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THE NATAL AND BREEDING DISPERSAL OF BIRDS

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INTRODUCTION

"The question of the return of birds to their homes is one of perennial interest. How faithfully do adult birds—males and females return to their territories? How far from their birth place do young birds settle? Over how much ground does one family scatter?" (91).

Over 40 years ago, ornithologists studying the movement of birds in relation to their birth and breeding sites were preoccupied with estimating the extent of mixing of individuals within a species's range. There were major disagreements about how far young birds dispersed. Some authors felt that young birds did not tend to return to their birthplaces (101) but selected a nesting site anywhere within the species's natural range (27, 81). Others concluded that birds attempting to breed for the first time did, on the whole, return to their birthplaces though the extent of this fidelty was less than that of adults to their previous breeding sites (36, 69, 70, 91). It was generally agreed that adult birds did return to a previous breeding place.

Gradually the position of the supporters of the random dispersal theory was undermined as more data accumulated and methodological problems of measuring dispersal came to be better appreciated. A number of long-term studies were reported between the late 1930s and the early 1950s (4,

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5, 54, 68, 71, 91, 92) that enabled a more quantitative assessment of the dispersal patterns of young and adult birds across a wide range of species. This pioneering work could have provided the impetus for more detailed studies of bird dispersal, especially in relation to population structure [indeed, over 30 years ago it was suggested that when colonial seabirds exhibited fidelity not only to a site but also to a group, the latter fidelity probably originated in kinship (5)]. It is surprising that it did not, since simultaneously a number of important theoretical papers on population genetics appeared that highlighted the importance of dispersal for gene flow, population size, genetic structure, and evolutionary change (122–124). Even more surprising was the overall lack of regard for patterns of dispersal and its obvious bearing on the arguments concerning the efficacy of group selection during the earnest debates of the early 1960s (83, 117, 125).

Instead, as some long-term studies came to an end and others were still in a preliminary stage, studies of dispersal experienced a quiescent period and a shift in emphasis. Researchers became more interested in population density and control, so that the target of investigation was more the group (or population) and its dynamics than the individual. Long-term studies of birds concentrated on population dynamics, reproductive rates, and mortality rates (78). With a few exceptions (16, 65, 66, 110), little regard was paid to the immigration and emigration of individuals. This neglect of the population structure and genetics of birds is exemplified by the paucity of data on enzyme polymorphisms (88) and the amount of time it has taken for any assessment to be made of effective population sizes of birds, despite a plethora of dispersal data stretching back over 40 years (11). In studies of other vertebrates where more detailed studies have been made of dispersal (e.g. small mammals), investigators were tackling the question of what controls population density rather than examining population structure (73, 80).

Over the last decade there has been a major upsurge in theoretical and empirical research on dispersal. These developments are largely a result of the recent synthesis of studies in behavioral and evolutionary ecology, particularly in relation to species' social structures and the relative importance of kin and group selection (55–57, 118). One approach has been to examine patterns of limited dispersal across a wide range of animals in order to test theoretical models for the genetic differentiation of populations, inbreeding, and the evolution of cooperative behavior. A complementary approach has involved more intensive studies of the proximate factors that cause individuals to move from one site or group to another, together with the consequences of that movement. In this review we concentrate on these two approaches in recent research on birds. After defining terms, we present a brief comparative survey of species, age, and sex differences in dispersal followed by a consideration of the causes and consequences of dispersal and their bearing on life histories, population structure, and behavior.

TERMS AND METHODS IN DISPERSAL

The definition of dispersal most frequently used by vertebrate ecologists is "the permanent movement an individual makes from its birth site to the place where it reproduces or would have reproduced if it had survived and found a mate" (63). This definition refers explicitly to the movement of prereproductive individuals. Although dispersal is often strongly biased towards juveniles, adults may also move from one breeding site to another. The causes and consequences of dispersal differ between the two categories. It is therefore important to draw a clear distinction between them. We have suggested (45, 51) that dispersal from the site or group of birth to that of first reproduction or potential reproduction should be termed *natal dispersal.* Subsequent movement between sites or groups would then be termed *breeding dispersal.* When a successful breeding attempt follows either type of dispersal, then the dispersal is *effective* (45, 103). Effective dispersal is similar to *migration* as used by geneticists but not by ornithologists.

In some cases it is important to distinguish movement between sites from that between groups. In studies of relatively asocial species it is often difficult to determine the spatial arrangements and movements of individuals. This is much less problematic when dealing with social species, such as communal birds, where reproductive groups are distinct. Here the term *transfer* has been used to describe the movement of individuals from one group to another. Transfer is one type of dispersal since it involves species movement between groups rather than sites.

We now come to a serious methodological weakness in many studies of dispersal. When considering the evolutionary consequences of dispersal, measures of dispersal should take into account both the dispersion and density of individuals. It has been standard practice, particularly among studies of vertebrates, to express dispersal between sites in terms of either (*a*) distance (15, 16, 47, 49) or (*b*) the extent to which individuals leave one area for another (74, 86). There may be some advantages to these methods in studies of population control but there are also a number of drawbacks. The problems concern the comparison and interpretation of patterns of dispersal within species and those between species. They can be illustrated by our work on the great tit, *Parus major.*

In Wytham Wood near Oxford, UK, great tits establish breeding territories that are normally 100–150 m in diameter. There are substantial fluctuations in population density between years: between 1964 and 1975 the median distance of natal dispersal ranged from 354 to 1017 m in males and from 543 to 1269 m in females (51). Although it is often assumed that population density is a major cause of dispersal, there is no relationship across years between density and distance dispersed for the males, while there is a *negative* relationship for the females. Such measurements have little biological meaning. It is territory size that should influence natal dispersal; the former will vary with number of breeding pairs in the study area. When distances are converted into territories traversed, males move a greater number of territories as density increases, while young females move a fairly constant number of territories each year, irrespective of population density. In addition, when comparisons are made between species it must also be borne in mind that territory or home range size increases with body size as well as varying between taxonomic and dietetic groups, and that in some species there may be sex differences in dispersion (28, 82). Studies of dispersal should take these factors into account. Dispersal should be measured in ways that are consistent and biologically realistic so that comparative studies are facilitated.

A second major problem in dealing with dispersal is that of measuring its extent. Part of the reason for the earlier disagreement (see above) stemmed from a poor appreciation of the factors that must be taken into account before estimates can be made. Most studies of bird dispersal have relied on the banding and recovery of young and adult birds within a finite study area. Some authors concluded that a low recovery of fledglings as breeding birds indicated a high level of dispersal, but they ignored the compounding factor of high mortality rates in young birds (39). Another problem arose from the limited size of the recovery site (23, 71, 115, 116). The usual procedure of estimating the pattern of dispersal from recoveries within a study area underestimates effective dispersal. The bias will be more marked the smaller the area, and will tend to shift the median value of dispersal closer to the natal area. Recently a method for correcting this bias and providing a more accurate description of dispersal has been developed (10).

Another problem concerns the skewed distribution of dispersal distances (skewed towards the point of origin). Frequently, mean values of dispersal have been given. With such skewed distributions a more useful measure is often the median value of dispersal (51, 54, 91, 92, 103).

Finally, a problem that arises particularly in discussions of the causes and consequences of dispersal is the interaction between mate and site. In many species, breeding dispersal is accompanied by a change in both site and mate. It is often difficult to decide which of the two variables, mate or site, has been responsible for the dispersal and which has the more important reproductive consequence after the change. Where possible, we highlight studies that provide some estimate of the relative importance of mate or site on natal and breeding dispersal.

In Table 1 we note 5 topics where sufficient data are available for quantitative conclusions to be drawn and where additional species examples would be largely superfluous. In addition, we list important areas where the empirical data base is currently inadequate.

PATTERNS OF DISPERSAL

Species Differences

Species vary widely in patterns of dispersal. Some show high levels of dispersal within all age and sex classes. These tend to be species whose food requirements or nesting habits fluctuate markedly or unpredictably from year to year, both within and between locations. Their life histories are characterized by a nomadic existence and periodic irruptions to areas outside their normal species range. Examples include many seed eaters of northern latitudes (e.g. crossbill, *Loxia curvirostra;* grosbeak, *Hesperiphona vespertina;* Siberian nutcracker, *Nucifraga caryocatactes;* and Clark's nutcracker, *Nucifraga columbiana*), which stay within their normal range when food is abundant but may emigrate as a consequence of seed-crop failure, particularly after a productive breeding season when the population density is high. This pattern is typical of species that feed on tree seeds, which tend to fluctuate in numbers more than do those of other temperate plants (89). Some birds may not return to their natal or previous breeding area but instead remain to breed in an area of high food abundance following irruption, though in occasional cases there are records of eventual return to the site of origin (108, 111). Similarly, a number of birds of prey that feed on cyclic populations of rodents (e.g. Snowy owl, *Nyctea scandiaca;* rough-legged hawk, *Buteo lagopus*) leave areas where small-mammal

Table 1 Current status of research on dispersal in birds[a]

Available data	Inadequate data
1. Occurrence of age and sex differences in dispersal	1. Life history consequences (e.g. mortality, reproduction) of natal and breeding dispersal
2. Median values of dispersal for particular age and sex categories	2. Proximate basis of site tenacity and philopatry
3. Poor reproductive performance as a cause of between-year breeding dispersal	3. Genetic structure of populations
4. Variation in population density and natal dispersal	4. Dispersal, mating preferences, and inbreeding avoidance
5. Philopatry and social organization in communal birds	5. Behavioral interactions (e.g. song dialects, kin recognition)

[a] For a complementary list of research topics on dispersal see (25).

densities are low and move to sites where the cycle is out of phase with their locality of origin and prey are more abundant (77). A mean natal dispersal distance of approximately 2000 km has been recorded for the rough-legged hawk (42).

Species that inhabit arid areas with unpredictable rainfall [e.g. honey eaters, Meliphagidae (67); and the pink-eared duck, *Malacorrhyncus membranaceus* (41) in Australia] may also have periods of nomadism, settling to breed where suitable habitats are locally abundant. It is not known for any case whether the population integrity of nomadic species is maintained during the irruptions or whether there is mixing and interbreeding of individuals from a wide geographical area.

Most species of birds undergo relatively low levels of natal and breeding dispersal. They are not subject to the periodic fluctuations in food supply and environmental conditions experienced by the nomadic species. Examples range from the colonially breeding seabirds such as the albatrosses [Diomedeidae (40)], gulls, and terns [Laridae (4, 26, 85, 112, 121)] to numerous passerines such as the great tit (23, 34, 51, 59), pied flycatcher [*Ficedula hypoleuca* (16, 54)], and song sparrow [*Melospiza melodia* (91, 92)]. Such species are usually described as philopatric.

Age Differences

Among the nomadic species it is usually assumed that large-scale dispersal to new areas is characteristic of both adults and juveniles. In most cases it is presumably advantageous for all individuals to emigrate following a complete failure in the food supply. It remains to be shown that, when only a small proportion of the population emigrates in response to a partial failure, individuals of particular ages are differentially represented among the emigrants.

Age differences in dispersal have been widely reported among philopatric species. Natal dispersal is always more extensive and covers a wider geographical area than does breeding dispersal. No examples have yet been recorded where adults leave an area to a greater extent than do juveniles, despite theoretical predictions that this could be the case in some species (58). For example, juvenile great tits move, on average, between 4 and 7 territories during natal dispersal, whereas adults usually return to within one territory's width of their previous breeding site (51, 59). Among colonial seabirds it is not uncommon for a young bird to join a colony other than that into which it was born. However, once established as a breeding bird, movement between colonies is a rare event [e.g. kittiwake, *Rissa tridactyla* (121)]. These age differences in dispersal are typical of many other species (17, 32, 79, 87, 106). In addition, although a systematic comparison has yet to be made, there do not appear to be any differences in the degree of philopatry shown by species that undergo seasonal migrations from wintering to breeding grounds compared to those that are permanently resident in an area. Among breeding birds there may also be a tendency for philopatry to increase with age (91, 109). This may be a consequence of increasing faithfulness to a site, mate, or both.

Sex Differences

Sex differences in dispersal have not been recorded in nomadic species. However, they do occur in a wide range of philopatric species (9, 45). In most species, both natal and breeding dispersal are more extensive among females. For example, nearly all male pied flycatchers return each year to their previous nesting locality, while over half of the females nest in a different place each year (54). The greatest reported disparity between the sexes in natal dispersal with a female bias occurs in species of communal breeders [e.g. babblers, *Turdoides* spp. (43, 127); Florida scrub jay, *Aphelocoma coerulescens* (120)]. Males either remain in their natal territory to breed or they sequester an area adjacent to it, whereas females leave their natal territory to breed.

In one family of birds the sex bias in dispersal is in the opposite direction. Among the Anatidae the females are extremely faithful to a previous nesting area or colony, while both natal and breeding dispersal of males are widespread (1, 2, 29, 107). The most detailed study is of the lesser snow goose, *Anser caerulescens,* where, following pair formation on the wintering grounds, the male returns to the female's natal colony to breed (29). A discussion of the factors that may predispose most species of birds to female-biased dispersal and the Anatidae to male-biased dispersal can be found elsewhere (45).

Classification

We have briefly described the major patterns of dispersal in birds. To what extent can species be assigned to particular categories and how many different categories are there? Recently, two attempts have been made to differentiate patterns of dispersal. One divides species into philopatric and dispersive types. An earlier definition of philopatry (84) is broadened so that species are referred to as philopatric if the median value of dispersal of the most dispersive group (usually young females in birds) is less than ten territories (or equivalent spatial dispersion) from the natal area (103, 104). Clearly, this is an arbitrary division but it does provide a useful distinction, particularly when comparing life history differences of the two types. The second and not mutually exclusive classification is that of Baker, who suggests three major categories of avian "removal migration" (equivalent to natal and breeding dispersal): (*a*) that typical of most passerines (e.g.

great tit), with limited breeding dispersal and more extensive natal dispersal; (*b*) that shown by nomadic species with wide ranging dispersal by young and adult birds; and (*c*) that exhibited by colonially nesting birds, with some movement between colonies by young birds before first breeding but with a minimum of breeding dispersal (9). Most species can be included in one of the three categories. However, two groups of birds would probably merit their own categories: first, the communal birds, where extreme philopatry is a feature not only of adults of both sexes but also of the young males; second, the Anatidae, where widespread dispersal of males may be typical of juveniles and adults, with the movement of breeding males being more extensive than that of young females. A summary classification is shown in Table 2. Species exist with patterns of dispersal that lie between two categories.

CAUSES AND CONSEQUENCES OF DISPERSAL

Breeding Dispersal

WITHIN YEAR Few studies exist of the patterns of breeding dispersal within one nesting season (53, 59, 97, 100). Two studies have shown that movement within a year between successive nesting sites is more constrained than that between years, presumably because suitable sites are already occupied. In the house sparrow, *Passer domesticus,* most males and about half the females keep the same site for successive attempts within a breeding season. Few birds return to the same site the following year, though most remain in the locality (100). In the great tit, changes of nest site occur after an unsuccessful breeding attempt. Breeding dispersal within years is less extensive than that between years and appears to be constrained by territorial boundaries. After a failed brood, pairs change sites but renest within the current territory (59).

A breeding failure is unlikely to be the only factor influencing the movement of adults that attempt to raise more than one brood per year. The only detailed study of factors other than nest failure that may be causes or consequences of breeding dispersal has been on the stonechat, *Saxicola torquata* (53). Movement between sites in this species may involve a complex interaction among a number of different variables (e.g. breeding success, predation, vegetation type), though these variables account for only a small amount of the variation in dispersal distances. If the previous nest had been preyed upon or if the parents successfully reared a larger than average number of young, pairs tended to move long distances to a new nest site within their territory and to a different type of vegetation. The first type of movement was not, however, shown to minimize the risk of subsequent nest

Table 2 Categories of dispersal

Categories	Examples	Sources
Dispersive		
Nomadic—extensive natal and breeding dispersal.	Crossbill *Loxia curvirostra*, Rough-legged buzzard *Buteo lagopus*, Clark's nutcracker *Nucifraga columbiana*	42, 89, 111
Extensive natal and breeding dispersal of males, limited dispersal of females, particularly adults.	Anatidae	1, 2, 29, 107
Philopatric		
Marked breeding site fidelity of adults, particularly males. Median natal dispersal of both sexes usually less than ten territories from birth site.	Most passerines	16, 23, 34, 51, 54, 59, 91, 92
Faithfulness to site and sub-group of adults within colony, particularly males. Intercolony movement of young birds, particularly females.	Laridae, Procellariidae	4, 17, 26, 85, 112, 121
Marked philopatry to group and site of adults and young males. Natal dispersal between groups and sites of young females.	Communal birds	43, 120, 127

predation. On the other hand, long distance movement as a consequence of rearing a large brood did appear beneficial; the growth rates of nestlings in the subsequent brood were high. Greig-Smith suggested that birds moved to avoid areas that were depleted of food while rearing the previous brood. Many of his conclusions are speculative, but this example is an important step towards attempting to disentangle the many factors that may affect short-term breeding dispersal. It also indicates that the causes and consequences of movements within a nesting season, such as the effects of food depletion, may differ greatly from those for dispersal between breeding seasons.

BETWEEN YEAR Once a breeding site has been established, in many species of birds individuals return repeatedly to the same locality or remain there permanently. While this review concerns primarily birds that change site, we briefly mention the advantages of site-tenacity since they may by implication provide insight into the reasons for breeding dispersal.

Reasons for site-attachment were summarized some 25 years ago under two headings (61). First, familiarity with food sources and refuges from predators would enable the adults and/or young to exploit an area more efficiently. Familiarity with food resources mediated through site fidelity and territoriality could involve a number of different hierarchical decision processes—e.g. maximizing food intake, minimizing the risk from predators, optimizing return times in relation to renewal rates, or minimizing the risk of territorial intrusion. Second, familiarity increases fighting potential if prior ownership gives an advantage in aggressive encounters. When these reasons were put forward, only circumstantial evidence suggested that familiarity was an advantageous consequence of site-attachment. Since then there have been both theoretical and empirical advances in studies of fighting in relation to residency and in relation to the short-term foraging advantages of familiarity and exclusive use of an area (75). However, we still do not know the relative importance of the various factors that influence whether or not birds retain a breeding site from one year to the next. Instead, the emphasis of current research has been on the effect of more readily quantifiable characters (e.g. overall territory quality or reproductive success) on breeding dispersal.

One frequent finding from a wide range of bird species is that individuals move to a new breeding locality following a poor or unsuccessful breeding attempt the previous year (24, 59, 98, 109). The immediate lack of success is usually caused by desertion, predation of the eggs or nestlings, or by the poor quality of the food supply in the territory. In the great tit, most birds that rear a brood to fledging nest within one territory's width of their former nesting site the following year, whereas there is a marked tendency to change breeding sites if the eggs or young have been taken by a predator (59). Even if a successful brood is eventually produced in one year after an abortive first attempt, the female tends to breed elsewhere the following year. In the sparrowhawk, *Accipiter nisus* (90), and the wheatear, *Oenanthe oenanthe* (19), differences in territory quality mediated through variation in reproductive success rather than predation appear to impel birds to change site.

A poor breeding attempt may also result in a sex difference in breeding dispersal. In a number of species, females change sites more often than males after a reproductive failure (24, 98). This pattern may be associated with two factors: first, the role of the male in territorial defense and the possibility that he could not establish a territory in an area other than the one with which he is familiar; and second, the greater potential for females to find a new site with an unpaired male (45, 47).

In discussing the factors implicated in the breeding movements of birds, we must distinguish between dispersal as a feature of particular sorts of individuals and dispersal that is primarily a consequence of the nesting locality. In many cases, variation in the quality of sites may act together with variation in the age or quality of individuals or their mates. Where this occurs, it may be difficult to disentangle the relative importance of the different variables.

Birds of some species breeding for the first time may occupy territories of poorer quality than those of older individuals. The settlement of new breeders is often determined by the behavior of previous breeders, which, particularly in migratory species, have reached the nesting grounds sooner and occupied the prime sites. The least successful and younger individuals may be relegated to a suboptimal area where, if male, they may remain unpaired or be prevented from establishing a territory altogether. In the Temminck's stint, *Calidris temminckii,* males will attempt and often succeed in changing to a better site as they become older (60). In the wheatear (19) it is advantageous to commence breeding as early as possible to maximize reproductive success. Territories on which egg laying occurs early during the season are occupied preferentially by older males, which arrive earlier than younger ones. These areas may provide better foraging conditions for the females, which occupy territories in the same order as the males. As males become older, they tend to shift onto the preferred territories. It is unclear whether females choose or change sites as a result of differences in the age or quality of the males, the size or quality of the territories, or the owner's time or period of occupancy. Similar considerations of the influence of mate or site on breeding dispersal are a feature of other studies (33, 102, 126).

Recent work has also indicated that a predisposition to disperse because of low reproductive success may be conditional upon the overall or long-term quality of the site or the age of the breeding individual. Magpies, *Pica pica,* hold territories of two sorts: those that are permanently occupied and defended throughout the year, and those that may be left vacant for several months outside the breeding season. Birds that hold the former have, on average, a higher reproductive success and are less likely to move after a breeding failure (6). In circumstances where some sites are of better quality than others, it may not pay individuals of long-lived species to shift to a new area as a result of one poor performance. Comparisons of lifetime reproductive success in relation to breeding dispersal are needed to clarify this issue. This species illustrates again how breeding dispersal may be linked to both mate and site. When magpies move to a new site they also usually divorce and pair with an unmated bird on a nearby territory. One possible explanation is that in a species that defends an exclusive territory, an individual that pairs with an unmated territory holder can take advantage of the latter's knowledge of territorial boundaries and foraging sites, thus minimizing the time and energy required for familiarization (6).

The influence of age on breeding dispersal has been examined in the sparrowhawk (90); the tendency to change localities declines with age. Yearlings always move from a poor territory whether successful or not, and from a higher quality territory after a failure. It is unclear why older birds with more experience show less dispersal than younger individuals. One suggestion is that breeding dispersal is caused only by differences in food abundance and that initially younger individuals may be seeking better feeding territories (90). Older birds may be reluctant to leave a good territory with abundant prey despite a breeding failure, or they may have reached the stage where they occupy a site commensurate with their age and experience and where the costs of removal may be outweighed by any subsequent improvement in reproductive output. Here again the interactions among and importance of territory establishment, food supply, nesting success, and mate fidelity in relation to breeding dispersal are uncertain.

We end this section by considering two recent studies. In one, the nesting locality appears to be primarily instrumental in causing any breeding dispersal (35), while in the other the age of the mate and status of the pair bond are of prime consideration (109). In the goldeneye, *Clangula clangula,* as with many other Anatidae, the male does not select or defend a nest site and he deserts the female shortly after egg laying. Females that return to the same nest box start laying earlier in the season and as a result have a higher hatching success and larger broods than females that change sites between breeding seasons. Because the role of the male is minimal, locality rather than mate is presumably the key factor for breeding dispersal. Females that change nesting localities, particularly those that move longer distances, have a lower reproductive success mainly because egg laying starts later; clutch size declines during the season. The time taken to locate and occupy a new site may be the critical factor delaying the onset of reproduction. Even so, such breeding dispersal may be advantageous in the long term since it frequently occurs after a breeding failure or when the previous clutch has been preyed upon. Competition between females for nest sites and the avoidance of intraspecific brood parasitism may also influence breeding dispersal, particularly among females that change localities after a successful breeding attempt the previous year (35).

In the colonially breeding kittiwake, most birds that retain the same mate reoccupy their previous site (30). When birds change mates, approximately one third of the males and two thirds of the females also change sites. Among females, breeding dispersal commonly results from divorce rather than the death of a mate. As with the sparrowhawk, the tendency to change site declines with age. Pairs within the center of the colony have, on average, a higher reproductive success than those on the edge (31). However, once the overall breeding position is established, the causes and consequences of breeding dispersal are invariably a product more of the pair bond and change in mate than of the nesting locality within the colony (109). So, for example, birds that fail to raise any young are more likely to divorce than are successful pairs, though divorce as a result of breeding failure is less likely among older birds. Females that retain the same mate subsequently produce larger clutches and larger eggs and have a higher hatching success than birds that change mates (109). Such differences in reproductive output will tend to operate irrespective of changes in site. This is not surprising in long-lived colonial birds where individuals remain in one colony throughout their reproductive lives and where familiarity with the habitat is only likely to be an important consideration during the first nesting attempts.

Finally, it has been frequently claimed that individuals that retain the same mate do so because enhanced reproductive success is a product of increasing familiarity and coordination within an established pair bond (18, 64, 87, 94). In addition, this claim is often used to explain why birds should retain the same site—i.e. because it increases the probability that the pair bond will reform at the start of the new breeding season. While the hypothesis is entirely plausible and laboratory experiments (37, 38) suggest that such familiarity could enhance reproductive success, there is little unequivocal evidence from natural populations to support what has become a pervasive generalization. A lower reproductive success of newly formed pairs may be explained entirely as a product either of the age and experience of the male and female or of a new nesting locality rather than of any lack of familiarity within the pair. Similarly, any increase in reproductive success of a pair may be a product of each individual's age or experience or the retention of a site and not necessarily the length of the pair bond. We know of only one published study that has controlled for these confounding variables. When pairs of a similar age and experience are compared in the kittiwake, those retaining the same mate do have a slightly higher reproductive success than those that have changed (109). Even so, the behavioral mechanisms that underly this advantage are unknown.

Natal Dispersal

In most species of birds natal dispersal is far more extensive than breeding dispersal. One major reason for this pattern stems from the site-tenacity of established breeding birds. Any limits to population size will inevitably mean that some individuals will be prevented from breeding in their natal area and therefore be forced to disperse in search of a vacant site (113). While young birds may endeavor to secure a territory close to their birth site they will often be disadvantaged in terms of age, experience, and habitat familiarity when competing with established breeders in a population. Evidence that territorial behavior or some equivalent interaction causes juveniles to disperse has come in three forms. First, direct observation that the movement of birds may be a direct consequence of older individuals' reestablishing territories in former breeding areas (110). Young birds are frequently excluded from optimal breeding habitats or localities close to their birth site but may take advantage of any opportunities to secure such a site when a vacancy occurs (105). An alternative pattern has evolved in some species (e.g. communal birds) where populations may be so stable, sedentary, and close to carrying capacity that remaining at home, particularly for males, in the hope eventually of a chance to breed may be the only option available when vacancies elsewhere are infrequent or difficult to obtain (20, 36, 44). Second, in long-term studies it is often possible to monitor the effects of changes in population density and age structure on the recruitment and dispersal of young individuals. In the great tit, young males disperse a greater number of territories in years with a high population density (51). This may be caused by two factors: first, the large number of young males looking for territories; and second, a high return of adults to the breeding population. In some of the Tetraonidae there may be a complex interaction between population cycles and dispersal comparable to that of small mammals (114). A third means of detecting the influence of population density on dispersal is to examine movements in relation to the time of fledging. In the great tit, birds leaving the nest later during the breeding season disperse further than the earlier fledglings. They are also usually lighter in weight (34). They have to compete for space not only with adults but also with the early young, which will have time and weight in their favor.

Other than the data on patterns of effective natal dispersal, little is known about the consequences of dispersing from the natal area. There is some evidence in the blackbird, *Turdus merula,* that males dispersing substantial distances are more likely to die in their first or second year than those settling close to their birth site (48). In the great tit, where dispersal was monitored over much shorter distances, there was no such mortality effect nor any reproductive disadvantage once breeding had commenced (51). The consequences of natal dispersal in terms of risk and reproduction must be examined in more detail.

INBREEDING AND AVOIDANCE Inbreeding and its avoidance have come to the fore in recent discussions of dispersal (12, 13, 14, 46, 50). Any dispersal from the natal area or group in philopatric species will inevitably reduce the probability of mating with a close relative. Once individuals have established a breeding area, they usually remain there for the whole of their reproductive life. Thus inbreeding avoidance is mainly achieved by the movement of young birds away from their natal area. Such movements should not, however, be interpreted as evidence that inbreeding avoidance is a function of dispersal nor that inbreeding is harmful. It should also be noted that the probability of inbreeding will be heavily skewed towards the point of origin.

It is generally assumed that inbreeding is harmful, though remarkably few data are available on (*a*) the effects of inbreeding in natural populations, (*b*) the frequency of inbreeding in natural populations, (*c*) the relationship between the frequency of inbreeding and dispersal, and (*d*) the mating preferences of individuals in relation to population structure. Close inbreeding has been recorded only rarely in birds. Data are available for the song sparrow [*Melospiza melodia* (91, 92)], the yellow-eyed penguin [*Megadyptes antipodes* (98)], the splendid wren [*Malurus splendens* (99)], the acorn woodpecker [*Melanerpes formicivorus* (72)], and the great tit [*Parus major* (23, 50, 93)]. The small number of examples probably reflects more the lack and difficulties of field studies on individuals of known genealogies than the true incidence of such matings in natural populations. The great tit is the only species for which any estimate of the effects of inbreeding has been calculated. In the population breeding in Wytham Wood, UK, the only significant difference in breeding performance between inbred and outbred pairs was in nestling mortality, which was, on average, 28% among inbreeders compared with 16% among outbreeders (50). This finding of inbreeding depression has been substantially confirmed in an analysis of a larger sample of inbred pairs from the Dutch population study (93). As well as the increase in mortality at the nestling stage there was also a 7.5% decrease in the viability of the eggs for every 10% increase in the coefficient of inbreeding. One of the study areas was an isolated island population, which probably accounts for the high level of inbreeding. The claim (93) that inbreeding is not ultimately disadvantageous due to a higher recruitment of inbred than outbred birds into the population cannot be substantiated by the limited data presented.

When mating with a close relative results in inbreeding depression, selection will operate to reduce the frequency of inbred matings. By dispersing from the natal area, individuals are less likely to mate with a relative but may incur the penalty of encountering an unfamiliar habitat or of breeding with an animal with a dissimilar genotype. The expression of genes maladapted to novel surroundings and the possible break-up of gene complexes through mating with dissimilar types might severely limit an individual's reproductive success. There is little or no evidence on three major questions concerned with this problem: first, whether some types of dispersal have evolved as a means of avoiding inbreeding; second, whether behavioral mechanisms exist that enable individuals to distinguish between relatives and nonrelatives or familiar and unfamiliar individuals; and third, whether mating preferences reflect those predicted by models of 'optimal outbreeding.'

Studies of communal birds indicate that the incidence of movement between groups and the process of pair formation within groups probably operate to minimize the chance of close inbreeding (21, 72). Such findings suggest that there are underlying means of recognition where inbreeding avoidance is not simply a demographic consequence of dispersal. More rigorous data are available from experimental laboratory studies of quail. These indicate that close kin are avoided as potential mates through a process of learning (imprinting) at an early stage of development (12, 13). Birds also avoid individuals too dissimilar but preferentially select those with an intermediate degree of novelty. The functional interpretation hypothesized is that they thereby avoid the effects of both inbreeding and outbreeding depression. Tests of the optimal outbreeding models (12, 103) have yet to be done on natural populations of animals.

PHILOPATRY AND KINSHIP Several aspects of social behavior can be understood in terms of the interests that individuals have vested in the successful reproduction of relatives (55). In philopatric species, some individuals inevitably breed near close relatives, but breeding close to the birth site does not prove that the proximity of relatives is anything but incidental. In birds, males are usually more sedentary than females. In the great tit, 25% of males nest within one territory's width of their birth place and a proportion of those nest next to their father (52). There is at present little evidence that birds benefit from nesting next to kin or that the acquisition of a territory in relatively asocial birds can be mediated by the presence of a nearby relative. However, these topics must be investigated in much more detail. On the other hand, in group-living species such as the communal birds the social organization that has evolved does reflect the overall pattern of dispersal and familial proximity (20, 22, 119). There is a traditional adherence of adults to one breeding locality and low levels of natal dispersal, particularly of young males. In those species, males may eventually have the opportunity to inherit the natal territory or delineate a subsection of it. As nonbreeding birds the offspring assist their parents in anti-predator behavior and in providing food for their siblings in the nest. The association between male philopatry and social organization found in many group-living species has evolved independently in a wide range of birds and has almost certainly arisen through the sex difference in dispersal that occurs in most asocial species. In the Anatidae, where females are the sedentary sex, it remains to be shown whether any aspects of their behavior or social structure are the products of a matrilineal kinship system.

CONCLUDING REMARKS

Only recently have we begun to accumulate enough data to answer some of the questions posed over forty years ago about the dispersal of birds. We have highlighted here those areas where the body of information is still relatively weak. We end this review by suggesting that the dispersal of birds should now be addressed, both theoretically and empirically, as a problem relating to three topics: life-histories, population structure, and behavior. We know little about the life-histories (e.g. reproductive and mortality rates) of species that undergo widespread dispersal compared with those that are philopatric (3, 62). Some headway has been made towards understanding the social organization of birds in relation to population structure, but evidence from finer aspects of behavior in relation to dispersal is equivocal [e.g. song (7, 8, 76, 95, 96)] or nonexistent (e.g. mating preferences). There is now a firm base from which to tackle these problems.

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