

# Allocation of parental investment by polygynous Pied Flycatcher males

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The parental roles in the feeding of nestlings were studied in the polygynous Pied Flycatcher *Ficedula hypoleuca*, with special emphasis on how the males allocated their investment between their broods. The study was carried out near Oslo, southern Norway, mainly during 1985 and 1986.

In general, primary females received more male assistance in raising their young than did secondary (including tertiary) ones, but there was a considerable variation in the investment pattern of individual males. This variation was apparently related to two main factors. First, male assistance at secondary nests was less frequent in one of the study years (1985) with unfavourable weather conditions. Second, the males invested more heavily in their secondary broods when the hatching interval between the primary and the secondary broods was short. Consequently, the body weight of primary broods on day 13 increased with increasing degree of breeding asynchrony between the broods, whereas the body weight of secondary broods declined. There was also a tendency of reduced male assistance at the secondary nest when it was located far from the primary nest. The variation in male investment pattern could not be explained by any differences in brood size, nutritional condition of the young, or body reserves of the females of the two respective nests.

The results are discussed in light of the polyterritorial breeding system of this species. We suggest that competition for male parental investment is the reason why mated females are aggressive towards female intruders and that males show long-distance polyterritoriality in order to reduce the likelihood of female-female interactions, thereby increasing their chances of obtaining a secondary mate.

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## Introduction

The concept of parental investment was defined by Trivers (1972) as any contribution invested in current offspring that reduces a parent's ability to invest in other current offspring or in future offspring. Polygynous species with male parental care are particularly suitable subjects for testing parental investment theory, because: (1) the males have to decide whether to invest in current offspring, or to try to acquire additional mates, i.e. invest in future offspring; (2), if they invest in current offspring, then they have to decide how to allocate the investment between their broods.

Parental investment by males is less common in polygynous than in monogamous bird species (Verner & Willson 1969, Møller 1986), which is consistent with the parental investment theory. Polygynous species with male parental care are characterized by a relatively low degree of polygyny, i.e.

the males attract only a few mates each. A good example here is the polygynous Red-winged Blackbird *Agelaius phoeniceus*, in which harem size varies geographically and the extent of male parental care in the populations is inversely related to the average harem size (Muldal et al. 1986).

The Pied Flycatcher *Ficedula hypoleuca* is frequently polygynous (v. Haartman 1951; Alatalo et al. 1981, 1982; Askenmo 1977, 1984; Winkel & Winkel 1984; Røskaft et al. 1986; Stenmark et al. 1988), but the males seldom acquire more than two mates. The females are attracted successively to separate territories, which often lie up to several hundred metres apart (v. Haartman 1951, 1956). Such a polyterritorial mating system has also been found in several other European passerines (Møller 1986).

Polygynous Pied Flycatcher males contribute a considerable amount of parental investment. Before hatching in the primary nest, polygynous males feed

their incubating primary and secondary mates at similar rates, and the total rate of incubation feeding by polygynous males is nearly the same as that recorded for monogamous males (Lifjeld et al. 1987). After hatching, the polygynous male favours the primary brood. However, the extent to which the secondary broods are fed by the male is not clear from the existing literature. Both v. Haartman (1951, 1969) and Askenmo (1977) have reported that the polygynous males assisted almost exclusively their first (primary) female in feeding the young, and that most of the secondary females had to raise their broods single-handedly. Alatalo et al. (1982) found that the secondary females did receive some assistance, particularly towards the end of the nestling period when the young of the primary brood had fledged. Alatalo & Lundberg (1984) reported that 26 (37%) of 70 secondary females were more or less assisted by their mates. Winkel & Winkel (1984) recorded 55 cases of polygyny in which the males were observed feeding both their primary and secondary broods.

The pattern of male investment is apparently highly variable within, and perhaps also between, populations. So far, very little is known about the factors underlying this variation. The present paper describes the feeding of nestlings by a relatively large number of polygynous Pied Flycatcher males and examines how male assistance affected the reproductive success of the respective nests. Our main objective is to identify the most important factors determining how the males allocate their feeding investment.

## Materials and methods

The study was carried out near Oslo, in southern Norway, in 1985 and 1986. Data for two trigynous males from 1987 have also been included. All nestlings took place in wooden nestboxes in three study plots in the mixed coniferous and deciduous forests of Haga (1985 only), Tangen and Sinober (see map in Slagsvold et al. 1988).

All cases in which we had good reason to suspect that a male was polygynously mated outside the study plot (e.g. long periods of absence) were excluded from the analyses. Some of the males that we classified as monogamous may still have been mated with secondary females outside the study plots, but these were probably very few. The rate of polygyny was increased by releasing females, which had been trapped soon after settlement in spring in another woodland area, into the study plots. In 1985, 49 fe-

males were released and in 1986, 76 females. A total of 41 females settled in the study plots and 24 of them (59%) became mates of a polygynous male (see Slagsvold et al. 1988 for further details).

The males were trapped and colour-ringed as soon as possible after their arrival in spring and their ownership of nestboxes and subsequent mating success were recorded continuously throughout the period of female arrival. The day of onset of nest building was defined as mating day. By regular inspection of the nestboxes, we were able to record the start of egg-laying, clutch size, time of hatching, hatching failures and nestling mortality in all cases. The incubation period was defined as the interval between the time the last egg was laid and the time the last young hatched.

Feeding rates of males and females (no. of feeds per 30 min) were recorded for all categories of nests on day 5 and day 13 after hatching. Feeding rates were also recorded on days 2, 8 and 11 for all secondary nests in 1985, and for the secondary nests of the two trigynous males in 1987. The nestlings were weighed on day 5 and day 13 in all nests. In 1985, most of the males were trapped once again on day 13 of the nestling period (i.e. of the secondary or tertiary nest of polygynous males), weighed and the stage of primary moult scored on a 0–50 scale (Lifjeld & Slagsvold 1988a).

All statistical tests are two-tailed.

## Results

### *Feeding rates*

For monogamous pairs, the two parents fed the brood at about the same rates (Fig. 1). On day 5 after hatching the mean feeding rates of males and females were equal (Wilcoxon paired-sample test:  $z = -0.50$ ,  $n = 84$ ,  $P > 0.60$ ). On day 13 the male feeding rates were slightly lower than those of the females ( $z = -2.41$ ,  $n = 76$ ,  $P = 0.016$ ). At four of these nests the male was absent on day 13, which might indicate that he was tending another nest outside the study plot. When the data for these four nests were excluded, the difference between the feeding rates of males and females was no longer significant ( $z = -1.77$ ,  $n = 72$ ,  $P = 0.08$ ). Male feeding rate was positively correlated with brood size (on day 5:  $r = 0.23$ ,  $n = 84$ ,  $P = 0.036$ ; on day 13:  $r = 0.23$ ,  $n = 76$ ,  $P = 0.047$ ).

Polygynous males distributed their feeds between the different broods, but in general the primary brood

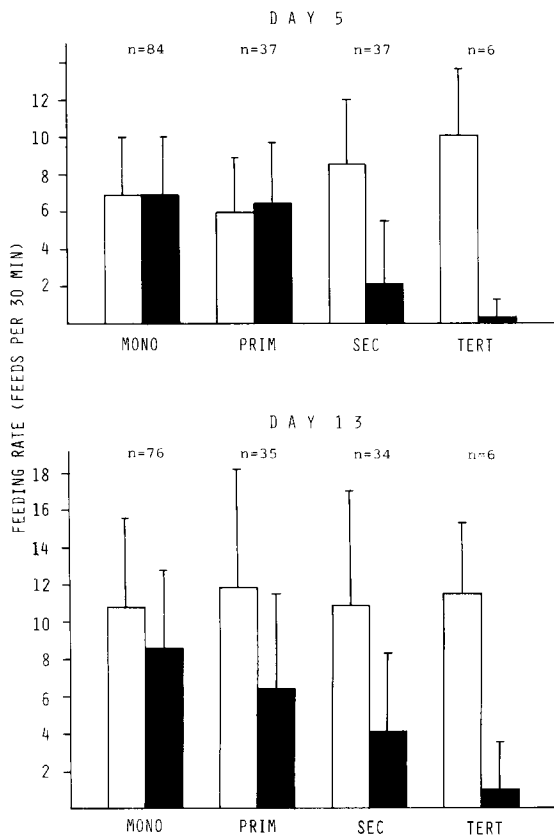


Fig. 1. Male and female feeding rates at two stages of the nestling period for the different categories of nests. 'Mono' refers to monogamous pairs, 'prim', 'sec' and 'tert' refer to the primary, secondary and tertiary nests of polygynous males. Open columns denote females, filled columns denote males. Vertical bars indicate SD.

received more food than the secondary brood. The favouring of the primary brood was particularly pronounced on day 5 after hatching, when 95% of the primary females and only 51% of the secondary females received male assistance ( $\chi^2=15.4$ ,  $P<0.001$ ), and male feeding rate in the primary nests was more than twice the rate recorded for the secondary nests (Wilcoxon paired-sample test:  $z=-4.27$ ,  $n=37$ ,  $P<0.001$ ). Primary broods were slightly larger than secondary broods; on day 5 the respective mean brood sizes were 5.8 and 5.4 (paired t-test:  $t=2.59$ ,  $n=37$ ,  $P=0.014$ ), but the male feeding rate, per nestling, was still highest for the primary nests (Wilcoxon paired-sample test ( $z=-4.16$ ,  $n=37$ ,  $P<0.001$ ). Consequently, mean body weight of the nestlings in the primary nests was higher than that for secondary

nests, viz. 7.9 and 7.2 g, respectively (paired t-test:  $t=3.46$ ,  $n=37$ ,  $P=0.001$ ). At this stage, the polygynous males' feeding rate of the primary broods was similar to that of the monogamous males (Mann-Whitney U-test;  $z=-1.10$ ,  $n=121$ ,  $P=0.27$ ).

On day 13, 80% of the primary females and 69% of the secondary females were assisted by the male ( $\chi^2=0.7$ , ns), and the difference between the male feeding rates for the primary and the secondary nests was less clearcut at this stage (Wilcoxon paired-sample test;  $z=-1.90$ ,  $n=34$ ,  $P=0.057$ ). Brood sizes were still slightly greater in the primary than in the secondary nests, viz. 5.6 and 5.0 young, respectively (paired t-test:  $t=2.37$ ,  $n=35$ ,  $P=0.024$ ). Primary broods received significantly fewer feeds from the male on day 13 than did the broods of monogamous males (Mann-Whitney U-test;  $z=-2.21$ ,  $P=0.027$ ).

Tertiary broods received even less food from the male than did the secondary ones; only one of the six tertiary broods was fed by the male on day 5, and one on day 13.

Polygynously mated females compensated for the loss of male assistance by increasing their own feeding rates. On day 5 female feeding rates varied significantly with female mating status (Kruskal-Wallis test;  $H=14.7$ ,  $n=163$ ,  $P=0.002$ ), being highest for tertiary females (Fig. 1). For all nests combined, the male and female feeding rates were negatively correlated (Spearman rank correlation;  $r_s=-0.22$ ,  $n=163$ ,  $P=0.005$ ). On day 13, female feeding rates did not vary significantly with mating status (Kruskal-Wallis test;  $H=0.4$ ,  $n=151$ , ns), and the male and female feeding rates were no longer significantly negatively correlated ( $r_s=-0.15$ ,  $n=151$ ,  $P=0.08$ ).

Polygynous males that assisted their secondary mates did not feed the secondary nestlings exclusively, but moved frequently between the primary and the secondary nests. The way our data were collected (i.e. during separate 30-min observation periods), did not permit any detailed analysis of the length of the feeding bouts and of the frequency of switching, but in general the males were absent for one or two intervals during the 30-min observation periods.

Fig. 2 presents a case study of the feeding pattern of one of the trigynous males. His secondary clutch hatched only one day after the primary clutch, the tertiary clutch hatched 10 days after the primary clutch. The male invested fairly equally in his primary and secondary broods and he fed the secondary brood during all five observation periods. The two last observation periods at the primary and the secondary nests were on the same days, and the male was seen

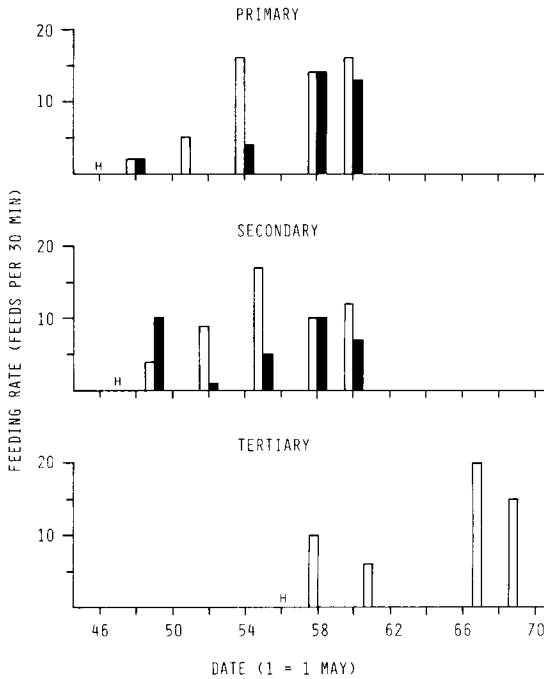


Fig. 2. Male and female feeding rates in the nests of a trigynous male in 1987. Open columns denote females, filled columns denote males. H = date of hatching.

feeding at both nests each day. The male was never observed feeding the tertiary brood. The primary, secondary and tertiary nests produced 6, 7 and 4 fledglings, respectively.

#### *Factors determining male assistance at secondary nests*

In the following section, we consider the variation in male investment pattern and examine some of the potential factors. The analyses in this section are mainly based on data collected from secondary nests in 1985 and 1987 ( $n=17$ ), i.e. five 30-min observation periods at each nest (see Methods).

*Trade-off between mating effort and parental effort.* Parental investment theory predicts that the males should reduce their investment in the current offspring if, by so doing, they gain a higher overall fitness by trying to attract further mates. If some female Pied Flycatchers arrive later than the time of hatching in the earliest nests one might expect al-

ready-mated males to expend some effort on secondary mate attraction.

We have never observed a polyterritorial male singing at an empty nestbox after the day of hatching in his primary nest. This is probably because there is little chance of a male getting any additional mates so late on in the breeding season. In 1985, the earliest clutch hatched on 8 June and only one of the naturally-arriving females, i.e. those not released by us, settled after this date. In 1986, the first clutch hatched on 10 June and only two females arrived after this date. Thus, in the present study we can exclude the possibility that a male's investment in feeding nestlings is confounded by his polyterritorial activity.

*Weather conditions.* The breeding activities and breeding success of the insectivorous Pied Flycatcher are strongly affected by the prevailing weather conditions (Järvinen 1983; Virolainen 1984; and own observations). The investment pattern of polygynous males may also depend on the weather conditions. In favourable weather, the females should be better able to compensate for the reduction in male assistance and the polygynous males will probably increase their chances of raising two broods successfully if they distribute their efforts evenly among their broods. In poor weather, on the other hand, the males may benefit more by concentrating their investment on one particular brood, to prevent a failure of both nestings.

The weather conditions in the two study years, 1985 and 1986, differed. During the period 15 June–5 July, i.e. the nestling period of most of the broods, the weather was more unfavourable in 1985 than in 1986. The mean daily temperature for that period was 14.8°C in 1985 and 18.6°C in 1986. The amount of precipitation was also greater in 1985 than in 1986, viz. 80 mm and 5 mm, respectively (source: Norwegian Meteorological Institute, mean values for the two stations Blindern and Tryvannshøgda). The weather conditions were even worse in 1987 than in 1985 and the data for the two trigynous males in 1987 were therefore pooled with the data for 1985 in the analyses of between-year differences. The difference in the weather conditions is also reflected in the body weights of the fledglings, which were lower in 1985 than in 1986 (Table 1).

Based on the difference in the weather conditions in 1985 and 1986 we would have expected to find that the males would have invested less in their secondary broods in 1985 than in 1986. This prediction was supported. In 1985, six of the 17 polygynous males were never observed feeding their secondary brood, compared with only one of the 18 males in 1986

Table 1. Comparisons of nestling body weights (g) in the two study years.

Nest category	1985 <sup>1</sup>			1986			t-test	
	Mean	SD	n	Mean	SD	n	t	P
Nestlings 5-days old:								
Monogamous	7.88	0.74	31	8.02	0.68	53	0.88	0.38
Primary	7.60	0.88	19	8.26	0.63	18	2.66	0.012
Secondary	6.79	1.07	19	7.66	0.79	18	2.83	0.008
Nestlings 13-days old:								
Monogamous	13.63	1.10	31	14.29	0.58	53	3.12	0.003
Primary	13.90	0.94	17	14.49	0.42	18	2.37	0.027
Secondary	13.28	1.63	17	13.99	1.07	18	1.51	0.14

<sup>1</sup> Including the nestings of the two trigynous males from 1987.

( $\chi^2=3.15$ ,  $P=0.08$ ). Secondary nests were monitored during five 30-min periods in 1985, but only during two periods in 1986. When the data for male assistance at the secondary nests were restricted to those for the same periods in both years (i.e. on day 5 and day 13) the difference between years was statistically significant ( $\chi^2=5.86$ ,  $P=0.016$ ).

*Nesting failures.* If, for some reason, the primary nesting attempt fails, the male would be expected to increase his contribution to the secondary nest. In a study of the Wood Warbler *Phylloscopus sibilatrix*, many secondary females received exclusive male assistance because of high predation of the primary nests (Temrin 1988).

In our study the rate of nesting failure was very low. In only two cases were no fledglings successfully reared in the primary nests. In one case both the primary and the secondary females abandoned their clutches. In the other case the primary nestlings died soon after hatching and the secondary female received exclusive male assistance. In three additional cases where the secondary nestings failed, the primary female received exclusive male assistance.

In yet another case the secondary female disappeared sometime between day 5 and day 8 after hatching. When the previous feeding observations were made, on day 2 and day 5, the female was not being assisted by her mate, which instead fed the 4-days-old primary nestlings. The male totally reallocated his feeding efforts after the secondary female disappeared. On day 8 and day 11 he fed the secondary nestlings at quite high rates (10 and 12 feedings, respectively). However, the young did not show a normal growth of feathers, probably because they

were not fully homeothermic at the time the female disappeared. Only one of the young fledged successfully and on day 13 the male was observed feeding both this secondary nestling and the fledglings from the primary nest.

*Brood size differences.* The reproductive value of a brood to a parent should be proportional to brood size. Parental investment theory therefore predicts that polygynous males should invest more heavily in the nest that contains the largest number of young.

Among the 17 Pied Flycatcher males whose secondary nests were monitored during five 30-min periods, there was no difference in the sizes of the primary broods (day 5) of the males that had assisted and those of the males that had never assisted their secondary mates (mean brood sizes 5.6 and 5.8 young, respectively,  $t=0.47$ ,  $n_1=11$ ,  $n_2=6$ , ns). Similarly, no differences existed between the sizes of the secondary broods (day 5: mean brood size of 5.7 young in each group,  $t=0.13$ , ns). It should be stressed that the mean brood sizes in the primary and secondary nests were the same (5.7 young). Therefore we cannot rule out the possibility that more a radical difference in brood size might have influenced the male investment pattern. However, we conclude that the variation in the investment patterns of the males observed in the present study cannot be explained by differences in brood size.

*The nutritional condition of the young.* Parents would be expected to increase their feeding investments when the young are hungry. Haartman (1953) demonstrated experimentally that Pied Flycatcher parents did increase their feeding investments when they were given hungry young. We would also expect

polygynous Pied Flycatcher males to allocate their feeding investment in accordance with the food demands of the broods, and we would therefore predict that the males reduce their assistance at the secondary nest when the primary nestlings are in poor nutritional condition.

The data did not support this prediction. The primary nestlings of the males that never assisted at their secondary nest were heavier on day 5 than the primary nestlings of assisting males (mean nestling weights of 8.0 and 7.4 g, respectively,  $t=1.40$ ,  $P=0.18$ ). Male-fed secondary nestlings were significantly heavier than those that were not fed by the male (7.3 and 6.3 g, respectively,  $t=2.67$ ,  $P=0.017$ ). These findings suggest that nestling body weight is affected by male food provisioning, and not vice-versa.

*Effects of female condition.* We have previously shown for monogamous Pied Flycatchers, breeding in homogeneous habitats (Lifjeld & Slagsvold 1988b), that females with high body weights produced fledglings with high body weights (Lifjeld & Slagsvold 1986). This is probably a reflection of a high quality of maternal care. The results reported here have shown that females can and do compensate for the loss of male assistance by speeding up their own food delivery rates. If two females mated with the same male differ with respect to their own nutritional reserves, the male would probably benefit from preferentially assisting the female with the smallest reserves, thereby obliging the other female to increase her investment. Hence it can be predicted that males should assist their secondary females only when the primary female has a high body weight.

In contrast to our expectation, the mean body weight of the primary females was significantly lower in cases when the male assisted than when he did not assist his secondary mate (14.4 and 15.2 g, respectively,  $t=3.25$ ,  $n=15$ ,  $P=0.007$ ). Also, the relative difference in body weight, i.e. the weight of the primary female minus the weight of the secondary female, was less in cases when male assistance was given at the secondary nest (-0.3 g and 0.8 g, respectively,  $t=2.46$ ,  $n=15$ ,  $P=0.029$ ). These results are probably confounded by an effect of hatching interval (see below), because, in the above cases, the difference in female body weights tended to increase with the hatching interval ( $r=0.41$ ,  $n=15$ ,  $P=0.13$ ).

*Hatching interval.* Male investment may be related to the hatching interval and hence to the age differences between the broods. According to parental investment theory this would be because older nestlings, compared to younger ones, represent a

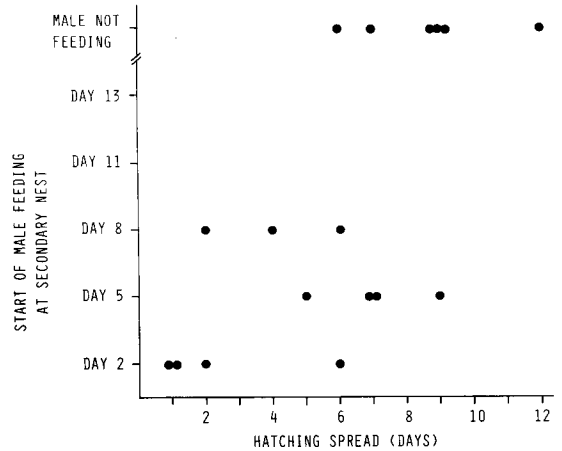


Fig. 3. The age of secondary nestlings when the male was first observed feeding them, plotted against the hatching interval between the primary and the secondary nest. Spearman rank correlation:  $r_s=0.64$ ,  $n=17$ ,  $P=0.006$ .

higher reproductive value because less further investment is required before they become independent. Older nestlings may also have a higher value because fledgling survival is higher the earlier the fledging time (Perrins 1965). Thus, males may preferentially invest in the primary nestlings because of their high reproductive value relative to that of the secondary nestlings. Alternatively, older, and hence larger, nestlings may simply demand more food, in which case the males may feed the primary nestlings because being older, at any given time, they need more food than the secondary nestlings. We would therefore predict, in both cases, that male assistance at secondary nests will be higher when the hatching interval is short.

Our data supported this prediction. The shorter the hatching interval the sooner the males started to feed their secondary broods (Fig. 3). In the cases where no male assistance was provided at the secondary nests the mean hatching interval was 8.5 days, as compared with only 4.5 days where the male did assist ( $t=3.08$ ,  $P=0.008$ ). The investment pattern of one of the trigamists in 1987 further supports this picture (Fig. 2); he invested fairly equally in his primary and secondary broods, and the hatching interval was only one day.

*Distance between nests.* When there is a long distance between the primary and the secondary nest, travelling between nests will be costly for the male. Theoretically, one would expect the male to reduce

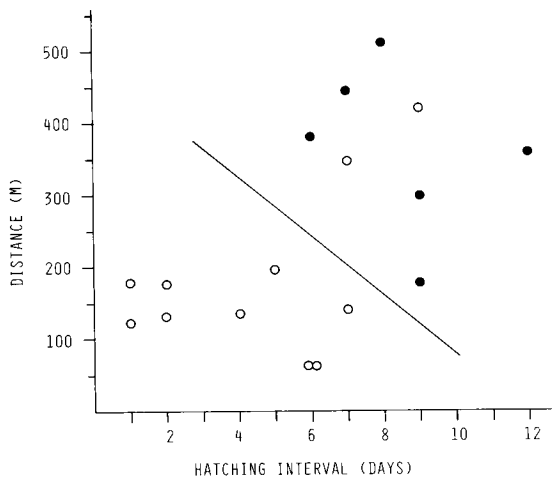


Fig. 4. The distance apart of the primary and the secondary nest plotted against the hatching interval ( $r_s=0.56$ ,  $n=17$ ,  $P=0.019$ ). The discriminant function indicated (distance =  $-41.4 \times$  interval + 490.5) separates cases with no male assistance (filled dots) from nests with male assistance (open dots). Fifteen of the 17 cases (=88%) were correctly classified.

his costs by feeding the nestlings in one particular nest for longer periods at a time, but this does not necessarily mean that he would allocate his total investment differently. If the two broods are not equally valuable for a male, the cost of travelling between nests should be considered as part of the cost of rearing a secondary brood. High travel costs would thus promote a further skew in male investment towards the primary nest. We would therefore predict that male assistance at the secondary nest should be low when the travel distance is long.

In support of this prediction, we found that unassisted secondary nests were characterized by being located a long way away from the primary nest (mean 363 m,  $SD=116$ ), as compared with assisted secondary nests (mean 180 m,  $SD=110$ ;  $t=3.20$ ,  $P=0.006$ ). However, the distance between nests was positively correlated with the hatching interval (Fig. 4), which makes it difficult to know if both variables, or only one of them, influenced male investment pattern. A stepwise discriminant analysis, with minimization of Wilk's lambda as the selection rule, was therefore carried out with male assistance as the dependent variable. Both the distance and the hatching interval entered the equation, which is indicated in Fig. 4. Use of this equation led to correct classifica-

tion of 15 of the 17 cases. Fig. 4 shows that all unassisted secondary broods hatched six days or more after the primary brood. When the data for all cases in which the hatching interval was less than six days were excluded from the analysis, there was still a tendency for the unassisted secondary females to be nesting further away from the primary nest compared to the male-assisted secondary females ( $t=1.82$ ,  $n=11$ ,  $P=0.10$ ). We therefore conclude that the distance between nests had a negative effect on male assistance at secondary nests, at least when the hatching interval was relatively large.

#### Male assistance and reproductive success

Male assistance during the nestling period can be expected to reduce nestling mortality and/or improve their body weights. One or more of the nestlings died in 16 of the 37 (43%) secondary nests. Nestling mortality (i.e. the proportion of nestlings dying between hatching and fledging) was negatively correlated with the male feeding rate recorded on day 5 ( $r_s=-0.39$ ,  $P=0.018$ ) and positively correlated with the hatching interval ( $r_s=0.33$ ,  $P=0.048$ ), but not related to the distance away from the primary nest ( $r_s=-0.08$ ,  $P=0.63$ ). Nestling mortality occurred in only 4 of the 37 (11%) primary nests and the mortality rate was significantly lower in the primary compared to that in the secondary nests (Wilcoxon paired-sample test:  $z=-2.00$ ,  $P=0.046$ ).

The mean body weights of the primary and the secondary nestlings on day 13 have been plotted in Fig. 5 against the hatching interval. The body weight of primary broods increased with increasing degree of breeding asynchrony between the broods, whereas the body weight of secondary broods declined. These patterns cannot be explained by any seasonal decline in body weight, because the mean body weight of 13-days old nestlings in monogamous nests was unrelated to the stage of the breeding season ( $r=-0.16$ ,  $n=84$ ,  $P=0.14$ ). The patterns are more likely to reflect differences in male feeding investment, because the mean body weight of secondary nestlings was higher the more they were fed by the male ( $r_s=0.52$ ,  $n=17$ ,  $P=0.033$ ), and the mean body weight of primary nestlings declined the more the male assisted at the secondary nest ( $r_s=-0.64$ ,  $n=17$ ,  $P=0.006$ ). These correlations were based on the average feeding rates of those males that were monitored during all five observation periods (i.e. in 1985 and 1987). The same trends were nevertheless found when the data for the males in

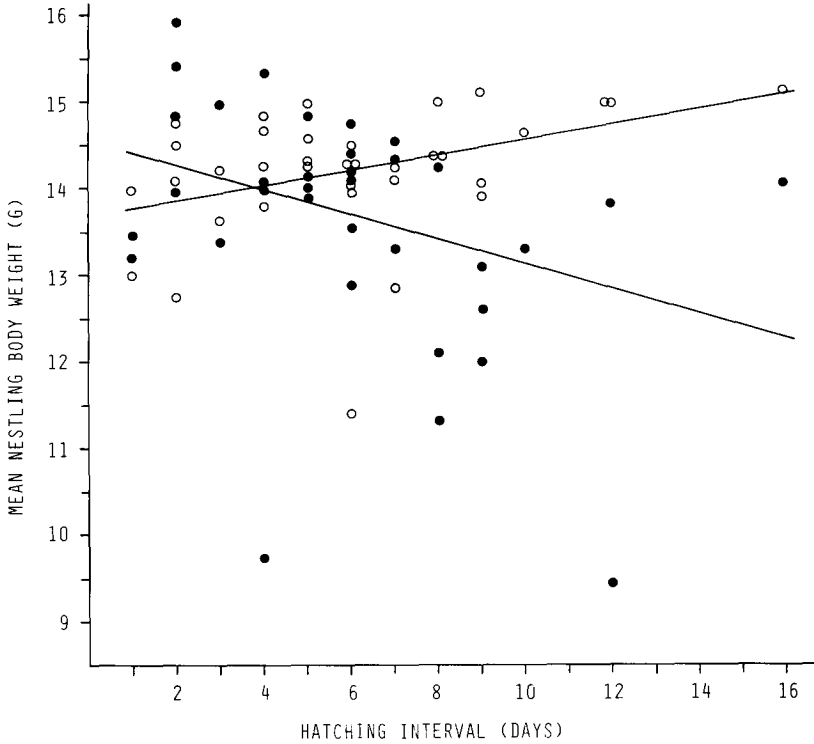


Fig. 5. The body weights of primary and secondary nestlings when 13 days old in relation to hatching interval between the primary and the secondary nest. Data for 35 pairs of nests. Regression line for primary nestlings (open dots)  $y=0.089x+13.67$ ,  $r=0.39$ ,  $P=0.021$ ; and for secondary nestlings (filled dots)  $y=-0.141x+14.55$ ,  $r=-0.36$ ,  $P=0.032$ .

1986 were included, using the average feeding rates on day 5 and on day 13 for all males; viz. the mean body weight of secondary nestlings was positively correlated with male feeding rate in secondary nests ( $r_s=0.50$ ,  $n=34$ ,  $P=0.003$ ), and mean body weight of primary nestlings negatively so, although not significantly ( $r_s=-0.22$ ,  $n=34$ ,  $P=0.22$ ).

The difference between the mean body weights for the primary and the secondary nestlings was not significantly correlated with the distance apart of the nests ( $r=0.23$ ,  $n=35$ ,  $P=0.18$ ).

#### *Did secondary females speed up their breeding activities?*

The results of the above analyses have shown that secondary females receive more help from the male and are thus able to achieve a higher reproductive success the sooner they hatch their clutch relative to the time of hatching in the primary nest. Secondary females should therefore speed up their breeding activities; they could lay their eggs sooner, start incubation sooner, or reduce the incubation period by in-

cubating more attentively. For the 40 pairs of polygynously mated females studied, the pre-laying period (i.e. the time elapsing from mating until the laying of the first egg) was 9.1 days for primary females compared with only 6.2 days for secondary females (paired t-test;  $t=7.51$ ,  $P<0.001$ ). However, there was a strong seasonal decline in the duration of the pre-laying period for monogamously mated females (Fig. 6); secondary females did not have a shorter pre-laying period than females that became monogamously mated on the same day (paired t-test,  $t=0.46$ ,  $n=46$ ,  $P=0.65$ ). Thus, the shorter duration of the pre-laying period of the secondary, compared to the primary, females was only due to the difference in their respective mating times. No difference was found in the duration of the incubation periods of the primary and the secondary females (mean values of 13.4 days in each group, respectively).

#### *Is polygyny costly for males?*

In a bigynous situation, three adults (two females and a male) produce two broods; in a monogamous situa-



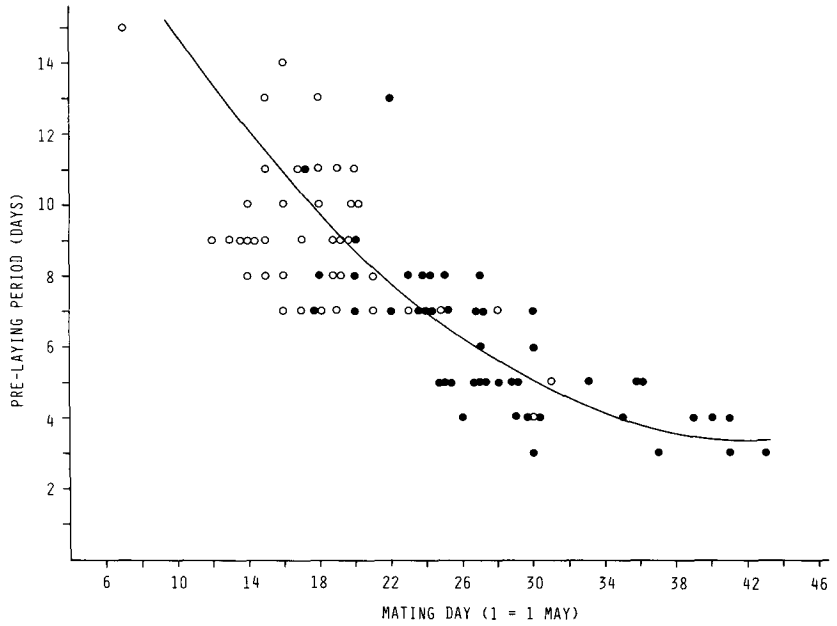


Fig. 6. The duration of the pre-laying period of primary (open dots) and secondary and tertiary females (filled dots) in relation to the time of mating. The curved line ( $y=0.011x(\text{mating date})^2 - 0.93(\text{mating date}) + 23.0$ ;  $R^2=0.65$ ) depicts the decline in the pre-laying period of 84 monogamous females.

tion two adults rear one brood. Although the average investment per adult should be higher in a polygynous situation, we know that females mated with a polygynous male do compensate, at least partly, for the reduction in male assistance by increasing their own investments. Thus, it is not immediately obvious that a polygynous male will have to make a higher total investment than a monogamous male. We examined whether any potential differences in the total investment made by males that reared different number of broods could be reflected in either male body weight or in the progress of the primary moult at the end of the breeding season. However, no differences in ei-

ther body weight or the start of primary moult were found between the males that had reared one and those that reared two or three broods (Table 2).

## Discussion

The male Pied Flycatcher clearly gives his primary brood priority. The same investment pattern has been reported for many polygynous species of birds, e.g. the Red-winged Blackbird (Yasukawa & Searcy 1982), the Yellow-headed Blackbird *Xanthocephalus xanthocephalus* (Patterson et al. 1980), the Bobolink

Table 2. Male body weight and progress of the primary moult at the end of the breeding season in relation to the number of broods produced. Data from 1985.

No. of broods	Body weight (g)			Date of weighing			Primary moult			Date of moult score		
	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n
1	12.2	0.6	20	1 July	5	20	6.1	7.8	12	5 July	5	12
>1	12.2	0.6	8	3 July	6	8	4.0	4.3	6	4 July	4	6
Test of difference	t=0.06 P=0.95			t=0.51 P=0.61			U=33.5 P=0.80			t=0.66 P=0.52		

*Dolichonyx oryzivorus* (Martin 1974; Wittenberger 1980, 1982), the Song Sparrow *Melospiza melodia* (Smith et al. 1982), and the Marsh Harrier *Circus aeruginosus* (Altenburg et al. 1982).

The frequency of extra-pair paternity has been postulated to be quite high among Pied Flycatchers (Alatalo et al. 1984). Confidence of paternity is a highly relevant variable for the determination of male parental investment, as shown for the Dunnock *Prunella modularis* (Houston & Davies 1985). However, no information is currently available about extra-pair paternity in primary versus secondary broods, and therefore no predictions can be made about how this factor should affect male investment pattern.

The hatching interval between the primary and the secondary broods seems to be one of the most important cues for male assistance at the secondary nests. For an intermediate hatching interval of 5–8 days, the normal pattern is that the primary female receives exclusive male assistance during the first part of the nestling period. Some days after hatching starts in the secondary nest the male begins to feed both broods, which means that male assistance to the primary brood decreases and that to the secondary brood increases during the course of the nestling period. This general pattern has previously been described by Alatalo et al. (1982).

The new finding in our study is that the variation in the hatching interval can explain individual differences in the male investment pattern. When the two clutches hatch relatively simultaneously, the male allocates a relatively larger share of his parental investment to the secondary nest and reduces his investment in the primary nest. With a very long hatching interval the males may not assist their secondary mates at all.

The parents continue to feed the young for at least one week after fledging (Creutz 1955; Järvinen 1983), which means that when the hatching interval is long, the male may still be tending the primary fledglings towards the end of the nestling period of the secondary brood. Nevertheless, the possibility exists that secondary fledglings receive exclusive male parental care after the primary fledglings have become independent, but this remains to be studied.

Male assistance at secondary nests is less frequent when the weather is unfavourable, as demonstrated by the difference found in the male investment patterns in the two study years. A similar result has also been reported for polygynous Bobolinks (Wittenberger 1980, 1982), in which male assistance at secondary broods was less frequent and began later in

years with bad weather conditions and when the primary nestlings were in a poorer nutritional state.

Wittenberger (1980) also found that the number of feeding visits made by male Bobolinks to the secondary nest was greater the smaller the primary brood. Polygynous male Dunnocks preferentially feed the brood that contains the greatest number of young (Davies 1986). Male Yellow-headed Blackbirds reallocated their feeding investment in favour of their secondary brood when the size of the primary brood was experimentally reduced (Patterson et al. 1980). We were unable to show that our male Pied Flycatchers allocated their investments according to the size of the primary brood, but any possible effect of this kind could have been masked by other more important factors, such as the hatching interval or the distance apart of the two nests.

A polyterritorial breeding system, as opposed to a monoterritorial one, implies a relatively large cost to the male in travelling between the nests, and male assistance was reduced when the distance apart was very long. Male polyterritoriality may also diminish his ability to prevent his primary mate from copulating with other males in his absence (Alatalo et al. 1987). Nevertheless, the males apparently prefer to acquire and defend nest sites situated far away from the primary nest even though several empty nest sites may be available nearer at hand. Thus, one should expect to find that such long-distance polyterritoriality confers certain benefits which more than outweigh these additional costs. Most likely, long-distance polyterritoriality increases the male's chances of obtaining a secondary mate (see Slagsvold & Lifjeld 1988 for a review of possible mechanisms).

In our view, female-female aggression is the most likely mechanism underlying such long-distance polyterritoriality by males. Mated females are highly aggressive towards any intruding females during the initial stages of breeding, occasionally even at the secondary nest site of their polyterritorial mate (Breiehagen & Slagsvold 1988). By locating the secondary nest site well away from the primary one, the male may thereby reduce the likelihood of such aggressive female interactions and hence increase his chances of attracting a secondary mate. This does not necessarily mean that the secondary females are deceived into polygyny, as suggested by Alatalo et al. (1981, 1982; see Stenmark et al. 1988 for a test of the deception hypothesis).

There are several explanations for such female aggression towards other females (see Breiehagen & Slagsvold 1988). Female-female aggression in Red-

winged Blackbirds is postulated to be a mechanism of competition for male parental investment, because the primary females are more aggressive than the rest and they usually receive the greatest amount of male assistance (Yasukawa & Searcy 1982). Female-female aggression is likely to have the same function in the Pied Flycatcher, because all females mated with a polygynous male suffer, more or less, from a reduction in male assistance, compared to the monogamously mated females. We have shown in this paper that primary females receive relatively less male assistance the earlier hatching takes place in the secondary nest. A female will therefore gain by being aggressive early on in the breeding cycle than later on. The 'investment-guarding' hypothesis, as an explanation for female-female aggression, is thus capable of explaining the weakening of the aggressive response by the female after incubation starts, as observed by Breiehagen & Slagsvold (1988).

### Sammanfattning: Föräldrainvesteringens fördelning hos polygyna svartvitflugsnapparhanar

Hanar hos den svartvita flugsnapparen är ofta polygama. Denna undersökningen beskriver föräldrarnas matningsfrekvens, speciellt hur polygama hanar fördelar sin insats mellan parallella kullar. Fältarbetet utfördes i närheten av Oslo, huvudsakligen under 1985 och 1986.

Det allmänna intrycket var att primärhonorna fick mer hjälp av hanen än vad sekundärhonorna fick. Det var emellertid en avsevärd variation i inventeringsmönstret mellan olika hanar. Denna variation berodde på två huvudfaktorer: (1) Hanarnas insats vid sekundärboet var lägre under 1985 än 1986. Denna skillnad berodde troligen på de sämre väderförhållandena under ungarnas botid 1985. (2) Hanarna investerade mer i sekundärkullen när det var liten ålderskillnad mellan primär- och sekundärkullen. Därför konstaterades en negativ korrelation mellan vikten på sekundärungar, registrerad vid 13 dagars ålder, och skillnaden i kläckningstidpunkt för primär- och sekundärkullen. Ungarna i primärboet visade en positiv korrelation mellan kroppsvikt och skillnaden i kläckningstidpunkt. Det fanns också en tendens att hanarna minskade sin insats för sekundärkullen när avståndet mellan primär- och sekundärboet var långt. Variationen i investeringsmönster mellan olika hanar kunde inte förklaras med olikheter i kullstorlek, boungarnas kondition i de två kullarna eller med resp. honas kondition.

Resultaten diskuteras i förhållande till artens polyterritoriella häckningssystem. Vi anser att inbördes konkurrens mellan honorna om hanarnas föräldrainvestering är orsaken till att parade honor är aggressiva mot främmande honor. Vidare anser vi att hanarna är polyterritoriella för att reducera risken för konfrontationer mellan honor. Därmed ökar hanarna sina chanser att få ytterligare en hona.

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