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# THE BREEDING BIOLOGY OF THE WILLOW TIT IN NORTHEASTERN SIBERIA

VLADIMIR V. PRAVOSUDOV AND ELENA V. PRAVOSUDOVA

ABSTRACT.—We studied the breeding biology of the Willow Tit (*Parus montanus*) during 1987–1990 in the Magadan region of northeastern Siberia. Clutch size and number of fledglings averaged 7.5 and 6.5, respectively, and both were correlated negatively with the date of the first egg. Nestling growth rate was correlated positively with the date of the first egg, but was not related to brood size. Body mass at fledging was related negatively to brood size. Males fed nestlings significantly more often than did females, while females spent more time attending nestlings. The number of parental visits per young did not change significantly with brood size. During the first 13 days of the nestling period, female feeding rate per young was positively related to brood size while for males this relationship was negative. The nestling diet consisted mostly of Lepidoptera larvae, Arachnoidea, and Diptera. *Received 20 April, 1995, accepted 21 Sept. 1995.*

Most studies of the Willow Tit (*Parus montanus*), a small hole-nesting Palearctic passerine, have focused on the species' non-breeding biology in northern Europe (see Ekman 1989, Matthysen 1990). Fewer studies have been done on its breeding biology (Orell 1983, Orell and Ojanen 1983, Pravosudov 1987, Orell and Koivula 1988, see review by Cramp and Perrins 1993). Here, we report details of breeding biology of the Willow tit in northeastern Siberia and compare it with breeding biology of other parids. Our study area is close to the easternmost part of this species' range.

## METHODS

We collected data between 1987 and 1990 in the southern part of the Magadan region of northeastern Siberia (60°N, 150°E). The habitat was comprised mainly of larch (*Larix cajandery*), poplar (*Populus suoveolens*), and chosenia (*Chosenia arbutifolia*). A detailed description of the study area has been published previously (Pravosudov 1993a, b). Most of the birds were fitted with unique combinations of color bands. Nests were opened with a knife, after which a patch of bark was used to cover the opening. Nestlings in 13 nests were weighed to the nearest 0.1 g and the fifth primary was measured to the nearest millimeter. Using nonlinear regression, we found that the logistic equation was the most suitable for describing rate of body mass increase, and we used the growth constant K to estimate nestling growth rate. As another index of nestling growth, we used the growth of the fifth primary. The rate of increase in length of this feather is very close to linear, so we used the slope of the linear regression as an estimate of the growth rate. The rates at which nestlings were fed were studied by repeatedly observing eight nests for 1-h intervals over the whole nestling period. All observations were made from 35–40 m, and the parents did not appear

Institute of the Biological Problems of the North, Academy of Sciences of Russia, Far East Division, K. Marx pr. 24, Magadan, Russia. (Present address: Behavioral Ecology Group, Department of Zoology, The Ohio State University, 1735 Neil Avenue, Columbus, Ohio, 43210-1293.)

to be disturbed by our presence. To collect food brought to each nestling by its parents, we used a thread tied loosely around each nestling's neck. After the parents made a number of feeding visits corresponding to the number of young in a nest, we collected the food loads from each nestling's throat with forceps and stored each load in a separate vial. Parents resumed feeding as soon as collared nestlings were put back in the nest. This method did not appear to harm the young tits. In 1987, we determined only the frequency of different prey items in the diet. In 1989 and 1990, we also weighed to the nearest mg each food load taken from a nestling and each individual item such loads contained. Over all years, we collected 296 food items contained in 108 individual loads from 11 broods, 185 of which were weighed. The number of food loads collected per nest was 5–23 loads. The food loads were collected from nestlings 6–12 days old, with most collected during 7–11 days of nestling age.

Multi-way general linear models (GLM) and multiple and simple linear regression analyses were used for the majority of tests. General linear model (GLM) is a multivariate analysis that is used to perform analysis of variances (ANOVA) with balanced and unbalanced designs, analysis of covariance (ANCOVA), and regression (Neter et al. 1990, Anonymous 1991). All analyses were performed using MINITAB routines (Anonymous 1991). All tests of the slopes in regression analyses and for covariates in the GLMs were two-tailed. For statistical analyses of parental feeding rates, we used two methods (1) we analyzed averages per nest for the whole nestling period (16 days), and (2) we used all observations (147 1-h periods) made repetitively at the eight nests in a GLM where each nest served as a factor. All models dealing with parental feeding rate consisted of a nest as a factor and nestling age and brood size as covariates. Analyses of the length of time that parents spent in the nest during one visit while feeding nestlings was done on three nests only, and all 579 such observations were used in a GLM where each nest served as a factor and brood size and nestling age served as covariates. For statistical analyses of variance in food loads and main prey type in the diet among different years and different broods, we used average frequency of every prey type in a load per nest in ANOVA. Thus, the brood was the primary sampling unit. To analyze variation in the diet among different broods, we used average frequency of every prey type in a load and the load was the primary sampling unit. The variation among broods was tested separately for each year.

## RESULTS

Willow Tits almost always excavated their own cavities. Only two of 22 nests were in pre-existing natural holes, and in both cases, the birds altered the original hole by shaping the cavity. The average start of egg-laying differed significantly among years, occurring a week later during 1990 than during the two preceding years (ANOVA, $F_{2,18} = 5.7$, $P = 0.012$; Table 1). Mean clutch size was 7.5 eggs and varied significantly among years. Birds that started laying eggs later had smaller clutches (ANCOVA, effect of year, $F_{1,17} = 10.1$, $P = 0.006$; date of the first egg, slope $= -0.15$, $P = 0.006$; Table 1). The number of young that fledged was 6.5 and did not vary significantly among years, but pairs that started laying eggs later had significantly fewer fledglings (ANCOVA, effect of year, $F_{1,16} = 2.4$, $P = 0.124$; date of the first egg, slope $= -0.19$, $P = 0.03$; Table 1). Reproductive success as fledglings per egg averaged 0.85 and was nearly always higher than 0.7 (Table 1). The nestling body mass

TABLE 1

BREEDING CHARACTERISTICS OF WILLOW TITS IN THE MAGADAN REGION OF SIBERIA[a]

| Parameter | 1987 | 1989 | 1990 | Total | Range |
|---|---|---|---|---|---|
| No. of nests | 9 | 6 | 7 | 22 | |
| Mean date of first egg | 30 May | 30 May | 6 June | 1 June | 25 May–7 June |
| | 1.6 days | 1.9 days | 1.7 days | 5.6 days | |
| Clutch size | 7.1 | 8.0 | 7.7 | 7.5 | 6–10 |
| | 0.4 | 0.5 | 0.4 | 1.1 | |
| No. of fledglings | 6.4 | 6.2 | 6.8 | 6.5 | 3–9 |
| | 0.6 | 0.7 | 0.7 | 1.6 | |
| Reproductive success[b] | 0.89 | 0.75 | 0.89 | 0.85 | 0.42–1.00 |
| | 5.2 | 6.1 | 6.1 | 15.5 | |
| K constant | 0.376 | 0.372 | 0.411 | 0.385 | 0.331–0.436 |
| | 0.017 | 0.015 | 0.016 | 0.035 | |
| Primary growth rate | 3.28 | 3.44 | 3.45 | 3.39 | 3.02–3.60 |
| (mm/day) | 0.07 | 0.06 | 0.07 | 0.16 | |
| Body mass of young | 11.91 | 12.49 | 12.54 | 12.33 | 11.34–13.16 |
| on day 14 posthatch | 0.43 | 0.69 | 0.27 | 0.56 | |

[a] Within each cell of the four rows on the left, the upper number is the mean and the lower number is the standard deviation.

[b] Reproductive success = fledglings/eggs.

growth constant (K) did not vary significantly among years or with brood size (ANOVA, $P > 0.2$). The nestlings in the later nests, however, grew significantly faster (regression on the date of the first egg, $b = +0.005$, $P = 0.011$, constant $K = 0.213 + 0.005$ date; Fig. 1). Body mass of nestlings on day 14 posthatch did not vary significantly among years (Table 1) or with date of first egg (ANOVA, $P > 0.2$). However, day-14 body mass appeared to be related to brood size; nestlings in smaller broods were heavier (regression on the brood size, $b = -0.163$, $P = 0.064$, $N = 13$, mass $= 13.4 - 0.163$ brood size). Body mass of fledglings was not significantly related to their growth rate (regression, $P = 0.80$). The growth rate of the fifth primary varied similarly with the growth constant, K. Feather growth was not significantly affected by either year or brood size (ANOVA, $P > 0.2$), but the nestlings in later broods tend to grow their fifth primary faster (regression on the date of the first egg, $b = 0.017$, $P = 0.082$, $N = 13$, rate $= 2.83 + 0.017$ date).

Males made significantly more feeding trips to nest than did females (paired *t*-test, $t = 3.56$, $N = 8$ nests, $P = 0.009$, Fig. 2). Females increased the number of feeding trips per brood as brood size increased (Regression, $b = 0.82$, $P = 0.046$, $N = 8$ broods, number of trips $= 1.18 + 0.82$ brood size), while total number of visits and number of visits by males per nest were not significantly affected by brood size ($P > 0.2$, calculated

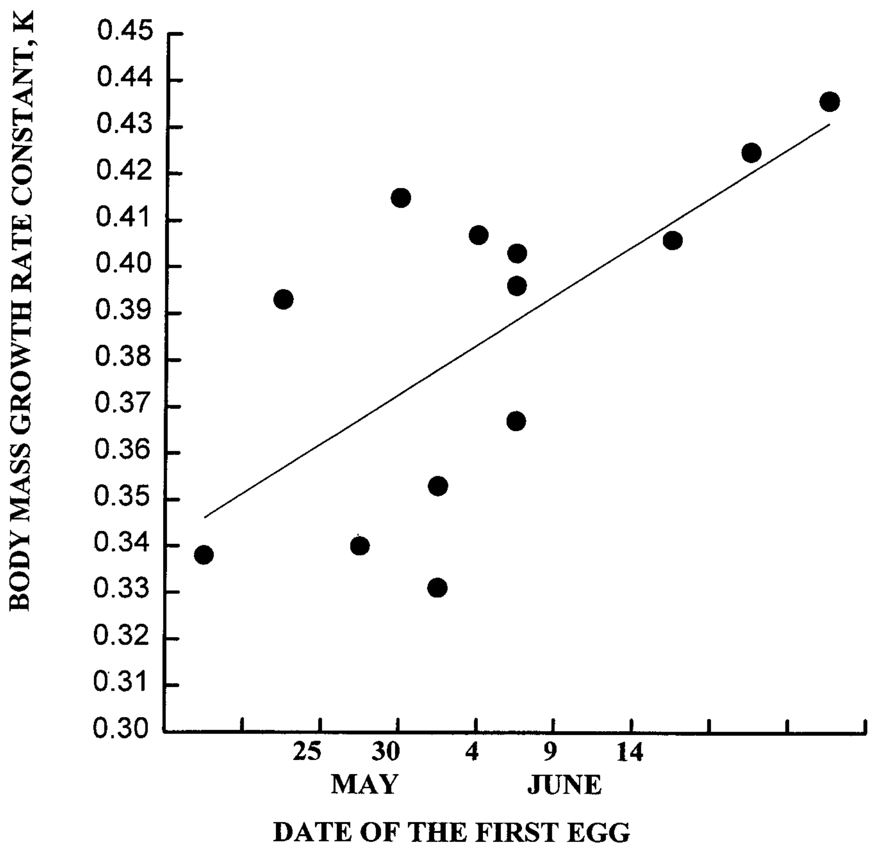

FIG. 1. Relationship between body mass growth rate constant, K, of Willow Tits and the date of the first egg.

on averages per nest for the entire nestling period). GLM analysis using all feeding observations and brood as a factor during the entire nestling period showed no significant relationships between the number of visits per nest (total, male and female separately) and brood size ($P > 0.2$). Both total number of visits per nest (slope = 3.12, $P < 0.01$) and number of visits by females (slope = 3.95, $P < 0.01$) significantly increased as nestlings grew older, although male feeding rate was affected by nestling age only suggestively (slope = 1.56, $P = 0.095$). The number of feeding trips per young (total, male and female separately) was also not significantly affected by brood size ($P > 0.4$, calculated both for nest averages for all nesting period and with a nest as a factor for all feeding observations). Both total number of feeding trips (GLM with a brood as a

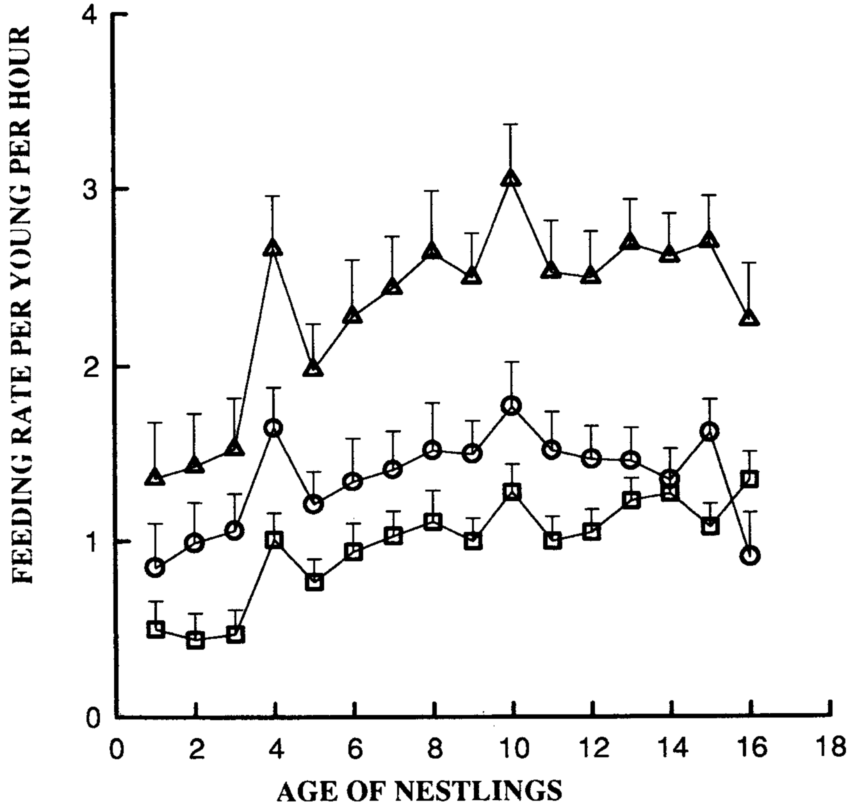

FIG. 2. Number of feeding visits of Willow Tits per nestling per hour as related to nestling age. Open circles and squares represent feeding rates of males and females, respectively. Triangles represent rates for males and females combined. Vertical lines represent ± one SD of the means.

factor, slope = 2.64, $P < 0.01$) and number of visits by female per young (slope = 3.30, $P < 0.01$) increased significantly as nestlings grew older, while male feeding rate was not significantly affected by nestling age (slope = 1.29, $P = 0.22$). Since some young left their nest on the 14th day posthatch and nestling body mass (Fig. 3) and parental feeding rate (Fig. 3) started slowing down by the 13th day posthatch, we analyzed the frequency of parental feeding visits separately for the first 13 days of nestling age (N = 116 1-h periods for 8 nests). This separate analysis of the first 13 days may be very important since the young reach their fledging body mass and are able to fledge by that time, so the heaviest pressure on parents should fall in this period. The results were strikingly different

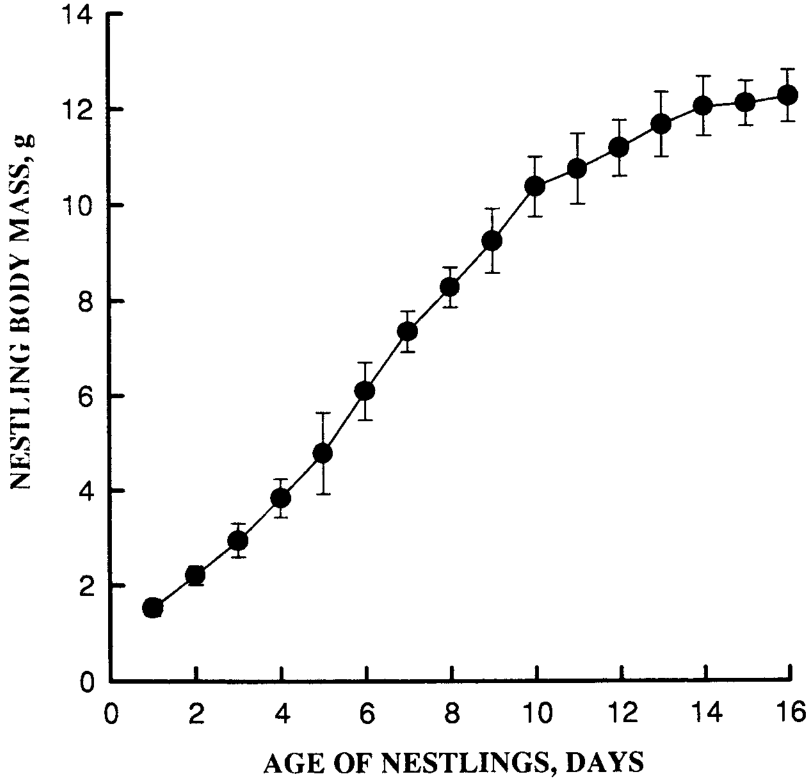

FIG. 3. Nestling body mass of Willow Tits as related to nestling age.

from those of the whole nesting period (Table 2). Both total number of feeding trips and number of feeding trips by female per brood and per young increased significantly as nestlings grew older. Male feeding rate, though, did not change significantly with nestling age (Table 2). Both males and females increased number of feedings per nest as brood size increased. Feeding frequency per young showed a dramatic difference between sexes (Fig. 4). Females made more feeding trips per young in larger broods, while males made significantly fewer of them as brood size increased (Table 2, Fig. 4).

Females, but not males, spent more time attending nests containing fewer young during the entire nesting period (GLM with nest and brood size as factors, $F_{2,579} = 8.27$, $P < 0.001$). Both male and female decreased their attendance time as nestlings grew older (GLM with a nest as a factor, $P < 0.01$, Fig. 5).

Arachnoidea, Lepidoptera, and Diptera comprised the majority of the

TABLE 2

RELATIONSHIPS BETWEEN PARENTAL FEEDING RATE AND NESTLING AGE (DAY 1–13) AND BROOD SIZE IN THE WILLOW TIT

| | Age | | Brood size | |
|---|---|---|---|---|
| No. of visits/h | Slope | *P* | Slope | *P* |
| Male per brood | 0.16 | 0.13 | 1.10 | 0.00 |
| Female per brood | 0.44 | 0.00 | 1.37 | 0.00 |
| Total per brood | 0.59 | 0.00 | 2.49 | 0.00 |
| Male per young | 0.03 | 0.11 | −0.12 | 0.01 |
| Female per young | 0.06 | 0.00 | 0.08 | 0.01 |
| Total per young | 0.09 | 0.00 | −0.03 | 0.58 |

nestlings' diet (79%, Tables 3 and 4). The number of prey items contained in each individual food load brought to nestlings averaged 3.0 and did not vary significantly among years ($F_{1,8}$ = 1.76, $P$ = 0.23, Table 5) or different broods (no two pairs were different at $P$ = 0.05, Tukey's test). Average mass of a load taken during 1989–1990 also was not statistically different ($t$-test, $t$ = 1.74, $P$ = 0.22, N = 7) between these years (Table 3), although there were significant differences among broods during both years (in 1989, one nest was different from one out of 3 broods and in 1990, one nest was different from the rest, all differences at $P$ = 0.05, Tukey's test). The mass of a food load was positively and significantly related to the number of prey items in a load when differences among years and broods were accounted for (ANCOVA with year and brood as factors and the number of items in a load as a covariate, individual load is the primary sampling unit; slope = 15.64, $t$ = 5.49, $P < 0.001$). Even though all major prey items showed a great deal of variation there were no significant difference in average frequency of any major prey type per load either among years or among broods (no pairs compared were different at $P$ = 0.05, Tukey's test).

## DISCUSSION

The breeding biology of the Willow Tit in northeastern Siberia and western Europe appears to be very similar (Orell and Ojanen 1983). Average clutch size (7.62) and number of fledglings (6.19) in Finland (Orell and Ojanen 1983) are nearly identical to those in Siberia (7.5 eggs and 6.5 fledglings). The trend toward reduced clutch size with later breeding seems to be general not only for Willow Tits but for many other bird species as well (Orell and Ojanen 1983). Nestling growth rate (K) of Siberian Willow Tits (0.331–0.436) is very similar to that of Willow Tits

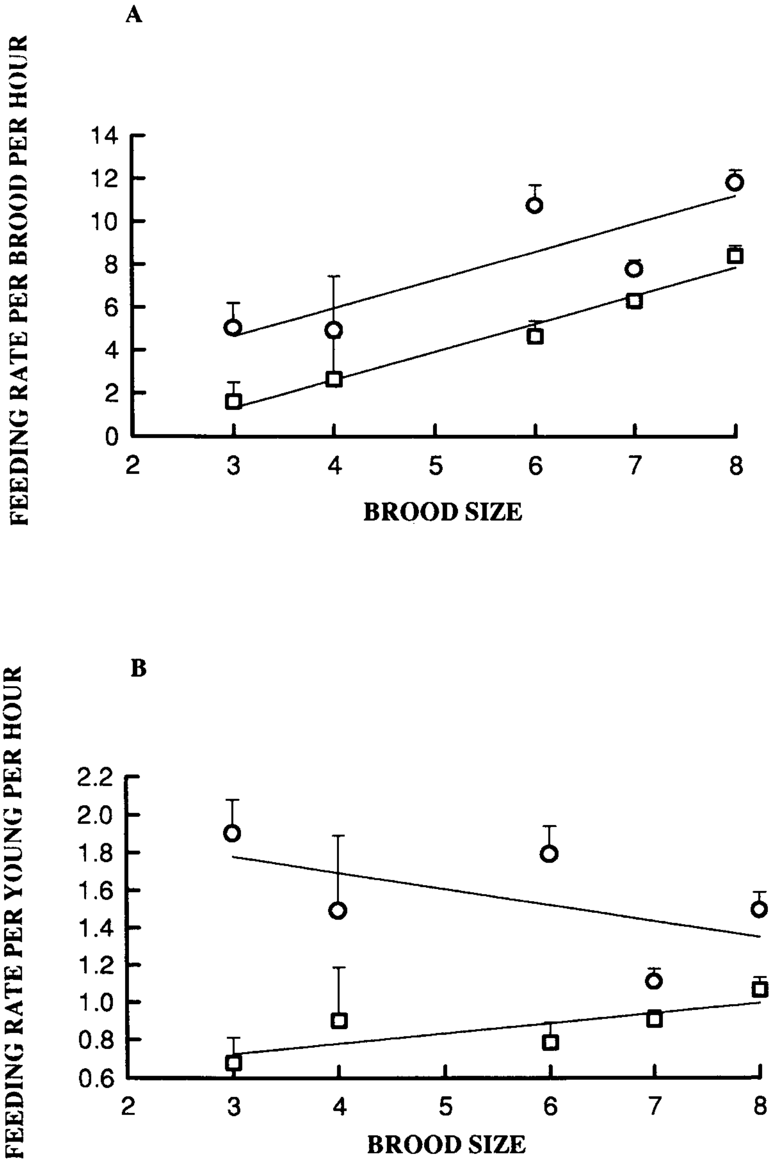

FIG. 4. Feeding rates by male and female Willow tits per brood (A) and per nestling (B) as related to brood size. Feeding rates are taken as averages for the first 13 days of nestling age, and lines represent standard deviations of the means. Males are represented by circles and females by squares.

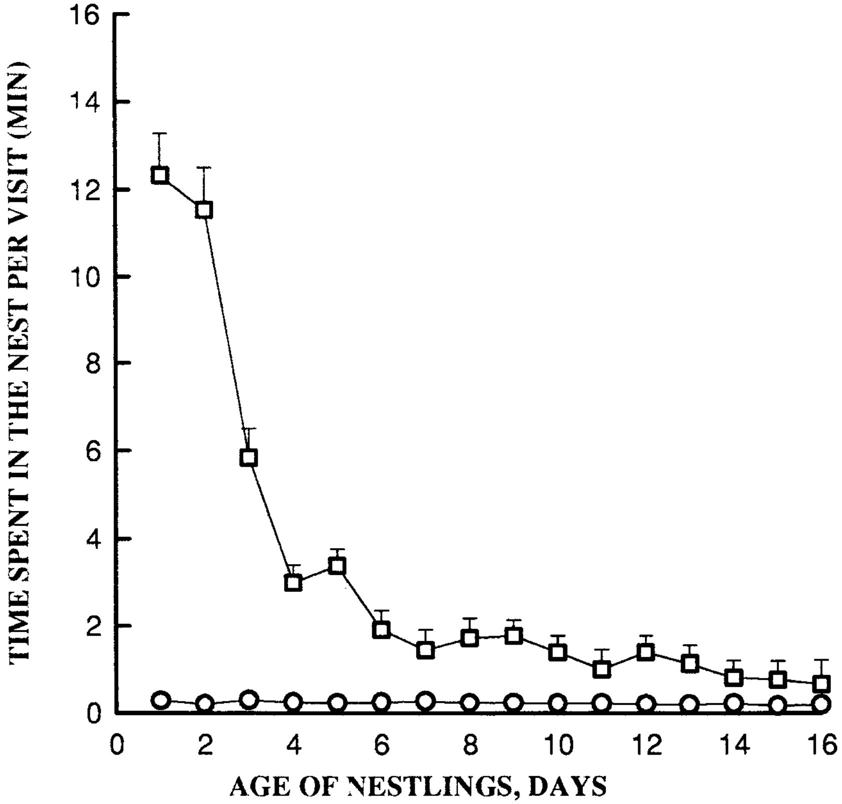

FIG. 5. Length of time spent in the nest cavity during one visit by male and female Willow Tits as related to nestling age. Vertical lines represent standard deviations of the means. Males are shown by circles and females by squares.

in other studies (0.380–0.406; Foster and Godfrey 1950, Inozemtsev 1962, Song 1980, Orell and Ojanen 1983). The negative correlation between fledgling body mass and brood size has also been demonstrated before (Nur 1984, Orell and Koivula 1990).

It seems that birds that start breeding earlier typically produce more fledglings. However, we found that nestling growth rate was positively correlated with the start of breeding. Nestlings that hatched later grew significantly faster although there was no effect of the timing of breeding on fledgling body mass. The fledgling body mass was also unrelated to their growth rate. This result may suggest that although late-breeding pairs produce fewer fledglings, their young could be better off nutritionally. Timing of breeding has long been thought of as a life-history trade-off.

TABLE 3

FREQUENCY OF DIFFERENT FOOD TYPES IN THE DIET OF NESTLING WILLOW TITS IN SIBERIA

| Prey taxon | 1987 | 1989 | 1990 | Total | Percent |
|---|---|---|---|---|---|
| Arachnoidea | 9 | 20 | 20 | 49 | 16.5 |
| Total Lepidoptera | 25 | 63 | 45 | 135 | 45.6 |
| Larvae | 18 | 59 | 45 | 122 | 41.2 |
| Imago | 7 | 4 | 0 | 13 | 4.4 |
| Total Hymenoptera | 15 | 3 | 2 | 20 | 6.8 |
| Larval Hymenoptera | 0 | 2 | 0 | 2 | 0.7 |
| Tentridinidae | 1 | 0 | 0 | 1 | 0.3 |
| Pamphilidae | 0 | 1 | 0 | 1 | 0.3 |
| Formicidae | 1 | 0 | 2 | 3 | 1.0 |
| Total Coleoptera | 16 | 4 | 2 | 22 | 7.4 |
| Larval Coleoptera | 15 | 2 | 2 | 19 | 6.4 |
| Diptera | 38 | 10 | 2 | 50 | 16.9 |
| Limoniidae | 25 | 0 | 0 | 25 | 8.4 |
| Tipulidae | 10 | 9 | 2 | 21 | 7.1 |
| Unidentified | 3 | 1 | 0 | 4 | 1.3 |
| Plecoptera | 2 | 4 | 0 | 6 | 2.0 |
| Chloroperlidae | 0 | 3 | 0 | 3 | 1.0 |
| Unidentified | 2 | 1 | 0 | 3 | 1.0 |
| Homoptera | 1 | 2 | 0 | 3 | 1.0 |
| Gastropoda | 0 | 1 | 1 | 2 | 0.7 |
| Fish bones | 2 | 0 | 0 | 2 | 0.7 |
| Total number | 111 | 114 | 71 | 296 | |

Birds may benefit by breeding earlier, possibly because food abundance is higher. However, for the Willow Tits breeding in Siberia, this is probably not true since when they start breeding there is still snow cover and food becomes abundant only later (pers. obs.). Other studies have shown that in some resident passerine birds, including the Willow Tit, there is another important benefit from breeding earlier; young fledged earlier stand a better chance of recruitment into both winter flocks and into the next season's breeding population (Nilsson 1988, Koivula et al. 1993, Pravosudov 1993b). Our results suggest that there may be a trade-off between early and late breeding in the Willow Tit. If nutritional condition of fledglings were independent of the start of breeding, birds breeding earlier would produce young that would have a higher chance of establishing themselves into a subsequent breeding population. However, birds breeding later may produce better nourished young, although fewer of them. The optimal time of breeding may thus reflect a trade-off between breeding early enough to produce early dispersers (and successful recruits) and breeding late enough to produce well nourished young.

TABLE 4
MASS (MG) OF DIFFERENT FOOD TYPES IN THE DIET OF NESTLING WILLOW TITS

| Prey taxon | 1989 | 1990 | Total | Percent |
|---|---|---|---|---|
| Arachnoidea | 833 | 702 | 1535 | 20.5 |
| Lepidoptera | 2392 | 2531 | 4923 | 65.8 |
| Larvae | 2175 | 2531 | 4706 | 62.9 |
| Imago | 217 | 0 | 217 | 2.9 |
| Hymenoptera | 160 | 85 | 245 | 3.3 |
| Pamphilidae | 60 | 0 | 60 | 0.8 |
| Formicidae | 0 | 85 | 85 | 1.1 |
| Larvae | 100 | 0 | 100 | 1.3 |
| Coleoptera | 57 | 104 | 161 | 2.1 |
| Larvae | 36 | 104 | 140 | 1.9 |
| Diptera | 310 | 119 | 429 | 5.7 |
| Tipulidae | 290 | 119 | 409 | 5.5 |
| Plecoptera | 84 | 0 | 84 | 1.1 |
| Chloroperlidae | 68 | 0 | 68 | 0.9 |
| Homoptera | 76 | 0 | 76 | 1.0 |
| Gastropoda | 16 | 14 | 30 | 0.4 |
| Total | 3928 | 3555 | 7483 | |

Parental behavior in which male Willow Tits fed young more often than females but females spent more time attending nestlings during the whole nesting period was quite similar to that of the Mountain Chickadee (*Parus gambeli*) (Grundel 1987). However, during the first 13 days of nestling life, Willow Tits differed significantly from Mountain Chickadees in the way the sexes responded to changes in brood size. In our study, both males and females increased the number of feeding visits per brood as the brood size increased. However, the number of feeding trips per young was negatively correlated with brood size in males but positively correlated in females. This result, and also the fact that male feeding rate

TABLE 5
MEASUREMENTS OF NESTLING FEEDING IN THE WILLOW TIT

| Parameter | 1987 | 1989 | 1990 | Total |
|---|---|---|---|---|
| Number of loads | 24 | 49 | 35 | 108 |
| Number of broods | 4 | 4 | 3 | 11 |
| Number of food items/load | 4.2 (2.6)[a] | 2.2 (0.7) | 2.5 (0.8) | 3.0 (1.8) |
| Mass of a food load | — | 81.1 (22.2) | 127.9 (42.4) | 101.1 (38.4) |

[a] SD.

did not change much with nestling age, may indicate that males worked as hard as possible and that is why their feeding rate was similar for broods of different size and age throughout the entire nesting period. On the other hand, females appeared to adjust their feeding rate to variation in demand caused by different ages of young and different brood sizes. Females, but not males, also adjusted their attendance time to brood size while feeding nestlings.

It is known that parental feeding rate by itself is not necessarily a good indicator of parental investment since the biomass of food brought by parents to their young per visit may differ between males and females (Grundel 1987). However, Grundel (1987) found in the Mountain Chickadee that differences in total volume of food per nestling in broods of different size were due to changes in feeding frequency rather than in prey size or load size. Therefore, the patterns of feeding frequencies by male and female Willow Tit parents of large and small broods appear to be a valid representation of their investment. The pattern of feeding rate with an increase in the beginning of the nestling stage, a plateau in the middle, and a decrease before fledging seems to be very common and has been shown for many parids (Gibb 1950, Royama 1966, Grundel 1987). Because of the sexes' opposite trends in feeding rate per young with an increase in brood size, the total number of feedings per young in Siberian Willow Tits was not significantly different in broods of different size. This pattern has not been found in many studies (Gibb 1950, 1955; Royama 1966, Walsh 1978, Grundel 1987), although it has been demonstrated before (Pinkowski 1978). Assuming that the changes in feeding rate associated with changes in brood size truly represent a change in parental investment, our results are consistent with the individual adjustment hypothesis (Hogstedt 1980, Pettifor et al. 1988) which assumes that birds adjust their clutch size to their own capabilities of raising young. The absence of any relationship between brood size and nestling growth rate also appears to support this hypothesis. The negative relationship between fledgling body mass and brood size seems to go against the individual adjustment hypothesis since post-fledging survival is known to correlate positively with fledging body mass (Nur 1984, Orell and Koivula 1990). Since young in large broods tend to be lighter compared with young from smaller broods, one can assume that those from larger broods should have lower survival. However, experimental results from studies of Willow Tits in Finland did not fully support this assumption, suggesting that any relationship among brood size, nestling weight, and juvenile survivorship can be complicated by environmental variability (Orell and Koivula 1990). Also, from all the relationships described above, we can assume that lighter young fledge earlier (earlier breeding start results in larger brood size which results in lighter body mass of fledglings) and, if they survive, would have a greater chance of breeding.

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