

Clutch size of the Pied Flycatcher *Ficedula hypoleuca* — an experiment

Rauno V. Alatalo & Arne Lundberg¹⁾

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We manipulated the sizes of Pied Flycatcher broods, to study whether females lay clutches that maximize their life-time reproductive success, and whether clutch size is mainly limited by the capacity of the parents to feed the offspring. Soon after hatching brood sizes were increased or reduced by one or two nestlings. The number of young leaving the nest was higher in broods with extra young, but the fledging weight was lower. As Pied Flycatchers in Scandinavia have high natal dispersal, we could not count the number of offspring surviving to adulthood. In the sibling species, the Collared Flycatcher *Ficedula albicollis*, on the island of Gotland the young return to breed in their natal areas and in this species the likelihood of survival was observed to increase with the weight at fledging. When we used this relationship to estimate the likelihood of survival for the Pied Flycatchers, the broods with extra young were not found to be more productive than broods of the original size, which suggests that brood size is mainly limited by the capacity of the parents to feed the young. The manipulation did not influence the likelihood of survival of the parent birds, which suggests that trade-off between adult survival and reproductive effort is not important.

Rauno V. Alatalo, Department of Biology, University of Jyväskylä, Yliopistonkatu 9, SF-40100 Jyväskylä, Finland and Arne Lundberg, Department of Zoology, Uppsala University, Box 561, S-75122 Uppsala, Sweden.

Introduction

Clutch size in birds has been one of the main subjects of the research of Lars von Haartman. He has written a major review on clutch size determination (v. Haartman 1971), and studied many of its aspects in his favourite study object, the Pied Flycatcher *Ficedula hypoleuca* (v. Haartman 1951a, 1954, 1967a, 1967b, 1969, 1979). In particular, he has paid attention to patterns of clutch size variation, e.g. in relation to season, geographical location and the age of the females. These studies consider both the proximate mechanisms that control the clutch size and the ultimate factors that cause evolutionary change in clutch size.

Lack (1954, 1966, 1968) argued strongly for the view that birds set their clutch size at the level that maximizes the number of offspring contributed by the breeding pair to the next generation. For altricial birds, the limiting factor should be the amount of food

that the parents can bring their offspring. Initially, the most productive clutch size was expected to be the one that is most frequent in a population. However, there are many examples that the clutch size that produces most fledglings is larger than the modal size (for review see Murphy & Haukioja 1986). According to von Haartman's (1951a, 1967a) pioneering studies, this is the case in the Pied Flycatcher. This is also what we can expect for naturally varying clutch sizes, since the variation in itself should be adaptive. The females that have high quality territories and good prospects of rearing a brood should have a higher optimal clutch size than the females in poor territories. Högstädt (1980) demonstrated this, using experimental manipulation of clutch size in the Magpie *Pica pica* to show that an increase or a reduction in brood size would lower the number of fledglings leaving the nest. Clutch size manipulations have also been made with the Pied Flycatcher (Askenmo 1973, 1977, 1979), Great Tit *Parus major* (Boyce & Perrins 1987) and the Blue Tit *Parus caeruleus* (Nur 1984).

Besides the possibility that clutch size responds adaptively to the variation in breeding conditions, an-

¹⁾ Authors' names in alphabetical order

other problem in studies of optimization of clutch size is the difficulty of estimating the number of offspring that recruit to the breeding population. Brood size-dependent juvenile mortality may continue after fledging (e.g. in the Reed Bunting *Emberiza schoeniclus*, Haukioja 1970). Von Haartman (1967a) established that among natural broods of the Pied Flycatcher the probability of the offspring surviving to adulthood is as high in large as in small clutches, in spite of the tendency for fledging weights to be higher in small broods (v. Haartman 1954). A recent experiment by Gustafsson & Sutherland (1988) with the Collared Flycatcher *Ficedula albicollis* provides the best data available so far on the effects of brood size manipulation. The population on the island of Gotland has a high site fidelity and as most of the surviving young return to breed in their natal area, it is possible to estimate the number of recruits. An experimental increase in brood size resulted in an increase in the number of fledglings, but these were less viable than fledglings in control nests. As a result, the control nests were most productive in terms of offspring recruiting to the breeding population, as originally predicted by Lack.

The cost to the parents in terms of a reduction of the future possibility of successful reproduction may also reduce the clutch size from that which would maximize the output of each single breeding occasion (Charnov & Krebs 1974). Again, natural variation in the relationship between clutch size and parent survival cannot be used to test the idea (Högstedt 1981), since the factors that increase optimal clutch size may also enhance the survival. In many cases there is a positive correlation between parent survival and clutch size (see Murphy & Haukioja 1986). Radical increases in the brood size have frequently been made in the experiments and in the Pied Flycatcher male survival was reduced when the brood size was raised to 9 (Askenmo 1979). However, an increase of brood size by up to 50% exaggerates the costs of reproduction, and it is more interesting to see whether parent survival is influenced by an increase of only one or two young. Such an experiment with the Collared Flycatcher revealed no reduction of parent survival (Gustafsson & Sutherland 1988). In the present experiment with the Pied Flycatcher, we changed brood size by adding or removing one or two chicks soon after hatching, to test whether the original size is the most productive one, being limited by the capacity of the parents to feed the offspring. In the Pied Flycatcher the natal dispersal of the offspring is great (v. Haartman 1949, 1951a), and thus we were unable to

estimate the number of recruits directly. Instead, we have estimated the survival chances of the offspring indirectly from information on the relationship between offspring survival and fledging weight in the Collared Flycatcher (Gustafsson unpubl.).

Material and methods

The study was made in Uppsala, Central Sweden, in nest box areas also used for many other studies (e.g. Alatalo et al. 1981, Lundberg et al. 1981, Alatalo & Lundberg 1984, Alatalo et al. 1985). In this study we used mainly deciduous forests, in which the dominant tree was oak *Quercus robur* (87% of 204 nests); the remaining data come from coniferous forests in which pine *Pinus silvestris* predominated.

We manipulated brood size when the nestlings were 2 days old by moving one or two young from one nest to another with offspring of the same age. The chicks to be switched were chosen with the help of random numbers, including eggs that had failed to hatch. If the unhatched eggs were not included, the experiment would overestimate the true influence of the brood size. In control nests we exchanged pairs of chicks between two nests. We attempted to arrange that each type of manipulation (-2, -1, +1, +2 and control) was evenly distributed over each original clutch size. Among the 204 nests, the most common original clutch size was 7 (n=118), followed by 6 (n=55), 8 (n=25) and 5 (n=6). The original clutch size did not vary between the type of treatment in either of the years (1983, $F=0.33$, $df=4,72$, $P>0.80$; 1984, $F=0.15$, $df=4,122$, $P>0.95$). Nor were there any differences in the laying dates between the treatment types (1983, Kruskal-Wallis, $H=1.63$, $df=4$, $P>0.80$; 1984, $H=1.01$, $df=4$, $P>0.90$).

We switched newly hatched chicks rather than eggs to ensure that the switched offspring would be equally developed in the two nests. We also wanted to identify the switched young individually for other purposes. We are thus studying the possibility that clutch size is limited by the capacity of the parents to feed the young rather than the capacity of the females to incubate or to lay the eggs.

For each nest we recorded the number of young leaving the nest, and the weight and tarsus length of the young at the age of 13 days. To check whether the manipulation itself had an effect on the breeding success, for example because of the inevitable slight increase in the size hierarchy of artificially enlarged broods, we can compare the breeding success of the

Table 1. A comparison between totally unmanipulated clutches and the control clutches (chick pairs exchanged between nests). The number of unsuccessful eggs is the difference between the number of fledglings and the clutch size.

	mean	SD	n	Test
Unsuccessful eggs				
1983				
Unmanipulated nests	0.7	1.2	81	U-test
Control treatment	0.6	1.1	14	$z = 0.09, P > 0.90$
1984				
Unmanipulated nests	1.6	1.9	44	U-test
Control treatment	1.2	1.8	22	$z = 0.92, P > 0.30$
Fledging weight (g)				
1983				
Unmanipulated nests	14.3	0.9	79	t-test
Control treatment	14.3	0.5	13	$t = 0.36, P > 0.70$
1984				
Unmanipulated nests	13.6	0.9	40	t-test
Control treatment	13.6	0.8	21	$t = 0.44, P > 0.60$

control nests with a further 125 nests that were not manipulated at all. There was no difference in the number of young lost (=clutch size - number of fledged young) or the average fledging weight of the young between the untreated nests and the controls (Table 1).

Parent survival in relation to the treatment was estimated from the return rates of adults in the following year. Dispersal is high even between consecutive breeding seasons (v. Haartman 1949, 1951a), so only a part of the surviving adults could be captured. However, these will indicate the effect of the experiment, provided that the experiment did not influence breeding dispersal.

The survival of the offspring could not be estimated directly since they only seldom return to our nest box areas (less than 1%). In the sibling species, the Collared Flycatcher, survival is greatly influenced by the weight of the offspring at fledging. Among the 1768 offspring born in that species during 1981–82, the relative survival chances (standardized to an average of unity) in relation to weight at 13 days of age were as follows: <12g = 0.000, 12.0–12.9g = 0.185, 13.0–13.9g = 1.084, 14.0–14.9g = 1.058, 15.0–15.9g = 1.384, >15.9g = 1.052 (Gustafsson unpubl.). We have used this distribution to estimate the survival of Pied Flycatcher young of a given fledging weight, with the modification of +0.2g in fledging weight, to account for the fact that Collared Flycatcher young

are that much heavier on average than Pied Flycatcher young. For each nest we summed the relative survival estimates for the fledglings, and finally standardized this sum with the average fledgling number for the nests in our experiment (5.184) to obtain a relative estimate with an average of unity. Admittedly, the approach is only indicative, but it is justified by the fact that according to our scanty recapture data, in the Pied Flycatcher also the fledging weight of the offspring that had survived to at least two months (14.2 g, SD=0.8, n=18) was higher than that of all the offspring at fledging (13.6 g, SD=1.2, n=3604, $t=3.45, P<0.001$).

Results

Natural broods

The number of fledglings increased with clutch size (Fig. 1a, Spearman's rank correlation, $r_s=0.49, P<0.001, n=602$, data from 1979–1984 see e.g. Alatalo et al. 1985). There was also a slight increase in tarsus length with clutch size (Fig. 1b, $r_s=0.10, P<0.05, n=452$). As the weight of the offspring was not related to the clutch size (Fig. 1c, $r_s=-0.03, P>0.10, n=452$), the relative estimate of the recruit production, based on fledging weights showed as clear a positive relationship with clutch size (Fig. 1d, $r_s=0.39, P<0.001, n=466$) as did the number of fledglings. A single egg was as likely to produce a viable chick irrespective of clutch size; if anything there was a very slight positive correlation ($r_s=0.07, P=0.11, n=466$).

Experimental broods

Among the 204 experimental broods, the number of offspring leaving the nest increased from treatment -2 to +2 (Fig. 2a, $r_s=0.48, P<0.001$), the correlation coefficient being as high as for the natural broods. The number of fledglings was also significantly higher for enlarged than for control broods (Mann-Whitney U-test, $z=2.08, P<0.05$). In contrast, the correlation estimate between tarsus length and the change in brood size was negative, though not significantly so (Fig. 2b, $r_s=-0.11, P>0.10$). For fledging weight the correlation was significantly negative (Fig. 2c, $r_s=-0.21, P<0.01$). This decreases the correlation between the estimated relative number of viable offspring and the change in brood size (Fig. 2d, $r_s=0.25, P<0.001$). The estimate for the broods with

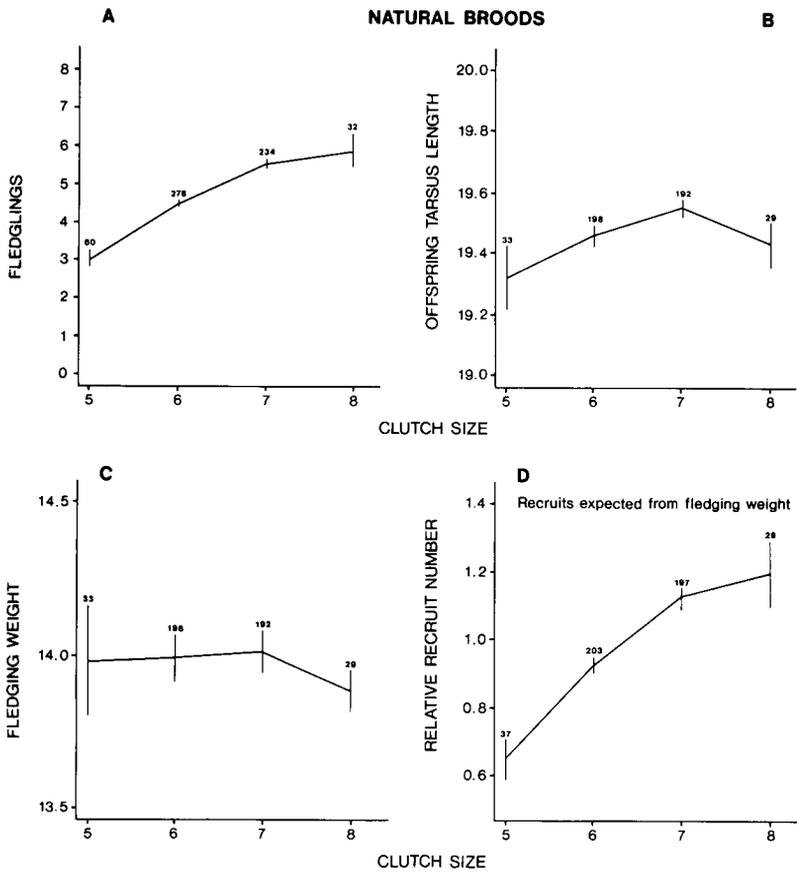


Fig. 1. Reproductive success in natural broods plotted against the clutch size. The vertical lines represent standard errors and the figures above them are the numbers of nests of the given clutch size.

extra young was no higher than for the control clutches (U-test, $z=0.29$, $P>0.77$), though the control broods had a clearly higher recruit estimate than the reduced broods ($z=3.66$, $P<0.001$). The relative success of each egg in producing viable offspring decreased with the experimental increase of brood size ($r_s=-0.15$, $P<0.05$).

Yearly variation

There was a clear difference in the outcome of the experiment for the two breeding seasons (Fig. 3). In 1983, the correlation between the change in brood size and the number of fledglings was high (Fig. 3a, $r_s=0.74$, $n=77$, $P<0.001$). Although the increase in brood size had a negative influence on the fledgling weight ($r_s=-0.27$, $P<0.05$), the correlation for the esti-

mated number of surviving offspring was highly positive (Fig. 3c, $r_s=0.62$). In 1984, the correlation between the change in brood size and the number of fledglings was much lower (Fig. 3b, $r_s=0.32$, $n=127$, $P<0.001$). Since fledgling weight was again negatively influenced ($r_s=-0.23$, $P<0.05$), there was no increase in the estimated relative number of recruits with the manipulated increase in brood size ($r_s=0.06$, $P>0.10$).

This difference is probably related to the clear difference in the breeding success of Pied Flycatchers in the two years. In 1983, the number of fledglings was higher in all the treatment categories, averaging 6.12 (SD=1.90, $n=77$), as compared with 4.83 in 1984 (SD=2.28, $n=127$, U-test, $z=3.78$, $P<0.001$). The average fledgling weight in 1983 (14.3 g, SD=0.88, $n=76$) was also clearly higher than in 1984 (13.4 g, SD=1.04, $n=114$, $z=6.34$, $P<0.001$).

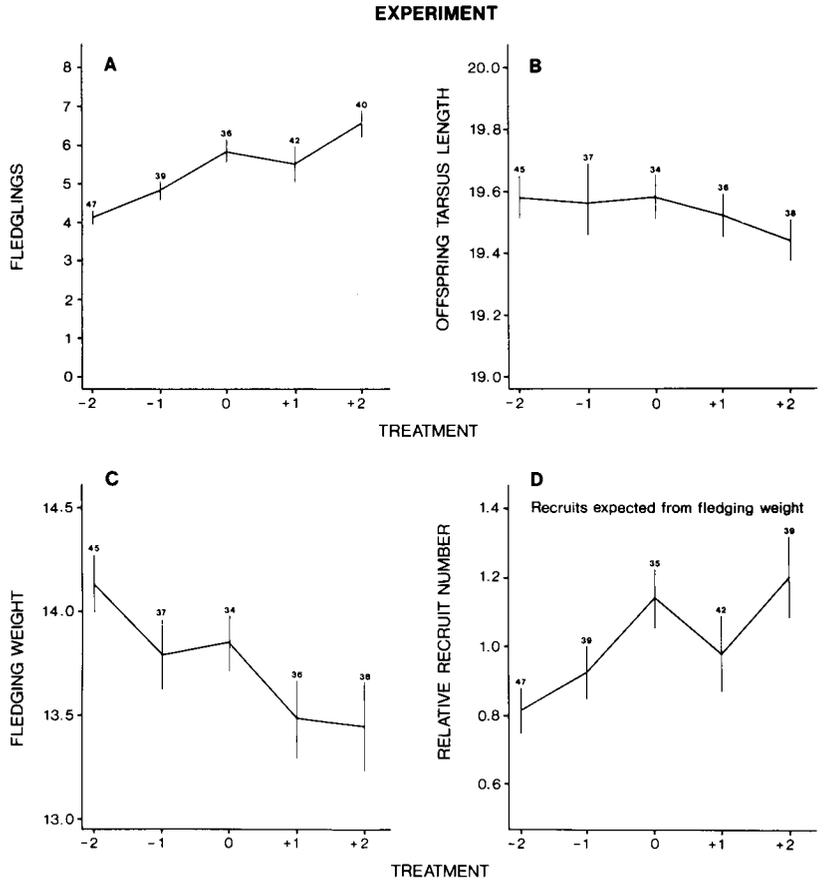


Fig. 2. Reproductive success in manipulated broods separately in 1983–84.

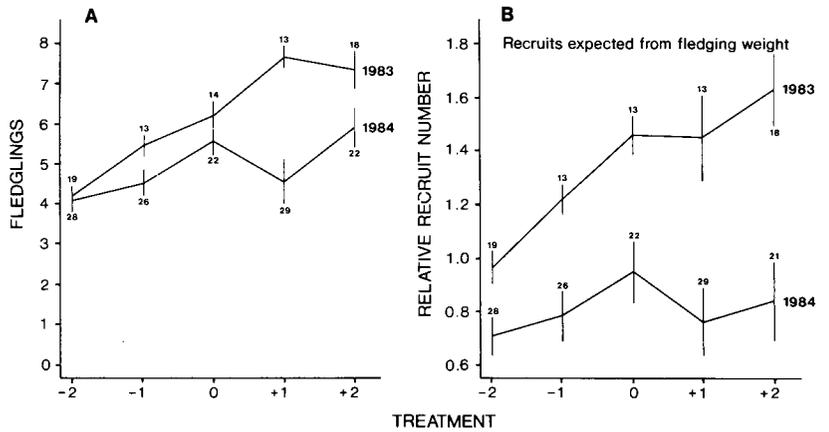


Fig. 3. Reproductive success in manipulated broods separately for the two summers.

Parent survival

There were no indications that the return rates of the parents were affected by the treatment (Table 2). This

applies to both males and females, though the data for females are scanty, forcing us to combine some of the treatment categories for the test.

Table 2. Rates of return in the following year for parents of differently treated broods.

	Returned %	n	Chi-square test
Males			
-2	18.2	44	Chi ² = 1.04 P > 0.90
-1	17.2	29	
0	20.0	35	
+1	13.9	36	
+2	22.9	35	
Females			
-2 or -1	7.6	79	Chi ² = 0.96 P > 0.95
0	7.9	38	
+1 or +2	6.6	76	

Discussion

The experiment supports the idea that individuals tend to lay the clutch size that is most productive for their average breeding conditions. However, the data are not quite sufficient to test whether an increase or reduction of only one egg gave a significantly reduced number of viable offspring. So far, that test has not been made in any species. It is likely that not all the effects of our treatment on offspring survival were revealed by the number of fledglings and the weight at fledging, and our approach probably overestimated the success of enlarged broods.

The experiment likewise provided support for the idea that it is the feeding of the offspring that determines the optimal clutch size, rather than the costs of laying or incubation. Still, it is possible that the capacity to lay or incubate have some, though slight, effects on clutch size. In particular, new studies of the costs of incubation using the double-labelled water technique in the Pied Flycatcher have indicated that this period is more demanding than was earlier believed (J. Moreno, in prep). In marginal populations in the subarctic areas, adverse weather frequently causes incubation failures (Järvinen & Väisänen 1983, 1984). Furthermore, Pied Flycatcher females incubate alone and they are partly dependent on the feeding by the male (v. Haartman 1951b, Lifjeld & Slagsvold 1986, Lifjeld et al. 1987). The aid of the male is particularly important in harsh weather, and the females of polygynous males may then have problems.

Many studies have suggested that clutch size has only slight effects on the future reproduction of the

parents. According to our experiment this is also the case in the Pied Flycatcher, although greatly increased brood sizes resulted in lowered return rates in the study of Askenmo (1979). The idea that the cost of reproduction for the adults limits the clutch size for birds was derived from the general life-history theory. However, prolonged parental care may limit the operation of such long-term effects (see e.g. Murphy & Haukioja 1986, Alatalo & Lundberg 1988). If parents work too hard for the benefit of their offspring, at the cost of their own survival, this may easily lead to the death of the parents before the offspring reach independence. In that case the success of the offspring will also be at risk. The situation is quite different in animals whose offspring are not dependent on parental care. In altricial birds the trade-off between present and future reproduction can work only for the costs that can be transferred to the period when the offspring have already reached independence, and the mechanisms for this may be limited.

The next question is how well the females adjust the clutch size in response to all the variation in breeding conditions. In our experimental nests, the average clutch size was practically the same for the two summers (1983: 6.82, SD=0.70, n=77; 1984: 6.78, SD=0.70, n=127, t=0.39, P>0.70), but the breeding success was much lower in 1984, presumably due to poor feeding conditions in that summer. During the nine days when the main part (>75%) of the nests had 10–13 day old nestlings, the average daily maximum temperature in 1983 was 20.5°C (SD=4.0) and in 1984 17.2°C (SD=2.8, t=2.03, P=0.06, data from Uppsala meteorological station). During the same period only one of the nine days was rainy in 1983, while eight were rainy in 1984, and the average daily rainfalls were 1.0 mm (SD=3.0) and 5.6 mm (SD=6.0, U-test, U=10, P<0.01), respectively. It seems that in 1983 the females would have benefited by laying larger clutches than they did, while in 1984 they succeeded in optimizing the clutch size.

Presumably females can respond only to the predictable variation in breeding conditions, and when laying they cannot precisely estimate the possibilities for feeding the offspring later in the summer. The breeding success of Pied Flycatchers varies greatly between years in relation to the weather conditions (Järvinen 1983, Virolainen 1984). The abundance of food changes with the weather; in particular, the larval outbreaks in deciduous trees vary greatly in magnitude. Furthermore, rainy weather for several days may cause great problems in feeding the offspring,

probably due to difficulty in searching for food in the wet canopy. A further unpredictable factor seems to be assistance by the male in feeding the nestlings. The secondary females of the polygynous males have to do most of the feeding alone (v. Haartman 1951b, Alatalo et al. 1982, Lifjeld & Slagsvold 1989). The polyterritorial behaviour of the males may conceal their true status from many of the females (v. Haartman 1951b, Alatalo et al. 1981, Alatalo & Lundberg 1984), and it seems that the females do not respond to their secondary status by reducing the clutch size as much as should be expected (Alatalo & Lundberg in prep., see also Stenmark et al. 1988).

On the other hand, there are many predictable cues to future breeding conditions. Females clearly respond to the progress of the season by reducing the clutch size with time. Von Haartman (1951, 1967a, 1969, 1979) calls this the 'calendar effect'; females produce clutches of the same average size at a given time, irrespective of the year. The reduction of clutch size with time can be attributed to the deterioration of feeding conditions later in the summer. However, the rigidity of the relationship over the years suggests that the females use rather rough rules-of-thumb in the proximate control of the clutch size. Among other factors, type of habitat (Berndt & Winkel 1967, Alatalo et al. 1985) or altitude (Zang 1980) may have a slight influence on clutch size. There is also variation in clutch size between populations (v. Haartman 1967b, Berndt et al. 1981), which is to be expected, as there should be differences in the predictable feeding conditions between areas.

Low predictability of the feeding conditions may allow some heritability to be retained for clutch size, in the same way as is found in the Great Tit, with variable selection pressures on clutch size in different years (Noordwijk et al. 1981). In the Collared Flycatcher, the heritability of clutch size, estimated by mother — female offspring resemblance, was 0.32 (Gustafsson 1986). In the Pied Flycatcher comparable data have not been published, but the correlation of clutch size from year to year in the same female is $r=0.48$ ($n=48$, $P<0.001$) in our data, which suggests that there may be some heritability. However, it is likely that these values overestimate the heritability, due to the same environmental factors acting on mothers and their offspring.

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Selostus: Kokeellinen tutkimus kirjosisiepon munaluvusta

Lack esitti jo vuosikymmeniä sitten hypoteesin, että linnut munivat munaluvun, joka maksimoi lisääntymisikään selviävien poikasten määrän. Pesäviipyyisillä lajeilla rajoittavana tekijänä olisi nimenomaan emojen kyky ruokkia poikasia. Aluperin hypoteesiä testattiin vertaamalla poikastuottoa ja munamäärää odotuksella, että populaation yleisin munaluku olisi kaikkein tuottavin. Yleensä kuitenkin havaittiin, että lentopoikasten määrä kasvaa munaluvun kasvaessa. Näin on myös kirjosisiepolla, esimerkiksi meidän Uppsalassa keräämämme aineiston mukaan (kuva 1A). Useimmiten ongelmana on, että todellista lisääntymisikään selviytyvien poikasten määrää ei voida arvioida, koska poikaset levittäytyvät tutkimusalueiden ulkopuolelle pesimään. Näin käy myös kirjosisiepolla. Poikasten kasvu ei kuitenkaan ole huonompi suurilla pesyekoilla (13 vrk:n ikäisten poikasten nilkan pituus kuvassa 1B ja paino kuvassa 1C). Lähisukuisella sepsiesiepolla Gotlannin saarella pesivien lintujen poikaset palaavat pesimään tutkimusalueille. Gustafssonin tutkimusten mukaan paluutodennäköisyys on pieni, jos poikaset ovat pesästä lähtiessään kevyitä. Hänen tuloksiaan hyväksi käyttäen voimme karkeasti arvioida lisääntymisikään selviävien poikasten määrää niiden pesästälähtöpainon perusteella (kuva 1D). Näin ennustaan myös todellinen poikastuotto kasvaa selvästi pesyekoon kasvaessa.

Högstedt esitti, että poikastuoton kasvu munaluvun kasvaessa johtuu yksinkertaisesti siitä, että kunkin yksilön kullakin kerralla munima munaluku vastaa yksilön senhetkisiä pesintäolosuhteita. Jos yksilöllä on hyvä reviiiri se munii ison pesyeen, kun taas poikasten ruokinta mahdollisuuksien heikessä yksilöt pienentävät munalukua. Niinpä, Lackin hypoteesi voidaan testata vain kokeellisesti pesyekokoa muuttamalla. Me teimme kokeen kirjosisiepolla kesinä 1983 ja 1984 Uppsalan tammivaltaisissa lehtimetsissä. Muutimme pesyekokoa yhdellä tai kahdella poikasella pian kuoriutumisen jälkeen. Kontrollissa kaksi poikasta vaihdettiin pesyekokoa muuttamatta. Pesinnän onnistuminen kontrollipesissä ja pesissä joita ei manipuloitu lainkaan oli samanlainen (taulukko 1), joten poikasten siirtely sinänsä ei vaikuttanut pesintämenestykseen.

Lentopoikasten määrä (kuva 2A) oli suurempi pesissä, joiden pesyekokoa oli lisätty, mutta pesyekoon kokeellinen lisääminen pienensi poikasten painoa (kuva 2C). Niinpä arvioitu lisääntymisikäisten poikasten määrä ei ollut kontrollia suurempi pesissä joissa pesyekokoa oli kasvatettu yhdellä tai kahdella poikasella (kuva 2D). Tämä tulos tukee Lackin hypoteesiä ja sitä, että pesyekokoa rajoittaa pääasiassa emojen kyky ruokkia poikasia eikä esimerkiksi kyky munia tai hautoa munia. Pesyekoon muutos ei vaikuttanut emojen todennäköisyyteen palata takaisin pesimään seuraavana vuonna (taulukko 2). Tämä viittaa siihen, että pesinnän aiheuttamat kustannukset tulevien kesien poikastuoton pienentämisen kautta ei rajoita kirjosisiepon pesyekokoa.

Linnut pystyvät muuttamaan pesyekokoaan vain ennustettavissa olevien seikkojen suhteen. Esimerkiksi kirjosisiepolla munaluku pienenee pesinnän aloitusajan viivästyessä ilmeisestikin siksi, että keskimääräisesti ravinnon saatavuus pienenee pesinnän myöhästyessä. Eri vuosina samaan aikaan aloitettuihin pesiin munitaan kuitenkin samankokoisia pesyeitä, vaikka poikasajan sääolosuhteet vaikuttavat hyvin paljon pesintämenes-

tykseen. Tämä vaihtelu, joka liittyy sateisuuteen ja lämpötilaan ei kuitenkaan ole ennustettavissa munintahetkellä. Niinpä näyttikin että kesällä 1983 hyvän sään vallitessa munaluvun kasvattaminen olisi voinut olla edullista (kuva 3), kun taas sateisena kesänä 1984 kokeellisesti kasvatetut pesyeet menestyivät suhteellisesti huonommin.

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