $9.6 \pm 1.2$  g ( $n = 5$ ) for the control nests. The difference is nearly significant (one-tailed paired  $t$ -test:  $t = -1.96$ ,  $df = 4$ ,  $P = 0.06$ ). The real average day length per nestling (accounting for the foodless period) did not correlate significantly with the mean asymptotic weight ( $r = 0.50$ ,  $P = 0.14$ ,  $n = 10$ ; Fig. 1). This was due to the fact that the nestlings in one control brood grew exceptionally well, and those in one manipulated brood all died from starvation, which increased the variance. If those two broods were omitted, the asymptotic weight increased significantly with day length per nestling ( $r = 0.87$ ,  $P < 0.01$ ). This may be an indication that the results can also be affected by weather conditions. The air temperature at the time of the exceptionally successful case exceeded the long-term average. In the case of total brood failure, air

temperature was below the long-term average (Table 1). There were no rainy days during the experimental period for the first of the experimental broods.

Overall, mortality during the experimental period was higher among the nestlings in the experimental broods (8 deaths) than in the control broods (1 death). Day length per nestling was shorter in those nests where the deaths occurred (one-tailed Mann-Whitney  $U$ -test,  $U = 1$ ,  $P < 0.02$ ,  $n = 10$ ; Fig. 1). It is quite exceptional for the Treecreeper to lose nestlings, and brood reduction (O'Connor 1978) is not typical of this species (Kuitunen 1987).

The weather conditions were quite variable during both breeding seasons, although the study period in 1987 conformed closely to the long-term average values. The corresponding period in 1988 was exceptionally warm. A multiple regression model was calculated to explain the asymptotic weight ( $W$ ) in terms of three independent variables: day length ( $D_n$ ), mean ambient temperature ( $T$ ), and precipitation ( $P$ ) during the experimental period. None of these variables were correlated. The model explained 90% ( $F = 17.6$ ,  $df = 3$ ,  $P = 0.002$ ) of the variance, and all three independent variables were included in the solution. Partial correlation coefficients ( $r_{W,D_n,T} = 0.58$ ,  $P = 0.05$ ;  $r_{W,D_n,P} = 0.61$ ,  $P = 0.04$ ; and  $r_{W,D_n,TP} = 0.90$ ,  $P = 0.001$ ) emphasized the importance of day length.

The average daily feeding rate ( $\pm$ SD) was  $278.2 \pm 68.1$  visits/day ( $n = 5$ ) in the experimental nests, and  $294.8 \pm 50.1$  ( $n = 5$ ) in the control nests. The difference is not statistically significant (one-tailed paired  $t$ -test,  $t = 0.39$ ,  $df = 4$ ,  $P = 0.36$ ), and these figures do not differ from the daily feeding rate observed previously for unmanipulated chicks of the same age in the same population (Kuitunen and Suhonen 1989). The most critical time for the adult birds was the last day of the experiment, when the energy demand of the nestlings was highest. The average feeding rate ( $\pm$ SD) at this stage was  $292 \pm 89$  visits/day ( $n = 5$ ) for experimental nests and  $332 \pm 78$  ( $n = 5$ ) for control nests. The difference was not significant (one-tailed paired  $t$ -test,  $t = 0.62$ ,  $df = 4$ ,  $P = 0.27$ ). The hourly feeding rate should as a consequence be greater in experimental nests than in control nests. Indeed, this appeared to be the case, but the difference is not significant. The values are  $17.0 \pm 3.8$  trips per hour ( $n = 5$ ) for experimental, and  $15.1 \pm 2.4$  ( $n = 5$ ) for control (paired  $t$ -test,  $t = 0.7$ ,  $df = 4$ ,  $P = 0.50$ ). The hourly feeding rate for 13-day-old nestlings is ca. 17.0 trips per hour (Kuitunen and Suhonen 1989). These values suggest that the prevention of feeding for 3 h should reduce the total daily feeding rate by approximately 51 visits, although the actual value is probably difficult to identify. It seems probable that adult Treecreepers can partly compensate for the lost feeding time. We reject the idea that the adult birds cannot increase their hourly feeding rate very much (cf. Kuitunen & Suhonen 1989). Because earlier results suggested that load size did not vary significantly be-

tween brood sizes or nestling age groups (Kuitunen and Suhonen 1989, Suhonen and Kuitunen 1990), it seems possible that the loads deteriorated in quality if parents no longer had enough time to select the larger food items available or those with the maximum energy content.

We conclude that the Treecreeper nestlings suffered an energetic deficit over the 3-h periods during which feeding was prevented. In the Treecreeper, variation in clutch size during the season may be partly a response to variation in day length. Presumably, adults maximize the number of young they can successfully raise under foraging-time constraints at different times of the season (see Ashmole 1963 and Ricklefs 1980).

Because food supply of the Treecreepers occurs in low density in widely dispersed patches they must work harder than other species to collect sufficient amounts of food during the day. There are other passerine species that show an "increase followed by decrease" pattern in clutch size during breeding season and moreover the original idea of Lack (1966) included not only seasonal but also geographical changes in day length (see also Ashmole 1963).

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## Diet of Murres Caught Incidentally during Winter in Northern Japan

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In northern Japan, the mortality of murres (*Uria* spp.) in coastal fisheries is rarely studied. For those cases reported, no biological or environmental aspects of the kills are included. Carcasses are promptly dumped as troublesome garbage, even though as a scientific sample, those birds would provide valuable information on the distribution and ecology of seabirds during winter in this region. Consequently, the life histories of wintering neritic and pelagic seabirds remain poorly known.

On 10-15 January 1989, a large catch of murres was reported in the Sea of Japan near Yobetsu, Shiribeshi District, Hokkaido (43°19.6'N, 140°23.0'E). In that period 10 boats deployed gill nets to catch Japan Sea greenling (*Pleurogrammus azonus*) at the bottom in 50-60 m of water. Other boats fished for flounder (bastard halibut, *Pralichthys olivaceus*; brown sole, *Limanda herzensteini*) at a depth of 40 m. The incidental catch of the murres occurred only in the greenling fishery. Nets are set in the evening and hauled the next morning. Net sizes vary. For greenling, a net 60 m long, 5.4-6.4 m wide with 75-90 mm mesh is used. For flounders, nets are 150 m long, 4.8-5.2 m wide with a 120-mm mesh. Most fishing vessels are less than 20 tons, and catches are carried back to port in the nets. The fish are processed on the wharf to sort them for market. The seabirds are thrown back into the sea. The mortality of murres at Yobetsu reported here was for a 5-day period in early January 1989. The event was disclosed when the public complained of the high number of floating dead birds inside the port.

We received 431 seabird carcasses through arrangements with the Division of Wildlife Preservation, Hokkaido Regional Government. There were 42 Common Murres (*Uria aalge*; 9.7%), 386 Thick-billed Murres (*U. lomvia*; 89.6%), 1 Pelagic Cormorant (*Phalacrocorax pelagicus*; 0.5%), and 1 unidentified bird (0.2%). Large gulls and crows heavily scavenged an additional 221

carcasses, which made these unsuitable as scientific samples. Of the intact specimens, we studied stomach contents in 5 Common Murres and 50 Thick-billed Murres. Prey items found in proventriculus and stomach were identified to nearest taxon, weighed, and measured for body length.

Maximum food load was 174 g (12.2% of body weight) for the Thick-billed Murre, and 45 g (3.7% of body weight) for the Common Murre. Identified prey were Japanese sandlance (*Ammodytes personatus*) and Japanese anchovies (*Engraulis japonicus*). Sandlance were present in 30 stomachs (60%) of the Thick-billed Murre and 2 (40%) of the Common Murre. Anchovies were found in stomachs of only 3 Thick-billed Murres. Stomachs were empty (contents <1 g) in 3 Common Murres and 16 Thick-billed Murres. These individuals were excluded from calculations of diet composition by weight. In 2 Common Murres, sandlance made up 100% of total prey weight. In the 36 Thick-billed Murres, sandlance made up 97.6% of total weight, anchovies 1.8%, bivalves 0.007%, and unidentifiable matter 0.5%. Marine debris such as plastic pellets was not observed. The bivalve found in a Thick-billed Murre suggests that the bird dove 50-60 m to the sea bottom.

The fishing grounds of greenling near Yobetsu occur in coastal waters at depths of 40-60 m from early January to late February. Greenling feed exclusively on the eggs of sandlance at the bottom. The spawning ground of sandlance coincides with the fishing ground of greenling (Miyaguchi 1977). The spawning run of sandlance comprises 2-3-yr-old fish (170-220 mm long) that enter coastal waters, where they form large concentrations to spawn just above the sandy or pebbly sea bottom. Sperm of the fish rise to the surface and form a transient, white narrow strip along the coastline. This may attract murres to the site. Juvenile sandlance (<150 mm long) follow and intermingle