Mate selection in the Great Tit *Parus major* in relation to age, status and natal dispersal

PAUL J. GREENWOOD, PAUL H. HARVEY & CHRISTOPHER M. PERRINS

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An examination has been made of the mate combinations of Great Tits in Wytham Wood from 1964—75. On average, 67.5 % of first year males and 34.6 % of older males were paired with first year females; 43 % of first year females and 16 % of older females were paired with first year males. As a result, the average age of their mate was higher for females than males and for both sexes higher for older birds than first years.

Those born in the study area were more likely than expected to pair with other residents and immigrants with immigrants in both sexes. Older birds, when re-pairing on the death or divorce of their mate, did not subsequently acquire older mates than Great Tits breeding for the first time. There was a suggestion that immigrant males were more likely to mate with a first year female and resident males with older females.

Older females when paired with a first year male were more likely than other categories to subsequently re-pair with an older male. Resident females were also more likely than other categories to re-pair with an older male following the death or divorce of a first year male.

The greater the number of territories that a resident Great Tit dispersed from its natal to first breeding site the further apart it was born from its eventual mating partner. The median number of territories separating the birth sites of resident birds which subsequently paired was 6.6.

Paul J. Greenwood & Christopher M. Perrins, Edward Grey Institute, Department of Zoology, South Parks Road, Oxford OX1 3PS, England
Paul H. Harvey, School of Biological Sciences, University of Sussex, Falmer, Brighton, Sussex BN1 9QG, England

Introduction

Long term studies of hole-nesting passerines have yielded perhaps the most detailed information on the population ecology of any bird species. Such studies have been centred in Europe. The most extensive and continuing investigations have been those on the Great Tit *Parus major*, Blue Tit *Parus caeruleus* and Pied Flycatcher *Ficedula hypoleuca*. Modern ecologists can acknowledge an enormous debt to the insight of a number of pioneers for initiating these studies, among them von Haartman in Scandinavia, Lack in Britain and Wolda and Kluijver in Holland.

One of the most important features of long term studies has been the value of studying populations of known individuals. This has enabled many components of population structure to be examined. We have already made a detailed study of dispersal in the Great Tit (Greenwood et al. 1978, 1979a, b, Harvey et al. 1979). It is perhaps fitting in this volume that we should consider further aspects of population structure, an area of research to which Lars von Haartman himself made a considerable contribution (e.g. v. Haartman 1949, 1951, 1954, 1960).

The breeding population of Great Tits in Wytham Wood consists of individuals which can be allocated to a number of different categories. A large proportion of birds which breed are themselves born in the study area (residents), but a sizeable fraction come from outside (immigrants). Approximately half the Great Tits in any one year are breeding for the first time. These can be designated simply as first year birds to distinguish them from older birds (at least 2 years old) which, in most cases, have bred before.

Some of the aspects of breeding structure which we wish to consider in this paper concern the pairing procedures of individuals within and between these different groups. Do immigrants pair with residents in the frequencies expected from their abundance in the population? Do first year birds pair with older birds as often as expected from their proportions? One would expect both on empirical and theoretical grounds to find deviations from a random mating assortment. For example, if it is advantageous for Great Tits to pair with individuals similar in phenotype to themselves then one way of achieving this might be to preferentially mate with a bird having a similar status (resident or immigrant). In terms of age, the benefits of experience in increasing reproductive success could result in older birds, on losing one mate, discriminating, in a subsequent choice of mate, against those breeding for the first time. A further problem is whether prior experience with one type of mate influences the selection of a partner the following year after the death or divorce of the former. An assessment is also made of the importance of natal dispersal on mate selection; whether dispersing from the birth to first breeding site affects the site of origin or type of mate with which an individual pairs.

Methods

The data presented in this paper were collected in Wytham Wood from 1964—75. The study area of 231 hectares of mixed deciduous woodland is described in detail by Elton (1966). An up-to-date synthesis of much of the information on the breeding ecology and behaviour of the Great Tit in Britain can be found in Perrins (1979).

Nest boxes are provided in excess in the study area and are used by Great Tits almost exclusively in preference to natural holes. The breeding data are collected systematically each year by several observers. All Great Tits which fledge are marked with a numbered ring prior to fledging. Since 1964 attempts have been made to catch both parents of all broods. Females are usually caught when incubating the eggs, males when they visit the nest boxes to feed the young. The proportion of breeding birds identified in any one year has varied from 19—81 % for males ((average 50.8 %) and from 71—89 % for females (average 79.0 %) (Greenwood et al. 1979a).

The breeding population of Great Tits in Wytham Wood is composed of residents and immigrants. Residents are defined as those born and subsequently breeding in the study area. Fledged birds unringed when first caught we define as immigrants; virtually all of these are born outside the wood and have dispersed into the study area to breed. The place of birth of such birds is usually unknown. However, their year of birth is usually known since the large majority are caught and ringed in their first year, either as juveniles in the autumn and winter or as members of the breeding population the following summer. First year birds can be distinguished from older ones on plumage characteristics. Those immigrants which are first caught after their first moult (which occurs when they are about 13—14 months old) cannoth be aged; such birds when breeding are a minimum of 2 years old.

The analysis is restricted, in the main, to pairs in which the age and status of both male and female are known. Two age categories have been used, first year and older; the term older referring to all those birds 2 years old and above. Further subdivisions of the older category would have severely limited the scope of the analysis since the sample sizes in higher age classes are small. Thus, in terms of the age and status of males and females the following subdivisions have been used:

- — First year resident
- — First year immigrant
- — Older resident
- — Older immigrant

The data for all years 1964—75 have been combined for the analysis.

In the first two sections we examine the mating combinations of all known pairs of Great Tits breeding from 1964—75. We have included birds irrespective of whether they changed mates or not from one year to the next. The remainder of the paper concerns the mate choices of (a) those breeding for the first time and (b) older birds acquiring a new mate following the death or divorce of a previous partner. Those individuals which re-pair with the same bird in consecutive years are excluded. The analysis is concerned with differences between groups in their tendencies to mate within and between these different groups. We do not examine the mate combinations of Great Tits in relation to the overall abundance of each of the four categories in different years.

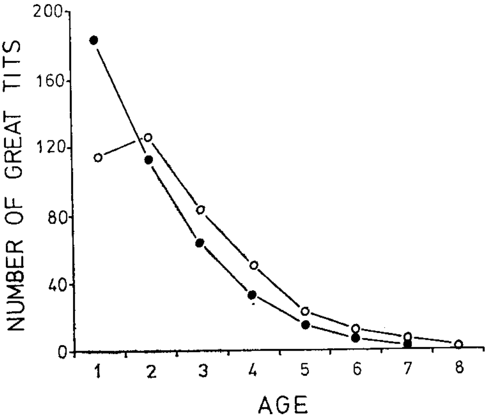

Fig. 1. The age distribution of Great Tits in Wytham Wood 1964—75 where the ages of both members of a pair were known; o = male, ● = female.

Results

Age structure. Illustrated in Fig. 1 are the age distributions of males and females in the population from 1964—75 where both members of a pair were identified. The figure includes birds known to have bred up to several times with the same mate, those that changed mates and those recorded only once. Individuals are counted as many times as they are known to have bred with an identified mate. It is a slightly inaccurate representation of the age structure of the population during this period since it does not include those Great Tits of known age paired to birds of unknown age. As such it will understimate to a small extent the proportion of older birds; 12 % of females and 6.5 % of males of known age were paired with older males and females respectively whose precise ages were unknown. It is also assumed that when both the male and female of a pair are identified they represent a random sample of the population. This may not be the case if certain age groups (e.g. first years) are more prone to breeding failure before the male is caught or certain areas of the wood have atypical age structures. The values shown in Fig. 1 confirm an earlier finding for the Great Tit of there being a shortage of first year males in the breeding population (Bulmer & Perrins 1973); it is believed that the

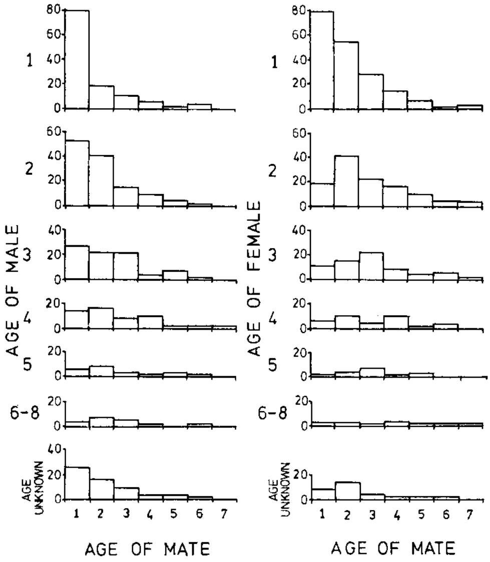

FIG. 2. The number of males and females of known age paired with mates of known age.

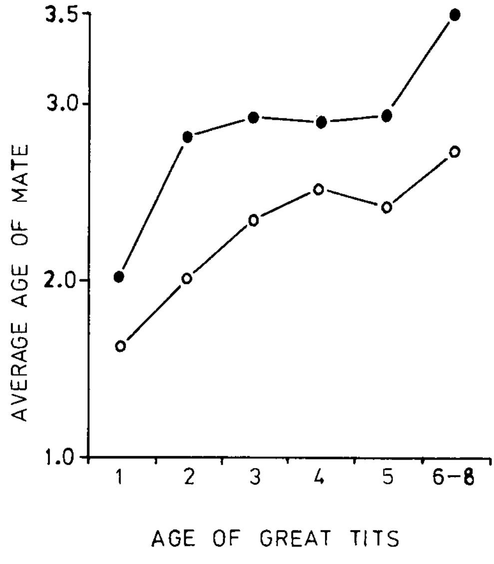

FIG. 3. The age of male and female Great Tits in relation to the average age of their mates; o = male, ● = female.

missing males are present, but unable to find a mate.

Age of mate. Fig. 2 shows the ages of males and females in relation to the ages of their mates. A higher proportion of males than females are paired with young individuals. 67.5 % of first year males and 34.6 % of older males are paired with first year females; 43 % of first year females and 16 % of older females are paired with first year males. The average age of the mate for each year group is always higher in females than males and for both sexes is higher for older birds than first years (Fig. 3). The increase in the age of mate with the age of both sexes reflects, in part (see below), the tendency of most birds to retain their mate from a previous year if both have survived. We estimate that approximately 30 % of all matings end in divorce when both members of a pair survive to breed in a subsequent year (Harvey et al. 1979).

Age and status of mates. The breeding performance of Great Tits varies in relation to the age of both parents. On average older females have a higher reproductive success than first year females (Perrins & Moss 1974), although the lower success of first year females is partially offset through breeding with an older male (Harvey et al. 1979). Given that success eventually declines with age in females (Perrins & Moss 1974), it is probably advantageous for both sexes to pair with older individuals. In this section we examine whether there are differences between individuals in their tendencies to acquire mates of a particular age or status. Although it is currently uncertain if breeding success is dependent upon an individual's status and that

TABLE 1. Mate selection of older resident and immigrant males and females following death or divorce of previous mate and mate selection of first year resident and immigrant males and females at first breeding attempt.

		Male				
		Older resident	Older immigrant	First year resident	First year immigrant	Total
Female	Older resident	30	20	30	18	98
	Older immigrant	29	27	33	31	120
	First year resident	47	45	65	36	193
	First year immigrant	55	66	62	101	284
	Total	161	158	190	186	695

of its mate it is conceivable that, as with age, differences do exist between the reproductive performances of the various combinations of resident and immigrant.

The sample in the analysis is restricted to first year birds of known status and older birds where the mate is known to have died in the preceding year or where a divorce has occurred and both members of the earlier pair took new mates. We have specifically excluded those individuals that re-pair with the same mate in consecutive years.

The age and status of individuals with respect to that of their mate are shown for all categories in Table 1. There is a marked tendency for first year and older birds of both sexes to pair with an individual of similar status ($\chi^2 = 14.82$, $P < 0.001$). For females, 59 % of residents paired with with a male of similar status whereas the proportion of immigrants paired with residents was only 44 %. For males, 49 % of residents mated with residents and only 35% of immigrants with residents; 51 % of residents paired with immigrants and 65 % of immigrants with immigrants. The fact that a higher proportion of resident females paired with resident males than was the case with resident males paired with resident females reflects the fact that natal dispersal is further in females than males (Bulmer 1973, Greenwood et al. 1979a). Consequently, there are more immigrant females in the breeding population than immigrant males. The average proportion of immigrants breeding in the study area from 1964—75 was 58 % in females and 49 % in males (Greenwood et al. 1979a).

There is no tendency for birds of either sex in a particular age category to pair with those within the same group ($\chi^2 = 1.95$, n.s.). Approximately as many first year females pair with older males (44.7 %) as do older females (48.6 %). In males, 33.2 % of older males that re-pair following the death or divorce of a previous mate do so with an older female, the equivalent figure for first year males breeding for the first time is 29.8 %. Both percentages are lower than those for females. This is because there are fewer older females in the population than older males due to higher mortality in females (Bulmer & Perrins 1973). From 1964—75 there were on average 60.6 % of older males and 46.4 % of older females in the breeding population (Greenwood et al. 1979a). Consequently there are fewer opportunities for first year and older males to mate with older females.

TABLE 2. Association between age of male and female and the age of their mate prior to change (1 = First year, 0 = Older).

		Age of mate prior to re-pairing		
		1	0	
Age of female	1	32	29	$\chi^2 = 9.5$
	0	21	57	$P<0.01$
		Age of mate prior to re-pairing		
		1	0	
Age of male	1	40	26	$\chi^2 = 7.5$
	0	27	45	$P<0.01$

TABLE 3. Association between status of male and female and the status of mate prior to change (R = Resident, I = Immigrant).

		Status of male prior to re-pairing		
		R	I	
Status of female	R	39	27	$\chi^2 = 3.85$
	I	31	42	P-0.05
		Status of male prior to re-pairing		
		R	I	
Status of male	R	32	46	$\chi^2 = 1.28$
	I	19	41	n.s.

There is no interaction between the status of the female and the age of her partner ($\chi^2=1.69$, n.s.). Thus, resident and immigrant females are equally likely to acquire first year or older males. However, an immigrant male is more likely to get a first year female and a resident male an older female ($\chi^2=3.79$, $P<0.1$).

We have examined the mating tendencies of individuals of different age and status for all birds acquiring a new mate (either as a result of changing partners due to death or divorce or because they are breeding for the first time). We have also analysed the pairing procedures of birds in the light of an earlier or subsequent bond. In other words, is mate acquisition dependent on prior experience?

The first, perhaps not surprising, finding is that when both sexes change to a new mate their previous one is of a similar age to themselves (females, $\chi^2=9.5$, $P<0.01$; males, $\chi^2=7.4$, $P<0.01$). First year birds are likely to have been paired with a first year. Older birds, on the other hand, are more likely to have been paired with an older bird (Table 2). In females, but not males, birds change from mates of a similar status (females, $\chi^2=3.85$, $P<0.05$; males $\chi^2=1.28$, n.s.). Resident females are likely to have been paired with a resident, immigrant females with an immigrant (Table 3). The reason this effect does not occur in males is probably because there are fewer resident females in the population than resident males (see above).

An influence of the former mate on subsequent pairing in the Great Tit is only evident in females. In Table 4 are shown the mating categories of females in each of the two age groups with respect to the age of their mate in one year and that of a new partner in the

TABLE 4. Age of female in relation to age of mate in one year and age of mate the next, following a change (1 = First year, 0 = Older).

	Age of mate in year *n*	Age of mate in year *n+1*		
		1	0	Total
Age of female 1	1	13	19	32
	0	9	20	29
Age of female 0	1	4	17	21
	0	26	31	57
	Total	52	87	139

$\chi^2 = 4.47$, $P<0.05$

subsequent year. There is heterogeneity in the data ($\chi^2=4.47$, $P<0.05$) which is mainly accounted for by the fact that older females which paired with a first year male in one year are more likely to re-pair with an older bird in a subsequent year. Of the 21 individuals mated to first year males all but 4 changed to an older bird the next year. They did so to a greater extent than first year females paired with first year or older males and older females paired with older males in the year preceding a change. There is also heterogeneity in the mate changes of females of different status with respect to the age of their mate in one year and that in the next ($\chi^2=4.2$, $P<0.05$). The results are shown in Table 5. Resident females paired in one year to first year males are likely to change to older males the following year to a greater extent than residents paired with older birds or immigrants paired with either first years or older birds.

Dispersal and mate selection. We have considered the influence of age and status on mate choice, irrespective of the spatial distribution of Great Tits within Wytham Wood. Elsewhere we have shown that first year resident males which disperse particularly short or long distances from their natal site are more likely to pair with older females, either immigrant or resident (Greenwood et al. 1979a). For first year resident females, on the other hand, the probability of mating with a first year, older, resident or immigrant male remains constant with increasing distance from the natal site.

TABLE 5. Status of female in relation to age of mate in one year and age of mate the next, following a change (R = Resident, I = Immigrant, 1 = First year, 0 = Older).

Status of female	Age of mate in year n	Age of mate in year $n+1$		
		1	0	Total
R	1	5	20	25
	0	19	22	41
I	1	12	16	48
	0	16	29	45
	Total	52	87	139

$\chi^2 = 4.2$, $P<0.05$

The natal dispersal of Great Tits can be examined not only in relation to their birth sites (as above) but also, for some individuals, to the birth sites of their mates. If it is assumed that individuals are phenotypically adapted to conditions prevailing in their immediate locality, particularly in environments that are relatively stable and predictable, then it may be advantageous to mate with an animal of as similar a phenotype as possible without incurring the risks of close inbreeding depression (see Greenwood et al. 1978). An individual which disperses too far will not only encounter a new environmental regime but may also incur the risk of breeding with an animal unlike itself.

One question to consider is whether dispersing a greater distance produces a concomitant increase in the distance between the natal sites of birds which eventually breed together. We have argued elsewhere that the appropriate measure of natal dispersal is the number of territories traversed from birth to first breeding site and not the distance expressed merely in physical units (Greenwood et al. 1979a). Similarly, it is more realistic to transform the distance in metres between the natal sites of birds that pair into the number of territories between those localities. Average territory sizes have been calculated for each year from the population size and area of Wytham Wood (Greenwood et al. 1979a). These territory sizes can then be used to calculate the natal dispersal of residents in their year of first breeding. Nest site locations can be accurately determined from a detailed map of the study area. The sample is restricted to those born in the wood which subsequently pair with residents; the birth sites of immigrants are unknown.

The number of territories that individuals move from their birth site to first breeding site (natal dispersal) is positively correlated with the number of territories separating the birth sites of birds which subsequently pair (males, $r=0.367$, $P<0.01$; females, $r=0.592$, $P<0.001$; $N=58$). The correlation coefficients do not differ significantly from each other ($d=1.55$, n.s.). In other words, when a Great Tit disperses a large number of territories from its birth site, it increases the likelihood that its mate will have been born a long way away from it in the wood. Dispersing further does not however increase the chances that a resident of either sex will pair with an immigrant (Greenwood et al. 1979a). The number of territories between the birth sites of first year resident Great Tits when breeding for the first time are shown in Fig. 4. The median separation is 6.6 territories.

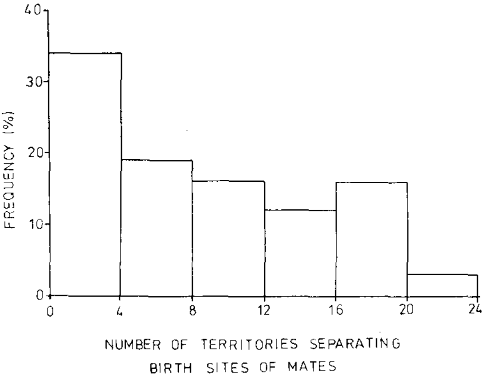

FIG. 4. The frequency distribution of the number of territories separating the birth sites of resident first year males and females which subsequently paired.

Discussion

The breeding population of Great Tits in Wytham Wood is a composite of individuals which differ in age and status. Approximately 50 % of breeding males and 60 % of females are born outside the wood. (These percentages have been increasing in recent years possibly as a result of heavy sparrowhawk predation on resident birds (Geer in prep.)). The higher annual mortality of breeding females, compared with that of males, also means that in any one year there are more older males than older females and hence more first year females than first year males amongst the breeders. Given the proportions of these categories in the population, it has been the purpose of this paper to eamine whether the mate choice of individuals deviates in any way from that expected from a random assortment. By mate choice we do not necessarily imply a behavioural basis of selection. Nevertheless, any deviations from the expected values would suggest that there may be ecological and behavioural correlates which influence the pairing procedures of birds within their respective categories.

One of the most striking effects is the tendency of Great Tits to pair within their own status group, resident with resident, immigrant with immigrant. This may not be a surprising finding for those birds pairing for the first time, particularly if, as is suspected, pair formation is initiated predominantly in winter flocks. Any local association of resident birds born in the same year would tend to bias encounters towards those of a simlar status. Conversely, groups of first year immigrants may already be in the process of pair formation prior to their arrival in the wood (see Kluijver 1951, Hinde 1952). Familiarity may be a prime determinant of eventual pair bonding. However, a comparable effect is also evident in Great Tits that have reproduced and are re-pairing following the death or divorce of a previous mate. This suggests a degree of positive assortment of individuals of similar status. Why birds might choose on such a character is currently a matter of conjecture. We would like to suggest that a detailed examination of breeding success might reveal those individuals preferentially mating within at least one of the groups have a higher reproductive performance than those between groups (see below); resident-resident or possibly immigrant-immigrant combinations or both being more successful than resident-immigrant pairs. It is worth pointing out though that positive assortment need only be expressed in one group to explain the observed distributions of pairs. For example, a preference for residents by residents would result inevitably in a higher than expected frequency of immigrant-immigrant pairs. If residents have different song types or repertoires from immigrants or established territories earlier than them, these could be used as a basis of selection or rejection.

There was little evidence that older birds on re-pairing mated with individuals that were on average older and more experienced than Great Tits breeding for the first time. This was perhaps an unexpected finding. Age affects a number of important factors that influence reproductive performance. The breeding success of females increases with age reaching a peak at 3 and 4 years old (Perrins and Moss 1974). It then declines, although by 5 years old and beyond there are relatively few females in the population. Males defend larger territories each year until about the age of four (Dhondt 1971). This would be expected to increase the reproductive potential of females mated to such birds. Even though older males can mitigate the inexperience of first year females and, to a lesser extent, experienced females offset the effect of first year males (Harvey et al. 1979), it is surprising to find such little evidence of discrimination on the part of older individuals, particularly males, in favour of birds of similar experience. A more detailed study of breeding success of pairs of known age and experience in relation to mate change may prove fruitful, particularly if it indicates no advantages accrue to those individuals that re-pair with older rather than young birds. The only indication that discrimination with respect to age does occur in Great Tits is found in females where prior experience to mates of certain types can influence their subsequent pairing tendencies. Thus, the reason that the average age of mates increases with the age of both sexes is due almost entirely to the retention of the same partner from one year to the next. Whether re-pairing with the same individual increases reproductive success in the Great Tit is unknown. In longer lived species, breeding success can increase for birds which retain their mates and there may also be discrimination in terms of age on changing mates (e.g. *Rissa tridactyla*, Coulson 1966).

In Great Tits, older females paired with a first year are more likely to re-pair with an older bird the following year than first year females or older females paired with older males. In addition, resident females paired with one year old birds are more likely to change to an older male the next year than other paired combinations. We have not analysed the breeding success of such individuals prior to and following a change. Nevertheless, the depressing effect on reproductive performance that first year males can have on older females (Harvey et al. 1979) may induce discrimination against inexperienced mates by such females for future breeding attempts. Again the causal basis, in terms of reproduction and any behaviourally mediated mechanisms for such a choice have yet to be elucidated. Likewise, the reasons for resident females to change mates from one year old to older birds more so than other categories remain to be determined. It may indicate an inferiority on the part of immigrant females to secure experienced males as readily as residents. If immigrants are those individuals which have had to disperse a long way in order to find a territory or mate then dispersal itself may have profound influences on mate selection.

We have shown elsewhere (Greenwood et al. 1979a) that natal dispersal from birth to first breeding site does not affect the age or status of a resident female's eventual partner. In males, those dispersing particularly long or short distances *within* the wood are more likely to pair with an older female. Although there are no recognisable costs to effective natal dispersal of residents in terms of mortality or reproductive success, one suggestion from the analysis in this paper is that immigrant males are more likely than resident males to pair with first year females. This may be indicative of a cost to more extensive dispersal or a reflection on the calibre of immigrant males in that it is those which are more sedentary as juveniles (i.e. residents) that acquire the experienced females. Whether familiarity with an area enables residents to obtain territories sooner, larger or of higher quality is unknown.

An additional way of examining dispersal is to look at the distances between the birth sites of individuals that subsequently pair. The distances that Great Tits disperse from their natal site make it inevitable that a large proportion of offspring breed close to their natal site and pair with birds from the same locality. The median number of territories separating the birth sites of residents that subsequently pair is 6.6. Those that remain too close to their birth site are more likely to inbreed with a sibling or parent (Greenwood et al. 1978). Even so, it is worth considering the possibility that mate selection that minimises close inbreeding but maximises the frequency of similar phenotypes breeding together in familiar surroundings has itself been a major ultimate factor determining the observed patterns of natal dispersal. Those Great Tits born in Wytham Wood which disperse a large number of territories are more likely to breed with an individual born a long way from them in the study area. If there are costs to breeding with phenotypically unfamiliar individuals then low levels of dispersal and the ability to discriminate between similar and dissimilar birds may be proximate means of 'optimally outbreeding' (see Bateson 1978). In this context it is again worth noting that residents pair with residents and immigrants with immigrants more than would be expected by chance. The costs, if any, of breeding with an 'unfamiliar' Great Tit have not yet been measured.

The results of this analysis also require a modification to be made to a previous assumption used to calculate the expected number of close inbreedings in the Great Tit. A model by Bulmer (1973), also used subsequently by Greenwood et al. (1978), assumed that individuals mated at random with respect to the proportions of the different groups in the population. As a result, the observed and expected numbers of inbreedings in Wytham Wood were similar given the observed patterns of natal dispersal. The finding that residents exhibit a propensity to mate with residents means that the expected numbers of inbred matings will have been underestimated and consequently will be greater than the observed frequencies. This may indicate that Great Tits can distinguish relatives from non-relatives and as a result refrain from breeding with close kin. Inbreeding depression occurs in the Great Tit (Greenwood et al. 1978). As yet though, it remains to be shown that there is a behavioural basis of inbreeding avoidance in wild birds based on the recognition of relatives.

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Selostus: **Talitiaisen parinmuodostuksen riippuvuus puolisoiden iästä ja synnyinpaikasta**

1. David Lackin v. 1947 aloittama ja C. M. Perrinsin johtaman työryhmän myöhemmin jatkama talitiaisen populaatiotutkimus Oxfordin lähistöllä on tuottanut lukuisia julkaisuja, joissa on voitu hyvin yksityiskohtaisesti tarkastella lajin populaatioekologian eri kysymyksiä. Käsillä oleva kirjoitus käsittelee parinmuodostusta ja sen riippuvuutta puolisoiden iästä (yksivuotiaat/vanhemmat), synnyinpaikasta (residentit l. alueella syntyneet/immigrantit l. muualta tulleet) ja aikaisemmasta kokemuksesta (edellisen puolison ikä ja synnyinpaikka).

2. Kuva 1 esittää talitiaisten ikäjakaumaa Oxfordin populaatiossa. Suunnilleen puolet linnuista on kunakin vuonna yksivuotiaita, ja ikäluokkien koko pienenee vuosittain noin puoleen; vanhimmat koiraat ovat olleet 8- ja naaraat 7-vuotiaita. Yksivuotiaiden koiraiden vähyys naaraisiin verrattuna johtunee siitä, että osa niistä jää parittomiksi. Keskimäärin 67.5 % yksivuotiaista ja 34.6 % vanhemmista koiraista oli pariutunut yksivuotiaan puolison kanssa; naaraiden osalta vastaavat luvut olivat 43 ja 16 %. Täten puolisoista koiraiden keski-ikä oli kussakin vuosiluokassa vähän korkeampi kuin naaraiden ja molemmilla sukupuolilla vanhojen lintujen puolisot olivat keskimäärin vanhempia kuin yksivuotiaiden (kuvat 2—3). Osaksi tämä johtuu siitä, että n. 70 % linnuista uusii parisiteensä silloin, kun molemmat puolisot säilyvät hengissä talven yli.

3. Ensipesijöistä ja uuden puolison kanssa pariutuneista vanhemmista linnuista alueella syntyneet osoittivat selvää taipumusta pariutua muitten residenttien yksilöitten kanssa ja immigrantit taas keskenään, kun taas kummallakaan sukupuolella ei ilmennyt pyrkimystä pariutumiseen samaa ikäluokkaa olevien yksilöiden kanssa (taul. 1). Immigrantit koiraat pariutuivat odotettua hiukan useammin yksivuotiaiden naaraiden, residentit koiraat taas vanhempien naaraiden kanssa.

4. Edellinen puoliso, joka oli joko kuollut tai eronnut, vaikutti myöhempään uudelleen pariutumiseen vain naarailla. Sellaiset vanhemmat naaraat tai residentit naaraat, jotka olivat olleet pariutuneina yksivuotiaan koiraan kanssa, suosivat uudelleen pariutuessaan vanhempia koiraita (taul. 4—5).

5. Mitä pitemmän matkan eli mitä useamman reviirin läpi alueella syntynyt talitiainen siirtyi synnyinpaikaltaan ensimmäiseen pesimäpaikkaansa, sitä kauempana toisistaan tulevat puolisot olivat syntyneet. Kuvassa 4 on esitetty ensi kertaa pesineiden residenttien talitiaispuolisoiden synnyinpaikkojen etäisyydet toisistaan, ilmaistuna niitä erottavien reviirien määränä. Keskimääräinen välimatka oli 6.6 reviiriä.

6. Diskussiossa pohditaan saatujen tulosten syitä ja biologista merkitystä.

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