

Relation of fitness of female Great Tits to clutch size and number of broods

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Data collected during 1969–85 from two areas at Oulu were used to study the clutch size in relation to the number of Great Tit offspring recruited to the breeding population, and to the survival and individual fitness values of the females. The number of fledglings was highest in large clutches, but the recruitment per brood was similar for all clutch sizes. Female survival was about the same, irrespective of the number of eggs laid, although there was a tendency for the females laying the largest clutches to have the highest survival at Taskila and the lowest at Sanginsuu. The individual fitness value of the females correlated positively with the clutch size at Taskila but not at Sanginsuu. This relationship disappeared at Taskila when the year effect on the clutch size was eliminated. This shows that large clutches were produced in favourable seasons, after which the survival of females and their descendants was high. Adjustment of the clutch size to the environment was less successful in the coniferous forest at Sanginsuu than in the more deciduous woodland at Taskila. Selection analyses confirmed the above results, failing to reveal stabilizing or directional selection for clutch size in either area. The populations are thus balanced in this respect. Females with second broods had higher fitness values than the others at Sanginsuu, but not at Taskila. Production of two broods per season is thus more profitable in the former area than in the latter.

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Introduction

The crucial point in the life-history theories is the hypothesis of reproductive cost. The cost hypothesis (Williams 1966) assumes a tradeoff between current and future reproductive success. Since the amount of resources is limited, investment of energy in reproduction withdraws resources from the maintenance or growth of an individual, decreasing its future fecundity or its chances of surviving to the next breeding season. The greater the reproductive effort the greater is the cost incurred.

The cost hypothesis has been used in constructing models for optimal life-history traits (e.g. Schaffer 1974, Stearns 1976, Pianka & Parker 1975, Murray 1979, Bell 1980, Stenseth 1984), and in explaining the evolution of the clutch size in birds (Cody 1966, 1971, Charnov & Krebs 1974, Ricklefs 1977, 1981). According to the reasoning of Charnov & Krebs (1974), the optimal clutch size should be smaller than the most common one, because females laying somewhat fewer eggs will live longer and have more opportunities for reproduction.

Field studies have yielded conflicting results regarding the existence of reproductive cost. Some investigations have supported the theory (Askenmo 1979, Bryant 1979, Gustafsson 1985, Roskaft 1985, Slagsvold 1985, Tinbergen 1985, Ekman & Askenmo 1986), while others have failed to do so (DeSteven 1980, Högstedt 1981, Smith 1981).

In many of these studies the material covers only a few years (e.g. Askenmo 1979, DeSteven 1980,

Smith 1981, Nur 1984a, b) and the relationship between reproductive effort and survival may be masked by the wide annual variation in the survival of the parent birds. In this paper we present long-term data on the individual fitness and fecundity of female Great Tits (*Parus major*). Natural selection in the size of first clutches was studied by the method of Lande & Arnold (1983).

Material and methods

The data were collected during a long-term study of hole-nesting birds started in 1969 in the Oulu area, northern Finland (see Orell & Ojanen 1983a). The records from Taskila and Sanginsuu are used here. The Taskila study area consists of mixed forest of Norwegian Spruce, Scots Pine, birch and other deciduous trees and bushes, the nesting boxes being located near suburban houses. The Sanginsuu area lies farther from human settlement; deciduous trees are sparser than at Taskila and pines and spruces predominate. A more detailed description of the study areas is given in Orell & Ojanen (1983a).

In regular visits to the study sites during the breeding season (mid April to late August), records were made of the number of breeding Great Tits, time of laying, clutch size, number of young fledged, and the proportions of repeat and second broods. The nestlings were ringed with aluminium rings before their departure. Both parents were captured, usually while feeding their young, and marked individually with aluminium and coloured rings. When a colour-ringed old breeder was identified with binoculars, it was not always captured. As it is easier to catch females than males during breeding, more females than males could be identified and in a number of failed nesting attempts only the female was known. For these reasons only the female material was used in this study.

The sex and age (yearling vs. older birds) were determined from the plumage characteristics as described by Drost (1937) and Svensson (1970). The incubation patch of the female was in some cases used to confirm the sexing.

As Great Tits are faithful to their breeding sites in northern areas (Hildén 1979, our own observations), the method of treating a parent as dead when it was absent in the following season, gives a reliable estimate of the mortality rate in the Oulu area. Survival estimates have been obtained by the same method in many previous studies (e.g. Askenmo 1979, Bryant 1979, DeSteven 1980, Högstedt 1981, Gustafsson 1985, Schmidt 1985, Tinbergen et al. 1985).

At Sanginsuu all the offspring (43) recruited to the next breeding population were local. At Taskila the local recoveries amounted to 76 juveniles, while 10 fledglings born there were found breeding in the nearby Kuivassjärvi area (ca. 2 km distant). To increase the material, the latter individuals were included in estimating the recruitment rate at Taskila. The data on female survival and recruitment of young were collected during 1969–85 at Taskila and 1971–85 at Sanginsuu.

Fitness values were calculated from the female survival rate and the number of young recruited to the next generation: female survival + (number of recruits)/2 (Gustafsson 1985, see also Nur 1984b).

In the selection analyses (Lande & Arnold 1983) these two components of fitness were also studied separately, the females surviving from one breeding season to another being assigned a fitness value of 1 and nonsurvivors a value of 0. For the recruitment data, fitness is the number of offspring surviving to the next season. Relative fitness is the absolute fitness value divided by the mean value of the population, so that the mean relative fitness value equals one. For example, female survival is transformed into a relative fitness component by dividing by the mean value of the population.

Selection intensity is measured by the standardized directional selection differential (S). S is the difference in character means before and after selection measured by standard deviation units. It was calculated as the slope of the univariate regression of relative fitness on the standardized clutch size (mean = 0, variance = 1, Lande & Arnold 1983).

For female survival, the significance of S was tested by calculating the rank correlations of the relative fitness with the clutch size (Lande & Arnold 1983, Grant 1985).

The stabilizing selection directionals (C) were calculated as the slope of the univariate regression of relative fitness on the square of the standardized character (Lande & Arnold 1983). A negative coefficient indicates stabilizing selection, while a positive one suggests disruptive selection.

The significance of C, when S was zero, was tested for the survival data by comparing the variances of the clutch size in two groups, survivors and nonsurvivors, with F-tests (Schluter & Smith 1986). For the recruitment data, the variances were compared between the group with more recruits than average and the group with fewer recruits.

In comparing the selection directionals for all the years combined, the clutch size was standardized within each year, to eliminate the year effect on the variable.

Results

On average, the first clutches at Sanginsuu were 0.7 eggs larger than at Taskila (mean 10.07 ± 1.36 S.D., $n = 257$ and 9.37 ± 1.47 S.D., $n = 302$, respectively; all full clutches included). There was a significant positive correlation between the number of fledged young and the size of first clutches (Tables 1 and 2). Large clutches have been reported to produce more fledglings than small ones in many other studies (e.g. von Haartman 1951, Kluyver 1951, Lack 1954, Perrins 1965, Haukioja 1970, Hussell 1972, Gustafsson 1985). When the number of young recruited to the next generation is considered, however, the differences between clutch sizes become much smaller or disappear. At Taskila, the contribution to the next breeding population was about the same in clutches of 8 to 11. Only small clutches (4–7 eggs) with a low recruitment rate, and large clutches (12–13 eggs) with a high recruitment rate, tended to differ from the more common clutches. At Sanginsuu, the smallest clutches also showed low recruitment, but clutches larger than 8 all produced about the same number of surviving offspring (Table 2).

At Taskila, there seemed to be a slight, though non-significant, trend for females producing larger clutches to survive better than those laying fewer eggs (Table 1). The individual fitness of the females was highest in the two largest clutch size classes (11 and 12–13 eggs) and lowest in the smallest class (Table 1). At Sanginsuu, the female survival rates varied less between the groups (Table 2), but were

Table 1. Average number of young fledged from first clutches and recruited to the breeding population. Survival of females to the next breeding season and their fitness values in relation to the size of the first clutches at Taskila.

	Clutch size						Rank correlation	
	4–7	8	9	10	11	12–13		
Fledglings	4.23	4.65	4.24	5.73	7.05	8.13	$r_s = 0.398$	$p < 0.001$
S.D.	2.69	2.78	3.08	3.40	2.94	3.56		
Recruits	0.097	0.275	0.203	0.232	0.270	0.478	$r_s = 0.077$	NS
S.D.	0.301	0.493	0.468	0.504	0.508	0.846		
Number of clutches	31	51	74	82	37	23	298	
Survival	0.185	0.308	0.356	0.333	0.371	0.476	$r_s = 0.103$	NS
S.D.	0.395	0.468	0.483	0.475	0.490	0.511		
Fitness	0.241	0.487	0.466	0.464	0.529	0.738	$r_s = 0.133$	$p < 0.05$
S.D.	0.401	0.556	0.516	0.531	0.593	0.700		
Number of females	27	39	59	69	35	21	250	

Table 2. Average number of young fledged from first clutches and recruited to the breeding population. Survival of females to the next breeding season and their fitness values in relation to the size of the first clutches at Sanginsuu.

	Clutch size					Rank correlation	
	5-8	9	10	11	12-14		
Fledglings	3.72	5.24	6.05	5.86	7.35	$r_s = 0.240$	$p < 0.001$
S.D.	2.58	3.09	3.30	3.74	4.01		
Recruits	0.056	0.156	0.181	0.196	0.115	$r_s = 0.025$	NS
S.D.	0.236	0.475	0.521	0.444	0.326		
Number of clutches	18	45	83	56	26	228	
Survival	0.235	0.378	0.217	0.370	0.200	$r_s = -0.014$	NS
S.D.	0.437	0.492	0.415	0.488	0.410		
Fitness	0.265	0.459	0.304	0.446	0.250	$r_s = -0.02$	NS
S.D.	0.504	0.545	0.487	0.580	0.414		
Number of females	17	37	69	46	20	189	

Table 3. Standardized directional selection coefficients (S) for survival of female Great Tits. The values refer to selection on size of first clutch. N = number of females at beginning of period. Years 1969-70 for Taskila and 1976-77 for Sanginsuu were not included owing to small data. * = $P < 0.05$.

Years	Taskila		Sanginsuu	
	S	N	S	N
1970-71	-0.12	25	-	-
1971-72	-0.41	20	-0.25	12
1972-73	-0.63	8	0.00	18
1973-74	0.48	19	0.20	27
1974-75	0.17	9	0.22	15
1975-76	-0.85	19	0.27	11
1976-77	1.15	12	-	-
1977-78	-0.26	12	0.18	11
1978-79	0.06	18	-0.87	6
1979-80	0.18	15	0.48	6
1980-81	0.72*	21	-0.86	17
1981-82	-0.16	37	-0.08	30
1982-83	-0.06	13	0.15	18
1983-84	-0.13	9	0.00	6
1984-85	0.73	9	0.79	9
Mean	0.06		0.02	

highest among the females with clutches of 9 and 11. The same females also had the highest average fitness values, but the correlation between clutch size and fitness was not significant.

Selection on clutch size was studied by calculating directional selection differentials for female survival at Taskila and Sanginsuu (Table 3). At Sanginsuu, female survival was not associated with the standardized clutch size in any of the years. The results were the same at Taskila, with the exception of 1980, when females producing large clutches survived significantly better than the others. However, the average of these differentials was about zero in both areas, which suggests that no directional selection took place in the populations during the study.

The material was too small to allow separate analysis of the recruitment rate in the different years,

but, as the years were independent in this respect, the data could be combined for overall comparison. No significant directional or stabilizing selection was found in either area (Table 4). So the recruitment of young from clutches of different initial size to the next breeding population did not deviate from random recruitment.

The significant positive correlation between fitness and clutch size (Table 1) at Taskila suggests that females with large clutches are fitter than those laying smaller ones. In contrast, stabilizing selection may exist at Sanginsuu, where the females with the smallest and largest clutches have low average fitness (Table 1). However, the above results may be affected by annual variation in the external conditions. If the largest clutches are produced in favourable seasons and the smallest clutches when the environmental conditions are poor, and survival is associated with the quality of season (e.g. 1980, see Table 3), the above positive correlation found for the Taskila females can be expected. To take out the year effect, the clutch sizes were standardized in such a way that the average for each year was zero and the standard deviation one. This was done by calculating the z-score for each clutch size, i.e. the deviation of the clutch size from the annual mean in standard deviation units; (clutch size — average clutch size)/S.D.

When the fitness values were calculated for females with different z-scores, the results changed slightly. At Taskila, the females who laid about the average clutch size (within 0.5 standard units of the mean) showed somewhat higher fitness than most of the others (Table 5), but those laying clutches that were 1.25 units larger had the highest fitness value. At Sanginsuu, the females laying large clutches (0.75 standard units larger than the average) seemed to be less fit than the others (Table 5). Slight directional selection for a larger clutch size may thus exist at Taskila, while stabilizing selection may be present at Sanginsuu.

These alternatives were studied by examining the regression of the individual fitness values on the standardized (within each year) clutch size for directional selection and their regression on the square of the standardized character for stabilizing or disruptive selection. In both areas, the deviation of the selection directionals from zero was slight, and not significant, in all cases (Table 6; see also rank correlations in Table 5). The results support the conclusion that the female fitness value shows no selection on the clutch size.

Females differ in their capacity to produce clutches during the season, some laying one, others more. At Taskila fitness did not seem to differ between these groups of females (Table 7). Females with repeat broods seem to be somewhat less efficient, though the differences between the groups were not significant. In any case the results suggest that females raising a second brood are not of better quality than those with only one brood.

At Sanginsuu the females rearing a second brood contributed significantly more descendants to the population and had significantly higher fitness values than those with only the first or a repeat brood (Table 7).

Discussion

What is the optimal clutch size? The reproductive success of an individual during its lifetime can be used as a measure of fitness. Importance attaches to the number of descendants surviving to breed and the survival of the parent itself (e.g. Charnov & Krebs 1974). For a reproducing bird it is decisive to achieve a clutch size that is optimal in the current situation and to maximize the number of recruits produced during its lifetime. According to the cost hypothesis (Williams 1966), reproduction decreases the individual's survival (survival cost) and therefore its future reproductive success (reproductive cost). The fittest individuals are those which gain the highest profit with the lowest investment. The optimal reproductive strategy of an individual is determined by the predictability of the environment it lives in. Theoretically, if the probability of the female surviving to the

next season is low, the strategy of maximum investment in the current season should be selected for (Schaffer 1974). On the other hand, if the survival of the fledged young is unpredictable, a small investment should be favoured (Stearns 1976, Gillespie 1977).

Högstedt (1980), who manipulated Magpie (*Pica pica*) broods, found that more young were raised to fledging in the natural broods than in the enlarged or reduced ones, and argued that the clutch size is phenotypically adjusted to correspond to the habitat quality. This means that females generally lay clutches whose size is optimal for the habitat and that the average clutch size is optimal for birds with territories of average quality.

If the major part of the clutch size variation is adaptive, survival should not be expected to differ with clutch size (e.g. Högstedt 1981, Källander 1983, Alerstam & Högstedt 1984). Hence, the relative investment in breeding should be about the same irrespective of the clutch size.

However, as the success of the female in adjusting clutches to correspond to the ability of the parents to raise the young to fledging may vary greatly from one year to another (e.g. Orell & Ojanen 1983b) selection for small, intermediate or large clutches can be expected in different years. In a balanced population, however, these forces must cancel each other out.

In both study areas the selection differentials for female survival, although barely significant, varied from negative to positive and the long term average was practically zero. The same result, no selection, was obtained when the other fitness component, the recruitment rate, was examined. Thus the results strongly suggest that these Great Tit populations are

Table 4. Standardized directional (S) and stabilizing (C) selection differentials for number of young recruited to the next breeding population, calculated from combined data at both study sites. Symbols and explanations as in Table 3.

Years	Taskila			Years	Sanginsuu		
	S	C	N		S	C	N
1969-85	0.12	0.02	298	1971-85	-0.05	-0.04	228

Table 5. Fitness values of the female Great Tits in relation to the size of first clutches expressed as z-scores at Taskila and Sanginsuu. The z-scores denote the mean of each class.

	Z-score							Rank correlation	
	≤-1.25	-1.00	-0.50	0.0	0.50	1.00	>1.25		
Taskila	0.278	0.370	0.553	0.564	0.390	0.468	0.621	$r_s = 0.085$	NS
S.D.	0.446	0.598	0.524	0.552	0.466	0.632	0.592		
N	27	27	47	39	50	31	29	250	
Sanginsuu	0.375	0.407	0.333	0.386	0.402	0.231	0.278	$r_s = -0.058$	NS
S.D.	0.592	0.555	0.504	0.543	0.539	0.439	0.428		
N	16	27	39	35	41	13	18	189	

Table 6. Standardized directional (S) and stabilizing (C) selection coefficients for individual fitness values of female Great Tits.

Years	Taskila			Years	Sanginsuu		
	S	C	N		S	C	N
1969-85	0.06	-0.01	250	1971-85	-0.02	-0.01	189

balanced with respect to the size of first clutches. These results support the hypothesis that females lay clutches whose size is optimal for parental care. In other long-term studies on the Great Tit, the juvenile recruitment rate per clutch has also failed to reveal directional selection (Perrins & Moss 1975, van Noordwijk et al. 1981, Steinbach 1983).

Comparison of the individual fitness value with the size of the first clutch revealed a significant positive correlation at Taskila but not at Sanginsuu. Högstäd (1981) and Smith (1981) found a positive relationship between fecundity and adult survival and Gustafsson (1985) noted that large broods contributed more recruits to the population than did the smaller ones. These results show that young from large clutches are not inferior in quality to young from smaller broods and have about the same probability of surviving. Nor was female survival impaired by large first clutches. On the contrary, it seemed that high-quality females laid the largest clutches at Taskila. However, when the year effect was eliminated by standardizing the clutch size, this relationship disappeared. The results suggest that in favourable conditions females lay large clutches and that after such seasons both female and juvenile survival is good resulting in high individual fitness values. Thus it is a question of the conditions during and after the breeding season and not of females with large clutches having higher fitness values in the long term. After the favourable summer of 1980, for example, female survival was significantly and positively related with the clutch size. This was a record year in the Oulu area, with practically no nestling losses (Orell & Ojanen 1983c).

If clutch size is phenotypically modified to the quality of the habitat and the capacity of the female, the optimal size cannot be found without experimental tests. Some manipulations of brood sizes have shown that birds are able to rear more young than were present in the initial clutch (e.g. Crossner 1977, DeSteven 1980, Cronmiller & Thompson 1980, Westerterp et al. 1982, Slagsvold 1982, Korpimäki 1986). As the fate of the young after fledging was not followed in these studies, the results cannot be used to judge the optimal clutch size, since the decisive variable is the number of young surviving to breed.

Manipulation of the clutch size of the Collared Flycatcher (*Ficedula albicollis*) in one year seemed to

show that females lay optimal clutch sizes (Gustafsson 1985). In this species the parents with unmanipulated broods had higher individual fitness values than those whose brood was enlarged or decreased, yet this difference was not seen by the time of fledging. The parents were able to rear enlarged broods to fledging, but the quality of such young was poor, judging from their low weight at fledging.

The results obtained by Nur (1984b), who manipulated the brood sizes of the Blue Tit (*P. caeruleus*), contradict Högstäd's hypothesis that clutch size is phenotypically adjusted to the quality of the habitat. In two years the clutch size which would lead to the highest growth rate in the Wytham population was larger than the most common one, 9 eggs. Therefore, in some years tits are able to rear larger broods than initially hatch. It may be that in such cases the food resources improved significantly during the season and the cues during laying were not predictable to adjust the clutch size to correspond to the conditions prevailing later in the summer. The clutch size may have been optimal for the females at the time of laying but not necessarily so when the young were being fed later in the season. In favourable years, such as 1980 in the Oulu area (see also Orell & Ojanen 1983b), quality differences, attributable to fledging weight (Perrins 1965), between the young from different broods may be too small to seriously influence their future survival and the individual fitness values of the parents. For this reason, Nur's results do not disprove the hypothesis presented by Högstäd (1980). However, in view of the conflicting results, it is important to continue brood size manipulations for many years in varying environmental conditions.

Reproductive strategies in an unpredictable environment. The individual fitness values cannot be compared between the study areas since the breeding Great Tits were caught more efficiently at Taskila than at Sanginsuu, and this is at least partly responsible for the higher survival and recruitment rates recorded in the former area (Tables 1, 2 and 5). Even at Taskila, not all the breeding birds were identified. For this reason and owing to the natal dispersal of juvenile birds, the individual fitness values for both areas are underestimates, the values for Taskila being closer to the real ones than those for Sanginsuu.

If the best qualified females lay the largest clutches, the results for Sanginsuu are difficult to explain: among the females with large clutches (12 or more eggs) and broods, the average survival at Sanginsuu was less than half of the corresponding value at Taskila. A similar relationship was found in the juvenile recruitment rate. The reason may be that mortality was in fact high among birds from large broods at Sanginsuu, but the same result would be obtained if natal dispersal is dependent on clutch size in this area. Dhondt & Hublé (1968) have shown that young from second broods emigrate farther than

older juveniles in the same area. This is perhaps due to the social relationships between young birds in Great Tit flocks (Garnett 1976). There are no data from Sanginsuu for testing this possibility, but at Taskila the clutches which contributed young to the Kuivasjärvi area, ca. 2 km distant, had an average of 10.4 eggs ($n = 9$), and the juveniles which remained at Taskila in the same years originated from clutches of the same size (average 10.3, $n = 32$). So at least such short-distance dispersal was not dependent on the clutch size and it is hard to imagine why such a relationship should exist at Sanginsuu, where the tit density in summer is much lower. Therefore, it seems probable that the young from large broods at Sanginsuu have a somewhat smaller chance of surviving than the other Great Tit fledglings.

The reason for the differences between the study areas can be differences in the habitat. The coniferous forest at Sanginsuu may be a less predictable environment for Great Tits than the mixed woodland at Taskila. Food may be plentiful in spring at Sanginsuu when the females are forming eggs, so that they can lay large clutches, and it may decrease or deteriorate later in the season, with a resultant decrease in breeding success.

Young from initially large broods are usually lighter than those from smaller broods in both areas (own unpubl. data). When the parents are unable to raise the whole brood, the number of chicks is reduced (e.g. O'Connor 1978, Orell & Ojanen 1983c). This is not always enough to compensate for the large initial number of young and the chicks are light at fledging (own unpubl. data). The condition of fledglings is important to their future survival (Perrins 1965). The environment at Taskila is perhaps good enough to allow underweight young to survive as

well although their starting point may be worse than that of the heavier fledglings. The superiority of the habitat at Taskila probably explains the relatively good survival of females rearing large broods. The chance of surviving to the next breeding season decreases if conditions become too poor, as is perhaps the case at Sanginsuu. In such a habitat the young from the largest broods and perhaps also the females caring for them may have a small chance of survival. It is possible that there is a certain threshold in the environmental conditions beyond which the reproductive cost becomes high enough to reduce the adult survival, and the quality of young at the time of fledging becomes decisive for future survival. The females breeding in the coniferous Sanginsuu area are evidently less successful in adapting the clutch size to the prevailing environmental conditions than those in the more deciduous Taskila.

At Sanginsuu the females more often have a second brood than at Taskila (13 % and 4 % of breeding pairs respectively, Orell & Ojanen 1983a and unpublished). Evidently only the females of highest quality are able to rear another brood later in the season (den Boer-Hazewinkel 1985). At Sanginsuu such females have much higher fitness values than the others. The size of the first clutch of females with second broods was somewhat smaller than average, the z-score being -0.253 ($n = 45$). The corresponding value for females without second broods was 0.066 ($n = 129$). The difference between these values was nearly significant (t-test, $p < 0.10$) and suggests that females with second broods invested less in the first attempt at Sanginsuu. Slagsvold (1985) and Tinbergen (1985) have shown that greater effort with the first brood was followed by lower output in repeat and second broods of the Great Tit (see

Table 7. Reproductive parameters of females in relation to the type of broods reared in a season at Taskila and Sanginsuu. The Kruskal-Wallis test applied to between group differences.

	Broods			
	First	Repeat	Second	
Taskila				
Recruits	0.271	0.209	0.333	$p = 0.876$
S.D.	0.532	0.412	0.679	
Survival	0.347	0.256	0.296	$p = 0.465$
S.D.	0.469	0.441	0.456	
Fitness	0.477	0.360	0.463	$p = 0.389$
S.D.	0.554	0.504	0.553	
Number of females	214	43	27	
Sanginsuu				
Recruits	0.108	0.042	0.360	$p = 0.023$
S.D.	0.358	0.204	0.875	
Survival	0.262	0.292	0.420	$p = 0.117$
S.D.	0.441	0.464	0.499	
Fitness	0.315	0.313	0.600	$p = 0.014$
S.D.	0.487	0.507	0.655	
Number of females	130	24	50	

also Roskaft 1985). It is possible that some Great Tit females maximize their fitness at Sanginsuu by breeding twice in the season. These females do not make a maximum investment in their first brood, which would result in low-quality offspring. They invest somewhat less and are later on able to raise another brood successfully.

At Taskila investment in second broods did not seem to be profitable. There were no fitness differences between females with and without second broods. In this area it is probably more important to breed as early as possible (earlier than at Sanginsuu, Orell & Ojanen 1983a) because of the higher competition between the young later in the summer and autumn due to the relatively high tit density. At Taskila the average number of Great Tits per unit area is about three fold that at Sanginsuu (4.6 pairs/10 ha and 1.6 pairs/10 ha respectively, Orell & Ojanen 1983b). Garnett (1976) has suggested that young from late broods have a low status in the hierarchy of tit flocks and therefore probably have a poorer chance of surviving (Tinbergen et al. 1985). Thus, maximal investment in first broods is perhaps a better strategy than breeding twice at Taskila. The rarity of second broods cannot be attributed to a shortage food, as the young of such broods are not significantly lighter than the young of first broods at Taskila (Orell 1983 and unpublished). In this area also, there is a tendency for females with second broods to have a small first clutch (z -score: -0.161 , $n = 26$) more often than the others (0.026 , $n = 210$), though the difference between the groups was not as pronounced as at Sanginsuu.

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Selostus: Pesyekoon ja tuotettujen pesyiden määrän merkitys talitiaisnaaraiden lisääntymismenestykselle.

Talitiaisnaaraiden elossasäilyvyyttä ja niiden seuraavaan (alueella pesivään) sukupolveen tuottamien poikasten (rekryytit) lukumäärää/pesye tutkittiin Oulussa kahdella pönttöalueella, Taskilassa (1969–85) ja Sanginsuussa (1971–85). Elossasäilyvyys määritettiin seuraavasti. Jos edellisenä vuonna pesinyt naaras tavattiin alueella seuraavana pesimäkautena, se sai arvon yksi. Jos sitä ei tavattu, se oletettiin kuolleeksi ja sai arvon nolla. Käyttämällä Gustafssonin (1985) menetelmää kullekin naaraalle laskettiin kelpoisuusarvo (fitness), joka mittaa naaraan kykyä tuottaa elinkelpoisia jälkeläisiä: naaraan elossasäilyvyys (+ rekryyttien määrä)/2. Näitä kolmea muuttujaa (elossasäilyvyys, rekryyttien tuotto/pesye ja fitness) tutkittiin pesyekoosta johtuvien kelpoisuuserojen selvittämiseksi. Lisäksi tutkittiin Landen ja Arnoldin (1983) menetelmää käyttäen, suosiiko valinta (suuntaava tai tasapainottava) tiettyjä pesyekokoja toisten kustannuksella.

Molemmissa pönttöpöpopulaatioissa suuret pesyekoot tuottivat eniten poikasia lentoon (Taulukot 1, 2). Pesyiden väliset erot hämärtyvät, kun tarkastellaan rekryyttien määrää/pesye. Pesyekoolla ei myöskään voitu luotettavasti

selittää naaraiden välisiä elossasäilyvyyseroja. Sen sijaan niillä naarailla, joilla oli suuri munamäärä, oli Taskilassa merkitsevästi parempi fitness kuin muilla. Sanginsuussa naaraiden väliset erot eivät olleet merkitseviä. Kun pesyekoosta poistettiin vuosivaikutus normoimalla, Taskilan naaraiden väliset fitnesserot eivät enää selittyneet munittujen munien määrällä (Taulukko 5).

Myös valintakertoimien alhaiset ja ei-merkitsevät arvot (vuosi 1980 poikkeus) osoittavat, että pitkällä aikavälillä pesyekoossa ei ole tapahtunut valintaa (Taulukot 3, 4). Toisin sanoen naaraan kunnosta ja pesinnän aikaista olosuhteista riippuen on edullista munia pieniä, keskisuuria tai suuria pesyeitä.

Alueiden välisiä fitnesseroja ei voida verrata suoraan, koska naaraiden elossasäilyvyysarvoihin ja todettuihin rekryyttien lukumääriin vaikuttaa tehokkuus, jolla pesiviä emoja on pyydytetty tai tunnistettu värirenkaista. Varsinkin alkuvuosina Sanginsuussa talitiaisemoja ei pyydytetty yhtä tehokkaasti kuin Taskilassa. Fitnesserot osoittavat kuitenkin, että keskimääräistä suurempia pesyeitä tuottaneet naaraat ovat menestyneet jälkimmäisellä alueella suhteellisesti paremmin kuin edellisellä (Taulukot 1, 2 ja 5). Tämä johtuu siitä, että havuupuuvaltainen Sanginsuu on epäennustettava verrattuna lehtipuuvaltaiseen Taskilaan. Siellä suotuisia olosuhteita keväällä, jolloin naaraat ovat pystyneet tuottamaan suuria pesyeitä, ei läheskään aina ole seurannut samanlaiset olosuhteet kesällä ja poikasten lähdeä pesästä. Näyttää siltä, että suurista pesyeistä lähteneet poikaset ovat olleet huonokuntoisempia eivätkä ole selvinneet elossa seuraavaan kevääseen niin usein kuin muista pesyeistä lähteneet. Samoin näitä poikasia ruokkioiden naaraiden elossasäilyvyys oli alentunut. Pesyekoon optimoiminen on siis onnistunut paremmin Taskilan naarailla; hyväkuntoiset naaraat ovat tuottaneet suurimmat pesyeet, joista on tullut myös eniten jälkeläisiä seuraavaan sukupolveen.

Verrattaessa naaraiden fitnessarvoja havaitaan, että toisen pesyeen tuottaminen onnistuneen poikueen jälkeen on ollut Sanginsuussa edullisempaa kuin Taskilassa (Taulukko 7). Syyinä saattaa olla, että täällä, missä kanta on tiheä (keskimäärin 4.6 paria/10 ha), myöhäisten pesyiden poikaset joutuvat itsenäistyttyään kilpailemaan ravinnosta ankarimmin kuin Sanginsuun (1.6 paria/10 ha) vastaavat poikaset. Tehostuneesta kilpailusta johtuen myöhäisten pesyiden poikasten elossasäilyvyys huononisi Taskilassa.

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