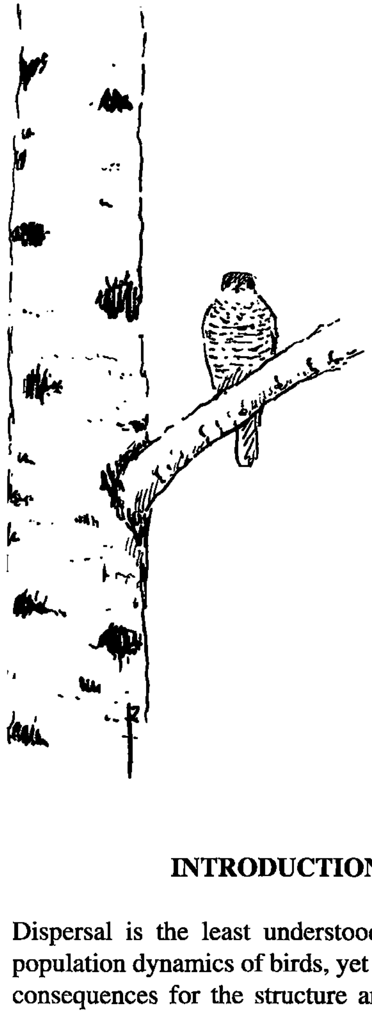
CAUSES AND CONSEQUENCES OF BREEDING DISPERSAL IN THE SPARROWHAWK *ACCIPITER NISUS*

IAN NEWTON



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Most Sparrowhawks *Accipiter nisus* were present on particular territories for only one breeding season, but others were present on the same territory for up to eight seasons. Short periods of occupancy were due partly to mortality and partly to about one third of surviving birds of both sexes changing territories between one breeding season and the next. The mean number of territories used per individual breeder in the study area increased from one territory in one-year birds to 2.8 territories in birds present for seven or more years. A change of territory was usually associated with a change of mate.

The tendency to stay on the same nesting territory, rather than move to a different territory, increased progressively with age (in females up to the oldest age groups of 7-10 years). Within any one age-group, birds were more likely to change nesting territories after a breeding failure than after a success. As a group, birds which stayed on the same territories from one year to the next showed high nest success, but no improvement between years, whereas females which changed territories showed improved success in the year after the move. While movements of breeding birds between nesting territories were related to the age and experience of the individual concerned, by inference such individual movements affected the long-term occupancy of territories, as well as the overall breeding success and distribution of the population. There was no evidence that breeding dispersal, in terms of the proportions of breeders that changed territories each year, was density dependent.

Key words: *Accipiter nisus* - breeding dispersal - movements - territory changes

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INTRODUCTION

Dispersal is the least understood aspect of the population dynamics of birds, yet it has important consequences for the structure and dynamics of populations (e.g. Greenwood & Harvey 1982; Johnson & Gaines 1990). Not only can it have much more influence on the fluctuations of local populations than can breeding and mortality rates, it is also central to such issues as source-sink and metapopulation dynamics (e.g. Pulliam 1988; Hanski & Gilpin 1991). Previous studies of breeding dispersal in birds have often revealed (a) sex differences in dispersal within species (Greenwood 1980; Gavin & Bollinger 1988; Payne & Payne 1993), possibly related to sex differences in territory acquisition and defence, (b) a tendency for greater site fidelity with increasing age (Newton & Marquiss 1982; Newton 1993; Harvey *et al.* 1984; Bried & Jouventin 1998), possibly related to increasing benefits through life of site-familiarity; and (c) a greater tendency to change territories after a breeding failure than after a success (Newton & Marquiss 1982; Beletsky & Orians 1991; Payne & Payne 1993), possibly related to site quality. These aspects are all concerned with the factors triggering individual dispersal decisions, and not with the consequences of dispersal for the individuals concerned or for the population as a whole.

In this paper, I shall discuss the factors that promote breeding dispersal in Sparrowhawks *Accipiter nisus*, and in addition, the consequences for individual performance, mate fidelity and territory occupancy. The data derive from a 28-year study in south Scotland, in which attempts were made each year to catch as many breeding birds as possible. Aspects of breeding dispersal were discussed in previous papers (Newton & Marquiss 1982; Newton & Wyllie 1992; Newton 1993), and in this paper I update these earlier analyses by the inclusion of new information, and explore other aspects not previously examined. The paper is concerned only with the movements of established breeders between different nesting places (i.e. breeding dispersal, *sensu* Greenwood 1980) and not with the movements between natal and first breeding sites (natal dispersal) which are discussed elsewhere (Newton & Marquis 1983; Newton & Rothery 2000).

Within their woodland habitat, Sparrowhawks usually nest in the same restricted localities in different years, forming regular nesting territories used over long periods (Newton 1986). The same territories may be used by a succession of different individuals, each present for one to several breeding seasons. At the same time, the individuals themselves may stay on the same territories in successive years, or they may change territories between one breeding season and the next. In the population studied, not all previously used territories were occupied in any one year, and previously-used territories were not used at random. Over a period of years some territories were used much less often than expected by chance at the population levels found, and others were used much more often. Furthermore, on the most frequently used territories, nests were most often successful, giving a strong correlation, over a period of years, between territory occupancy and nest success. On the basis of occupancy, therefore, territories were divided into five grades, poor (1) to good (5) (see Newton 1991).

METHODS

The study was conducted in two areas of south Scotland, centred on Annandale (55°15'N, 3°5'W) which covered 700 km^2, and nearby Eskdale (55°16'N, 3°25'W) which covered 200 km^2. These two areas were only 25 km apart at their nearest points. In these areas, as in the rest of Britain, Sparrowhawks were resident year-round, and as far as could be told, they bred monogamously. Each year all the woodland in both areas was searched to find the nests, and attempts were made to catch and ring as many breeding females as possible (66-80% of all female breeders caught each year during 1975-80 in Annandale and 56-83% during 1976-97 in Eskdale). My attempts to catch males were much less successful, so samples for males are smaller (5-35% of all male breeders caught each year in both areas). As it was largely a matter of chance whether particular males were caught, the findings for males should not be biased with respect to those for females, despite their smaller numbers. Both sexes were caught in baited cage traps placed on the ground near the nest, but most females were trapped on the nests themselves during incubation, a procedure which was found to have no adverse effects on nest success (Newton 1986). As there were no significant differences between findings from the two areas, the data were pooled for the analyses presented here.

Sparrowhawks that were trapped as breeders could be aged precisely if they had been ringed as nestlings, or if they were first caught in their first or second year of life when they were separable on plumage features (60% of all females caught). From the third-year on, the different age groups could not be distinguished, so at first capture could only be ascribed a minimum age of three years (40% of all females caught). However, since virtually all Sparrowhawks start breeding some time in their first three years of life (Newton 1985; Wyllie & Newton 1999), most new additions to the nesting population in definitive plumage could be assumed to be in their third year. Nevertheless, as some birds in definitive plumage changed territories between years, some may have entered the study area after previously breeding outside, and been older than the three years ascribed to them. Others may have bred in the area for one or more years without being caught and identified. The effect on the conclusions of these potential 'mistakes' in ageing are discussed later. Further details of the study areas and methods may be found in Newton (1986).

Birds that used the same territory (= nesting locality) in successive years were taken to have made no move between breeding seasons, while birds which changed territories between years were taken to have moved whatever distance separated their successive nests. On this basis no bird that changed territories moved less than 0.4 km, which was the minimum distance separating simultaneously occupied territories. A bird which raised young to fledging is counted as successful, regardless of the number of young raised, whereas one which did not raise young is counted as 'failed', regardless of the stage at which failure occurred. Most nest-failures were at the egg stage and probably resulted ultimately from food-shortage, with relatively few due to predation or other factors (Newton 1986).

Throughout the data are examined by use of chi-square tests, but, because several tests were sometimes performed on the same data set, some of the findings were also checked by logistic regression methods. The two procedures led to the same conclusions.

RESULTS

Occupancy periods and territory changes

Because on many territories birds were trapped and identified year after year, it was possible to calculate the full tenure periods of many individuals (Fig. 1). Most birds were present on particular territories for only one year (= one breeding attempt), but others were present on the same territory for up to eight consecutive years (or six in males). The average recorded tenancy period for females was 1.33 years and for males 1.41 years. Evidently, the long-term occupancy of some territories was produced by a succession of individuals occupying them consecutively, but most staying for a short time.

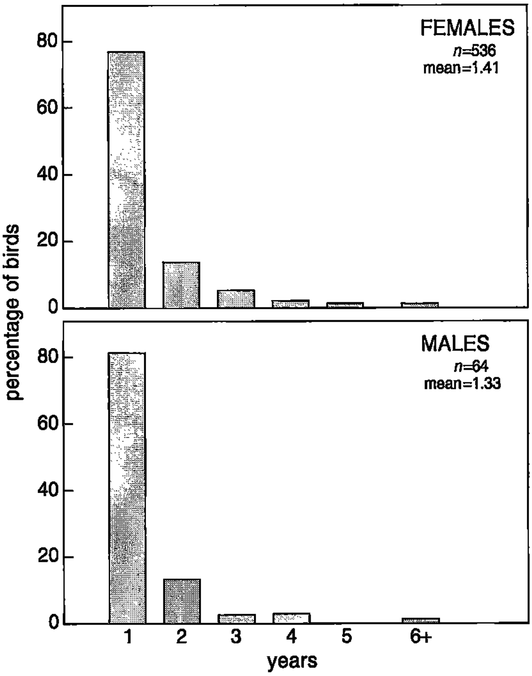

Fig. 1. Residence periods of individuals on particular territories. Birds whose time on particular territories was broken by one or more breeding seasons when another bird was present were recorded as having two separate tenancies.

Part of this turnover in occupants was due to mortality, and part to some of the surviving birds changing territories between years. Among 406 females caught in successive years, 73% were on the same territory, while 27% had changed territories. The equivalent figures for 46 males were 65% and 35%, giving no significant difference in the frequency of year-to-year changes between the sexes ($\chi^2 = 0.80$, $P = 0.37$). For birds caught at intervals longer than one year, the figures were broadly consistent with about one third of individuals changing territories each year.

Table 1. Numbers of territories occupied by individuals in relation to the numbers of breeding attempts recorded (one per year).

	Females							Males		
Years of recorded breeding	1	2	3	4	5	6	7+	1	2	3+
Numbers of birds	261	125	60	25	19	12	4	232	38	10
Number of territories occupied										
Mean	1.00	1.40	1.77	2.12	2.16	2.17	2.75	1.00	1.34	2.10
SD	0.00	0.49	0.70	0.97	1.01	1.19	0.96	0.00	0.48	0.99
SE	0.00	0.04	0.09	0.19	0.23	0.34	0.48	0.00	0.08	0.31

Number of territories occupied per breeding life

The numbers of different territories which particular individuals used is shown in Table 1 in relation to the number of years in which those individuals were recorded at nests in the study areas. Any years in which particular individuals were not identified as breeders in the study areas are excluded from the records for those individuals. In general, the mean number of territories recorded for particular individuals increased with the number of years that they were recorded as breeders, from one territory for birds found only in one year to 2.8 territories for females found in seven or more years. Individual variation was great, however: at one extreme one female found breeding in eight different years used the same territory each time, while two other females found breeding in six different years each used five different territories in that time. Data for males were fewer, but showed the same trend, at least up to the third year of life.

Some individuals used the same territory at different times in their lives, separated by a period on a different territory while their original territory was occupied by another bird. At least three other females went missing altogether for a year, when their territory was occupied by another female, then re-appeared on the same territory in the following year. Such birds may have attempted to breed elsewhere in the area but avoided capture or they may have bred outside the area and avoided capture, or they may have not bred at all in those years.

Factors that influenced territory changes

Confirming earlier analyses (Newton & Wyllie 1992, Newton 1993), the behaviour of individuals from one year to the next varied according to their age and previous nest success (Table 2, Fig. 2). In general, birds showed progressively greater site-fidelity, and less tendency to change territories, with increasing age. This trend was evident in females even up to the oldest age-groups of 7-10 years, but, because few birds survived that long, samples of such old birds were small. The trend to greater site-fidelity with increasing age was also apparent in the declining distances moved by birds which changed territories (Table 3). In addition, in all age groups, females that fail-

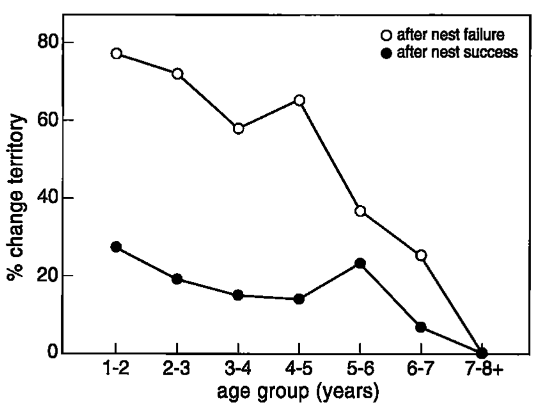

Fig. 2. The percentage of female Sparrowhawks that changed territory each year, according to age and previous nest success. See Table 2 for sample sizes and statistical details (in footnote).

Table 2. Frequency of territory changes by Sparrowhawks, according to age and previous nest success.

Age group (years)	After previous nest success: Stayed on same territory (%)*	After previous nest success: Moved to different territory	After previous nest failure: Stayed on same territory (%)†	After previous nest failure: Moved to different territory	Overall: Stayed on same territory (%)‡	Overall: Moved to different territory	Significance of variation between successful and failed birds: χ^2_1	Significance of variation between successful and failed birds: P
Females								
1-2	15(63)	9	5(24)	16	20(44)	25	5.31	0.0212
2-3	42(81)	10	6(29)	15	48(66)	25	15.86	< 0.0001
3-4	84(85)	15	13(43)	17	97(75)	32	19.11	< 0.0001
4-5	49(86)	8	4(36)	7	53(78)	15	10.47	0.0012
5-6	24(77)	7	7(64)	4	31(74)	11	0.24	0.6212
6-7	26(93)	2	4]	0	30(94)	2	0.31	0.581
7-8	10]	0	1] (83)	1	11]	1		
8-9	4] (100)	0	0]	0	4] (94)	0	1.50	0.221
9-10	1]	0			1]	0		
Overall	255(83)	51	40(40)	60	295(73)	111	69.08	< 0.0001
Significance of variation between groups	$\chi^2_6 = 13.80, P = 0.032$		$\chi^2_6 = 12.28, P = 0.056$		$\chi^2_6 = 32.29, P < 0.0001$			
Males								
1-2	2	2	1	0	3	2	0.052	0.820
2-3	5	0	0	3	5	3	4.302	0.038
3+	18	5	4	6	22	11	3.031	0.0817
Overall	25(78)	7	5(36)	9	30(65)	16	5.966	0.0146
Significance of variation between groups	$\chi^2_2 = 3.252, P = 0.197$		$\chi^2_2 = 3.547, P = 0.170$		$\chi^2_2 = 0.117, P = 0.943$			

Using binary logistic regression analyses for females, with site fidelity as the binary response variable, and age and previous nest success as independent variables, the association between age and site fidelity emerged as highly significant ($z = 3.84, P < 0.0001$), as did the association between previous nest success and site fidelity ($z = 7.27, P < 0.0001$). In males, trends were in the same direction, but only the association between previous nest success and site fidelity emerged as significant ($z = 2.66, P < 0.01$).
*Percentage of all successful birds of that age group.
†Percentage of all failed birds of that age group.
‡Percentage of all birds of that age group.

ed in their breeding attempt were more likely to change territories for the next year than were birds that succeeded (Table 2). This difference was statistically significant in each age class up to the 5th year, but not in the older age classes which were represented by smaller samples. Within both successful and failed breeders, the trend to greater site fidelity with increasing age was still apparent, but was especially marked among the failed breeders: old birds that failed to raise young were much less likely to change territories than were younger birds that failed. As indicated by the results from a binary logistic regression analysis (Table 2), these two associations, between age and

Table 3. Distances moved by birds which changed nesting territories between successive years. The same individuals may appear in more than one comparison.

	Ages (years)	Number of moves of the following distances (km) < 1.0	1.1-5.0	5.1-10.0	>10.0	Geometric mean distance (km)
Females						
	1-2	4	17	4	1	2.4
	2-3	9	10	6	1	1.9
	3+	18	44	3	1	1.6*
Males						
	1-2	1	2	0	0	1.2
	2-3	3	3	0	0	1.0
	3+	9	4	0	0	0.7

*omits one outlier of 28 km
Regression analysis of log distance against age: females, b = -0.237, $P = 0.013$; males, b = -0.224, $P = 0.147$.
On two way ANOVA, allowing for age effects, the sex difference was highly significant, $F = 11.75$, $P < 0.001$.

site-fidelity and between nest success and site-fidelity, were largely independent of one another.

Some similar trends were apparent in males, with about 35% of birds overall changing territories between years, but with a greater proportion changing territories after a nest-failure than after a success (Table 2). However, with smaller samples, these trends were not always significant in particular age-groups. The trend to greater site-fidelity, and smaller moves between territories with increasing age, was not significant in males, but samples were too small to draw firm conclusions. In general, however, males that changed territories between successive years moved over shorter distances than did females that changed territories (Table 3). Most males more than one year old moved to adjacent territories, whereas many females moved to more distant territories, the maximum record being 28 km from one study area to the other (but see below).

Movements outside the study areas

As in all studies of this type, any breeders that moved outside the study (or search) areas would not have been recaught, thus biasing the records in favour of short-distance moves. However, some information on long-distance moves was gained from birds reported dead by members of the public, as such recoveries were not confined to the study areas.

Of 40 female breeders that were reported dead over the years, thirteen had moved more than 10 km from their last recorded nest-sites (10 km being the greatest home range diameter recorded from radio-tagged Sparrowhawks in the study areas, Marquiss & Newton 1982). These thirteen birds had moved distances of 11-178 km and in various directions from their last recorded nest. Most were recovered outside the breeding season, but had not been identified in the study areas for up to three previous breeding seasons. However, three were recovered in a subsequent breeding season (April to mid-August), at 12, 58 and 120 km from their last known nest, having been missing from the study areas for 2-4 years. It seems certain, therefore, that at least these females that had bred in the study areas subsequently moved and bred long distances outside. Most of the birds that were recovered outside the study areas were in full adult plumage, with some up to 6 years of age when they moved. Some had bred successfully in their last known year in the study areas and others had not. At least one individual moved 70 km in mid-August, soon after breeding, at the same time that juveniles disperse from their natal territories. Similar records were obtained for thirteen males, of which three made movements longer than 10 km, namely 13, 19 and 56 km respectively. All three were recovered in a subsequent breeding season, 2-4 years after last capture within the study area, but only the last bird had moved outside the area. The implication was that some of the males that bred in the study area could also have moved long distances to breed elsewhere.

Potential causes of year-to-year movement at the population level

Analysis of this aspect was based only on the data from Eskdale where birds were trapped each year over a 20-year period, giving a much longer series of records than for Annandale, but with relatively small annual samples. Nest failure and youth were identified above as factors associated with territory changes by individuals. Because the percentage of nests that failed varied from year to year (between 24% and 57%), as did the percentage of yearling birds in the breeding population (between 0% and 44% in females), it would be expected that the proportion of birds that changed territories would also vary from year to year. In fact, on the samples of retrapped birds, this proportion varied from 0 out of 11 in 1984 to 7 out of 11 in 1989, an annual fluctuation that was statistically significant ($\chi^2_{19} = 33.89$, $P = 0.019$).

Territory changes may also have been affected by other factors, such as population density, acting on the whole population together. I therefore examined the annual proportions of birds that changed territories in relation to (a) nest numbers in the previous year (to test whether breeding dispersal was density dependent), (b) proportionate change in nest numbers from the previous year (to test whether dispersal was associated with population change), (c) survival from the previous year (to test whether local dispersal and local survival were linked), (d) the proportion of nests that produced young in the previous year (in view of the link between individual nest failure and tendency to change territory), and (e) the proportion of yearlings among female breeders in the previous year (in view of the link between age and territory changes). Survival was measured by capture-recapture analyses using the programme SURGE (Newton *et al.* 1993). In fact, on individual regression analyses, only one of these five relationships, namely between proportion of breeders which changed territory and the proportion of yearlings among breeders in the previous year, emerged as significant ($b = 0.97$, $r^2 = 0.366$, $P < 0.005$). Moreover, on a stepwise multiple regression analysis, none of the other variables explained significantly more of the overall variance. By implication, the other factors had so little influence on breeding dispersal, or were so closely correlated with age-composition, that none (other than age) emerged as important at the population level.

Consequences of territory changes

Because females were more likely to change territories after a failure than after a success, it was of interest to check whether they bred any better after the change (Table 4). Females of the same age group which stayed on the same territory from year to year acted as the control. As a group, the 289 female Sparrowhawks which stayed on the same territory from one year to the next showed high nest success, but no improvement between years (86% of nests successful in the first year as against 79% in the following year). In contrast, the 112 females which changed territories bred better after the move than before (45% of nests successful in the first year against 64% in the following year). This improvement after a move was evident in all the three age-groups shown in Table 4, but the pattern emerged as statistically significant only in the 1-2 year group, and in the overall data for all age-groups combined. However, after such a change, nest success was still significantly lower (64% of 112 nests) than in birds which had stayed on the same territory (79% of 289 nests, $\chi^2_1 = 9.64$, $P = 0.002$). The tendency to improvement in nest success after a

Table 4. Relationship between site-fidelity and subsequent nest success, according to age and sex.

	Breeding attempts in			
	Same territory		Different territories	
Age (years)	Successful	Failed	Successful	Failed
Females[a]				
1	14	5	9	17
2	15	4	20	6
Significance of variation	$\chi^2_1 = 0.15, P = 0.703$		$\chi^2_1 = 9.43, P = 0.002$	
2	41	5	10	15
3	40	6	14	11
Significance of variation	$\chi^2_1 = 0.10, P = 0.748$		$\chi^2_1 = 1.28, P = 0.258$	
≥ 3	193	31	31	30
≥ 4	174	50	38	23
Significance of variation	$\chi^2_1 = 5.44, P = 0.020$		$\chi^2_1 = 1.64, P = 0.201$	
Overall, one year	248	41	50	62
Overall, next year	229	60	72	40
Significance of variation	$\chi^2_1 = 4.33, P = 0.037$		$\chi^2_1 = 8.71, P = 0.003$	
Males[a]				
Overall, one year	20	5	10	9
Overall, next year	18	7	14	5
Significance of variation	$\chi^2_1 = 0.44, P = 0.508$		$\chi^2_1 = 1.31, P = 0.179$	

[a]In each age comparison, the same individuals are represented at both ages.

A logistic regression analysis for females was used to further examine the combined effects of site fidelity (or otherwise) and age on nest success. Allowing for age, this analysis confirmed a significant behaviour - year interaction ($\chi^2_1 = 9.16, P < 0.005$).

change of territory was also apparent in males, although the samples were much smaller. It thus seemed that, in both sexes, one advantage of a change in territory was an improved chance of nest success.

To determine the extent to which change of territory was associated with change of mate, analysis was necessarily restricted to those individuals whose mates were identified in successive years. All four possible behavioural patterns were recorded, namely a bird was found in the second year (a) on the same territory with the same mate, (b) on the same territory with a different mate, (c) on a different territory with the same mate, or (d) on a different territory with a different mate (Figure 3). In some instances where a bird had a different mate, the original mate was known to be alive and breeding elsewhere, whereas in other such instances the original mate was known to be dead, but most were of unknown status.

Birds that stayed on the same territory from one year to the next retained the same mate more often than did birds that changed territories. The difference between groups was significant in both sexes (Figure 3), with overall figures of mate retention of 55% per year in residents and 17% per

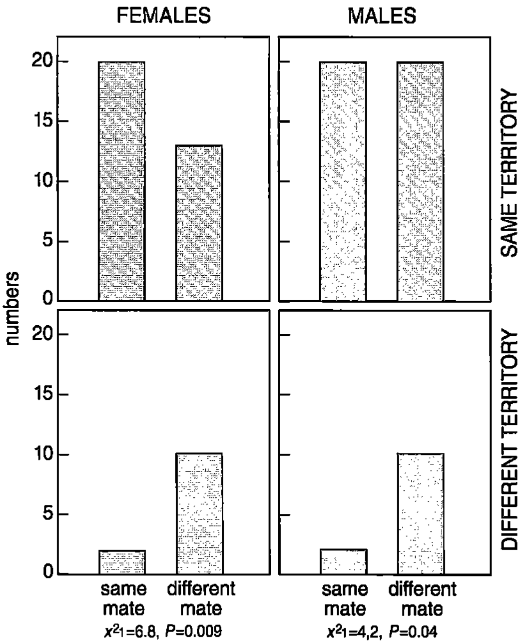

Fig. 3. Year-to-year fidelity to mate in relation to fidelity to territory.

year in movers respectively. Moreover, all moves in which the pair stayed together were to an adjacent territory in the same wood (about 0.5 km).

DISCUSSION

Present findings confirmed those of earlier analyses that site-fidelity among breeding Sparrowhawks was associated with breeding success or failure in the previous year and with age (Newton & Marquiss 1982; Newton *et al.* 1993; Newton 1993). Previous analyses revealed that the trend to increased site fidelity with age could be attributed entirely to age-related changes in the behaviour of individuals, and not to the progressive disappearance from the study population of individuals showing the greatest inclination to move (Newton 1993). Birds which disappeared may have simply moved outside the study areas, during the process of further changing territories, or they may have died.

One potential advantage of site-fidelity to the bird is familiarity with the area, which may enhance foraging success, predator avoidance, defence and other behaviour which contributes to performance. Other things being equal, the longer a Sparrowhawk has lived in a locality, the more it has to lose by leaving it, which may be one reason for the declining tendency to change territories with increasing age. In addition, the more often a bird has bred successfully on a territory, the more evidence it has accumulated that the territory concerned is a good one, and the more reluctant it might therefore become, after a single failure, to switch to another territory. Finally, as a bird ages, its social status may rise, increasing its ability to hold onto a high-grade territory in the face of competition from other individuals. Because most Sparrowhawks that moved shifted only to an adjacent or other nearby territory, they did not lose all the benefits of familiarity with the area. Only birds that moved more than 5-10 km are likely to have used completely new hunting areas.

In changing territories after nest failure, Sparrowhawks may have been responding to failure as such. Alternatively, both the failure and the move may have occurred in response to some third factor, such as loss of a mate or an unsatisfactory local food supply. The latter would fit with an earlier finding that Sparrowhawks were more likely to leave poor territories (with a history of poor occupancy and nest success) than good ones (with a history of high occupancy and nest success) (Newton & Marquiss 1982; Newton 1988, 1991). As radio-tracking showed, the better the food-supply the more sedentary Sparrowhawks became, and the worse the food-supply the more wide-ranging they became. Radio-tracking further showed that, outside the breeding season, the sexes acted largely independently of one another (Newton 1986). It was therefore not surprising that, when individuals changed territories, they usually acquired different mates. A greater tendency to change nesting territory after a nest failure than after a success has been reported in a wide range of other bird species, including passerines (Shields 1984; Gavin & Bollinger 1988;

Beletsky & Orians 1991; Payne & Payne 1993), waders and gulls (Jackson 1994; Robinson & Oring 1997; Oro *et al.* 1999), as well as other raptors (Court *et al.* 1989; Forero *et al.* 1999). The possibility that some territory changes may have followed mate loss could not be examined in Sparrowhawks (because only a small proportion of males was caught), but mate loss seemed influential in some other raptors, such as Merlins *Falco columbarius* and Black Kites *Milvus migrans* (Wiklund 1996; Forero *et al.* 1999).

The frequency of territory changes did not differ significantly between the sexes. However, almost all the moves recorded for males were to neighbouring territories, whereas many females moved over longer distances. At least in this respect, therefore, males showed greater site-fidelity than females. A difference in site fidelity between the sexes has been noted in a wide range of other bird species (Greenwood 1980), including other birds of prey (Mearns & Newton 1984; Korpimäki 1988; Court *et al.* 1989; James *et al.* 1989; Warkentin *et al.* 1991; Village 1990; Wiklund 1996).

Some Sparrowhawks, counted as 3-year-olds when first found breeding, may in fact have been older than three. Their age would then be underestimated in every year that they were present. The main effect of such underestimation would have been to lessen the trend of increasing site-fidelity within the 3-10 year olds. In other words, if such birds could have been aged more accurately, the trend of increased site fidelity over age groups 3-10 might have been more marked than actually recorded. Age-related or experience-related trends in site-fidelity have also been noted in the breeders of other bird species (Beletsky & Orians 1991; Montalvo & Potti 1992; Bried & Jouventin 1998), including birds of prey (Korpimäki 1988).

Breeding dispersal and population level

The way that individuals behave following nest failure could influence the numbers of birds nesting in the study area the following year, as well as the distribution of birds within the area and the occupancy of particular territories. At the population level, no relationship emerged between the proportion of birds that changed territory in particular years, and nest numbers, nest success or population change from the previous year. Evidently, factors acting at the individual level (notably age), were more important than those, such as population density, that are likely to have affected the whole population simultaneously. However, the fact that some territories were occupied more than others over a period of years was due partly to the attraction such territories had to a succession of occupants. On such favoured territories, the chances of breeding successfully were significantly higher than on less favoured territories (Newton 1991). An earlier analysis revealed that almost all individuals that changed territories moved to a territory that had previously been ranked as of equal or higher grade to the one abandoned. Hardly any individuals moved to a territory of lower grade (Newton 1991).

Breeding dispersal and territory occupancy

If some territories offered better breeding prospects than others, as seemed to be the case (Newton 1991), the greater tendency to move elsewhere after a breeding failure would itself result in greater and more consistent occupancy of high grade territories. This would occur whether the move was stimulated by the breeding failure as such or by some underlying factor, such as food-shortage, which could have influenced both the breeding failure and the move. Through this mechanism, birds would tend to occupy more consistently the more prey-rich parts of the area, and maximise their breeding success. In other words, it was largely this behaviour which caused territories of different quality to show different levels of occupancy over a period of years.

Breeding dispersal and individual performance

The fact that moves generally benefited those birds that changed territories was implicit in the fact that their nest success improved more, on average, than that of birds of equivalent age (and experience) that stayed on the same territory from one year to the next. Such changes at the level of individuals must presumably also have raised the productivity of the population as a whole above what it would be if all individuals stayed on the same territories (including poor ones) year after year.

Breeding dispersal and mate fidelity

A change of territory was frequently associated with a change of mate, and always if the move was further than to an adjacent territory. This may have been an incidental consequence of the fact that the two sexes acted independently of one another outside the breeding season, but, as breeding failures may have been territory-induced or mate-induced, the advantages of a simultaneous territory change and mate change were self-evident. It was then hard to tell how much the improvement in success that followed a territory change was due to the territory change itself or to the associated mate change. Too few males were caught to check whether birds that changed territories also gained better mates (mate quality being judged by age).

The link between territory change and mate change meant that individual Sparrowhawks had more mates during their lives than (they would have done than) if they had remained on the same territory throughout. The genetic constitution of their offspring was presumably therefore more varied than if they had retained the same mates, which may have carried some advantage, and as mentioned, some individuals may have gained better mates by moving to better territories. A link between site fidelity and mate fidelity also emerged in a study of Merlins *Falco columbarius* (Warkentin *et al.* 1991).

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SAMENVATTING

In dit artikel worden factoren die bijdragen aan de verandering van broedterritoria bij Sperwers *Accipter nisus* besproken, in het licht van de consequenties die zo'n beslissing heeft op het (individuele) succes als broedvogel, partnertrouw en territoriumbezetting. De meeste Sperwers in het studiegebied waren maar gedurende één broedseizoen op een bepaald territorium aanwezig, maar in andere gevallen vertoonden de vogels plaatstrouw tot in acht opeenvolgende seizoenen. Kort territoriumgebruik kon worden veroorzaakt door sterfte en doordat overblijvende partners (beide seksen) in latere jaren van territorium veranderden. Het gemiddelde aantal territoria dat door individuele Sperwers in het studiegebied werd gebruikt, nam toe van één territorium bij eenjarige vogels tot 2,8 territoria in vogels die zeven of meer jaren in het gebied tot broeden kwamen. Verandering van territorium viel vrijwel steeds samen met verandering van partner.

De neiging om hetzelfde territorium te blijven gebruiken, nam toe met toenemende leeftijd (bij wijfjes tot in de oudste groepen van 7-10 jaar oude). Bij elke leeftijdsklasse waren Sperwers na een mislukt broedseizoen sterker geneigd van partner en/of territorium te veranderen dan na een succesvol seizoen. Wanneer beschouwd als een aparte groep, vertoonden de plaatstrouwe vogels een hoog broedsucces, maar geen aantoonbare verbeteringen in de tijd, terwijl vogels die van territorium veranderden doorgaans betere broedsuccessen behaalden in jaren na de verhuizing. Er werden geen aanwijzingen gevonden dat de 'dispersie' (verandering van territorium), uitgedrukt als het percentage broedvogels dat jaarlijks van territorium veranderde, bijvoorbeeld door dichtheidsafhankelijke factoren werd bepaald. (CJC)

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