

INFLUENCE OF SITE FIDELITY ON MATE SWITCHING IN URBAN-BREEDING MERLINS (*FALCO COLUMBARIUS*)

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ABSTRACT.—From 1985 to 1989, we examined 120 nesting attempts by urban-breeding Merlins (*Falco columbarius*) in Saskatoon, Saskatchewan, Canada. Males showed significantly higher levels of site fidelity from year to year than females. Males returned to the same nesting area 61% of the time ($n = 28$), while females returned to the same nesting area a second year only 28% of the time ($n = 39$). Mate fidelity was low among Merlins in this population (only 20% of 60 pairings contained the same birds for two successive years), and it appeared largely related to the degree of site fidelity. The rate of interyear mate switching in this population (change of mate when both members of a pair were known to be alive the second year) was $>68\%$ ($n = 19$). Among males, mate and site fidelity were statistically independent. Thus, when males maintained the same nesting area between years, the probability of retaining the same mate was no better than by chance (58% of 12 males found retaining the same nesting area were paired with a different mate the second year, compared with 85% of 7 males who moved to a different nesting area and acquired a different mate). In contrast, among females, mate and site fidelity were not independent. Females who changed nesting area were unlikely to have the same mate (91% of 11 females), but those that remained on the same site were more likely to have the same mate (71% of 7 females).

There was no apparent benefit of site or mate fidelity to Merlin productivity, measured as the number of young produced per nesting attempt. Birds that had been paired for two or more years did not have significantly higher productivity than those pairs that remained together for only one year. Likewise, previous experience on a site did not significantly improve an individuals' productivity when both birds were the same or only one of the pair was the same, compared with that of pairs where both birds were new to the site. Low site and mate fidelity within this population may reflect the absence of selective pressure favoring fidelity. Received 23 April 1990, accepted 8 October 1990.

MANY avian species return in successive years to breed in the same general area, territory, or nest site. Greenwood (1980) suggested that it was possible, based on the species' resource-defense mating system, to predict which sex would be most likely to return (*philopatric*). Where males defend a breeding area (or its resources), they will be more philopatric and most females will disperse. In contrast, the opposite pattern will be found if females defend the resource. Birds that return to breed in the same area may benefit from past experience through easier exploitation of local resources (Moore and Ali 1984, Shields 1984, Dobson and Jones 1986).

High site fidelity has been hypothesized to directly affect the extent of mate fidelity found

within a population (Delius 1965, Soikkeli 1967), but little substantive evidence has been presented to support this hypothesis. Site fidelity may have its greatest impact on mate retention in migratory species. To reunite, these birds must contend with problems related to the timing of arrival on the breeding grounds, differences in mortality between the sexes, and differences in the level of site fidelity. However, pairs that reunite often benefit from higher productivity than newly formed pairs (Coulson 1966, Newton and Marquiss 1982, Rowley 1983).

We examined the adult breeding-site fidelity and mate retention patterns of Merlins (*Falco columbarius*) breeding in an urban environment. Merlins are small, Holarctic, bird-eating falcons (Cramp and Simmons 1980, Palmer 1988). They form monogamous pair bonds with strongly territorial nesting dispersion where they are clumped in space. Pairs nest in open habitat or

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interrupted forest, and within the last 30 yr some populations have moved into urban centers on the northern Great Plains of North America.

Typical of many of its congeners, male Merlins establish a nesting territory in spring, defend it from competing male conspecifics, and attempt to attract a mate (Cramp and Simmons 1980). Given this behavior and Greenwood's (1980) hypothesis regarding philopatry, we predicted that males should display greater nest-site fidelity from year to year than females. We have previously shown that male Merlins exhibit greater natal philopatry than females (James et al. 1989). In addition, based on results in Black-legged Kittiwakes (*Rissa tridactyla*; Coulson 1966) and Eurasian Sparrowhawks (*Accipiter nisus*; Newton and Marquiss 1982) where reunited pairs had higher productivity than newly formed pairs, we predicted that selection would favor birds that maintained pair bonds from year to year. Minimum annual survival rates for adult Merlins of both sexes in our population were ca. 70% (James et al. 1989). Thus, the odds were at least even that a previous mate had survived to the next year and would be available to reunite, take advantage of the experience gained, and improve productivity.

We also attempted to examine the interactions between mate and site fidelity in Merlins. This study population is partially migratory (James et al. 1987, Warkentin et al. 1990). Each year approximately 20% of the population (breeding adults and their offspring) remains in the city through the winter. This wintering component, consisting of females and males in similar proportions, is resident throughout the year. Therefore, many of these birds are on, or near, a breeding territory for much of the time (Warkentin and Oliphant 1990). The partially migratory nature of this population has developed in the last 20 yr (James et al. 1987) and could be considered a relatively recent phenomenon in evolutionary terms. Therefore, we predicted that in this traditionally migratory species, maintenance of the pair bond would be based largely on fidelity to nesting site rather than to a mate.

METHODS

As part of a larger study, we analyzed data collected from 1985–1989 on mate and breeding-site fidelity of Merlins nesting in the city of Saskatoon (52°07'N,

106°38'W). A detailed description of the study habitat is provided in Warkentin and James (1988). Merlins began to nest in Saskatoon ca. 1971 (Houston and Schmidt 1981). Since that time, we have monitored the population yearly. We determined (1) the location of all Merlin nests in the city of Saskatoon, (2) the number of young produced (and banded) in each nest, and (3) from 1985 onwards the identity of breeding adults associated with each nest (Oliphant and Thompson 1978, Oliphant and Haug 1985, Warkentin and James 1988, James et al. 1989). Each May the city was searched thoroughly to find all active Merlin nests. Although nest failures early in the season were likely missed, we believe that most pairs that reached the egg-laying stage were located. We banded the young ($n = 463$, 1985–1989) in each nest with USFWS aluminum leg bands (Oliphant 1974, Oliphant and Haug 1985). From 1982 onwards year-specific, anodized aluminum color bands were also placed on the leg opposite the USFWS band (James et al. 1989). Beginning in 1985, we mist-netted breeding adults (112 females and 94 males), with a Great Horned Owl (*Bubo virginianus*) as the lure bird (see James et al. 1989 and Warkentin et al. 1990 for trapping techniques); this was done in mid- to late June of each year. All captured birds not previously banded with USFWS bands were banded. Because of the highly dimorphic nature of Merlins (males are significantly smaller than females; Warkentin et al. 1990), the sexes could be easily distinguished in the hand. Among males, adults (birds ≥ 2 yr old) were differentiated from yearlings on the basis of plumage color. Adult males have a slate-gray or blue dorsal plumage while yearling plumage is brown and resembles both adult and yearling females (Temple 1972). Because of the similar nature of their plumages, adult and yearling females in this population could not be readily distinguished (except those which had been banded as nestlings). More than 95% of all known individuals were identified by the numbered USFWS band; we identified the remaining 10 individuals from plastic, color-coded leg streamers placed on birds during winter for other studies (Warkentin et al. 1990).

Merlins use abandoned corvid nests, primarily in spruce (*Picea* spp.) trees in Saskatoon (Warkentin and James 1988). Although the same neighborhoods of Saskatoon were often occupied each year, Merlins seldom returned to the same nest or nest tree. Therefore, we defined *nesting areas* as areas that may include several alternate nests used in different years. Following Newton (1986), we treated nesting area as synonymous with *territory*, which referred to that part of a male's home range that was used for nesting each year and defended against conspecific intruders. Nesting areas did not include all feeding areas. Because Merlins tend not to occupy the same nests from year to year, to assess site fidelity we arbitrarily assigned nests to nesting areas, based on the clumping of locations for previous year's breeding attempts

TABLE 1. Summary of breeding Merlins captured and indices of population productivity for Saskatoon, Saskatchewan (1985–1989).

Year	No. of nests ^a	No. of males identified (%)	No. of females identified (%)	No. young per successful nest
1985	20 (18)	17 (85)	18 (90)	4.1
1986	21 (21)	18 (86)	20 (95)	4.1
1987	24 (22)	17 (71)	22 (92)	4.4
1988	25 (25)	22 (88)	24 (96)	4.0
1989	30 (28)	20 (67)	28 (93)	3.8

^a Number of successful nests (producing at least one young) each year is indicated in parentheses.

(Warkentin et al. 1990). Thus, nesting areas were occupied 1–5 yr during the study depending upon their geographic location relative to nests occupied in previous years. To examine the reliability of our nesting-area assignments, we plotted nest locations for each year, calculated distances between nests, and combined these values for all 5 yr to derive an average internest distance ($\bar{x} \pm SD = 4.0 \pm 2.1$ km, $n = 1,411$). Because this value was significantly greater than the average distance between nests within nesting areas (0.4 ± 0.3 km, $n = 234$; t -value = 26.446, $P < 0.001$), we felt that our assignment of nests was representative of the actual clumping of nest sites into “traditional” nesting areas.

We defined *site fidelity* as occurring when birds returned to breed in the same nesting area that they used the previous year. *Mate fidelity* (reuniting) refers to the establishment of a pair bond and production of eggs by the same individuals in two or more consecutive years. Birds were considered to have *switched mates* (“divorced” *sensu* Rowley 1983) either when both members of the pair were found breeding with other partners (i.e. having produced eggs) the following year, or when one partner was found with a different mate the following year and the second was trapped in a later year. *Productivity* was measured as the number of young fledged per nest. We assumed that all chicks that reached bandable age successfully fledge.

We were unable to capture all breeding birds each year. Therefore, the reported values must be considered estimates for the categories outlined. For example, rates of mate switching may be biased because, in certain circumstances, both birds may be alive and breeding in the population the following year but one was not captured. Because we captured a large percentage of the breeding birds, we feel that our data will be an accurate reflection of the actual values. All values reported are mean \pm SD. Statistical significance was accepted at the 0.05 level.

TABLE 2. Site and mate fidelity among merlins breeding in Saskatoon, Saskatchewan (1985–1989). Sample sizes for each category are presented in parentheses. Significant differences (G -test) between male and female are indicated by asterisks ($* = P < 0.01$).

Pattern	% of males	% of females	% overall
Same mate	23.1 (26)	17.6 (34)	20.0 (60)
Same nest area	60.8 (28)*	28.2 (39)	41.8 (67)
Different nest area			
Different mate	90.0 (10)	96.0 (25)	94.3 (35)
Same mate	10.0	4.0	5.7
Same nest area			
Different mate	68.9 (16)	44.4 (9)	60.0 (25)
Same mate	31.1	55.6	40.0

RESULTS

We monitored 120 nesting attempts of Merlins within Saskatoon during 1985–1989 (Table 1). Between 80 and 92% of breeding birds were trapped each year at these nests.

Males returned to the same nesting area significantly more often than females ($G = 6.97$, $df = 1$, $P < 0.01$; Table 2). Males were found on the same site in two consecutive years >60% of the time, while females occupied the same site only 28% of the time. Given that there were 15% fewer breeding males caught per year than females, this difference may be attributable to sampling. But, if the number of males caught was inflated by 15% (4 males) and these were placed in the contingency table against the pattern (i.e. 17 of 32 males on the same site vs. 11 of 39 females), then the relationship remained significantly different ($G = 4.49$, $df = 1$, $P < 0.05$). The longest that a male was known to return to the same area was 4 yr in succession, whereas two females returned to the same areas for 3 consecutive years. When multiple reuse of sites by these individuals was included in the calculation, the average length of territory occupation was 1.2 yr for males and 1.1 yr for females.

The overall rate of mate switching in the population was 68.4% (13 of 19 times when both members of a pair were found in subsequent years they were associated with a different mate). Of those birds found with a new partner in subsequent years, 8 of 12 males re-paired with partners who had previously bred in the city, and 4 were with females previously unbanded

and presumably first-time breeders. Among females, 4 were with experienced mates (caught breeding in the city previously), and 4 were with presumably inexperienced males (two banded as nestlings but never captured as breeding adults and two previously unbanded adult birds). We also found that the rate of mate switching among pairs involving known non-migratory birds (7 of 12 changed partners from one year to the next) was not significantly different from that of pairs in which both birds were presumed to be migratory (5 of 6; Fisher's exact test, $P > 0.6$; see Warkentin et al. 1990 regarding identification of nonmigratory and migratory individuals).

When all individuals captured in at least two successive years were included in the data base, differences between the sexes were not significant in terms of mate retention ($G = 0.26$, $df = 1$, NS; Table 2). We found males with the same mate 23% of the time, while females retained their mate in the second year 18% of the time. In 5 of 6 cases where birds retained the same mate in subsequent years, the pair remained on the same nesting area. The pair that stayed together on a different nesting area moved to a site approximately 1 km distant from their original nesting area. Their previous territory was occupied that same year by another pair with similar breeding experience (i.e. both males were 3 yr old, and both females were at least 5 yr old). However, among birds that changed mates from one year to the next, females (24/28) were much more likely to move to a different nesting area than were males (9/20; $G = 8.78$, $df = 1$, $P < 0.01$). Again, by adding 15% to the total number of males (3 birds in this case) and placing them in the category against the pattern (i.e. 12 of 23 males changing mates vs. 24 of 28 females), the relationship remains significantly different ($G = 6.73$, $df = 1$, $P < 0.01$).

Considering these same data from the perspective of site retention rather than that of mate fidelity (Table 2), we found that birds that shifted to new nesting areas seldom retained the same mate. We compared site and mate retention in the most restricted case, where only those pairs in which both members were available to remate the following year (i.e. no "widowed" birds were included in the calculations; Table 3). Among males, mate fidelity was independent of site fidelity (Fisher's exact test, P

TABLE 3. Site and mate retention among male and female Merlins nesting in Saskatoon, Saskatchewan (1985-1989). Sample sizes for each category are presented in parentheses. Only those pairs in which both birds are known to be alive the following year are included.

Pattern	% of males	% of females	% overall
Different nest area			
Different mate	85.7 (7)	90.9 (11)	88.9 (18)
Same mate	14.3	9.1	11.1
Same nest area			
Different mate	58.3 (12)	28.6 (7)	47.4 (19)
Same mate	41.7	71.4	52.6

> 0.3). When males maintained the same nesting area, the probability of retaining the same mate was no better than that expected from random chance. Although there was a noticeable trend towards males on the same site reuniting more often than those that changed sites, the numbers had to be tripled before a statistically significant relationship was detected with the same proportions. However, in females, we found that mate fidelity and site fidelity were not independent (Table 3; Fisher's exact test, $P < 0.05$). Thus, females that changed nesting area were unlikely to have the same mate, whereas those that remained on the same nesting area were more likely to have the same mate. The values reported in this restricted subset for males and females (Table 3) are statistically similar to those found in Table 2, which includes "widowed" birds (heterogeneity log-likelihood test: males, $G = 0.008$, NS; females, $G = 0.800$, NS). We tested the same relationships with Fisher's exact test as we did among values in Table 3—but with the larger sample found in Table 2—and we found that site retention and mate fidelity were independent of each other among males ($P > 0.3$) but not among females ($P < 0.01$).

Productivity among pairs that stayed together for > 1 yr ($n = 6$) was not significantly better in the second year (4.0 ± 0.6 young fledged for first year and 4.3 ± 0.6 for the second year; Mann-Whitney U -test, $U = 14.5$, NS). Similarly, where members of a pair switched mates, the number of young produced before and after switching was not significantly different. Productivity in the first year, before switching mates, was 4.5 ± 0.7 ($n = 11$). Productivity of

the female with a different partner after switching was 3.8 ± 1.7 young per successful nest (including one female who failed to produce young the second year; $U = 69$, NS), and productivity of the male with a different partner after switching was 4.4 ± 1.0 young ($U = 62.5$, NS).

Based on our studies, we predicted that experienced Merlin pairs would have increased productivity over that of newly formed pairs. However, there was little apparent impact on the number of young produced by Merlins nesting in Saskatoon based on their breeding experience with a mate or on a nesting area. Except for one pair that remained together but moved to a new nesting area, all others fell into one of three categories: (1) both birds remained together on the same nesting area as the previous year (productivity = 4.4 ± 0.9 , $n = 5$), (2) one member of the pair was on the same nesting area as the previous year, but the second bird was new to the site (4.2 ± 1.1 , $n = 17$), or (3) both members of the pair were new to each other and to the nesting area (4.3 ± 1.2 , $n = 32$). There was no significant difference between any of the categories (Mann-Whitney U -test).

DISCUSSION

Site fidelity.—Familiarity with a nesting area conveys several potential advantages to an individual seeking to breed at that site. It facilitates obtaining food and mates, and it aids in territory defense and in evasion of predators (Moore and Ali 1984, Shields 1984, Dobson and Jones 1986). Experience in any area may also greatly increase an individual's lifetime reproductive success. However, individuals of many species are less likely to return the next year to the same area (or site) after reproductive failure (Martin 1974, Darley et al. 1977, Brooke 1978, Harvey et al. 1979b, Oring and Lank 1982, Newton and Marquiss 1982, Oring et al. 1983, Gratto et al. 1985, Weatherhead and Boak 1986). Although some birds, such as the Piping Plover (*Charadrius melodius*), return to a breeding site regardless of success, this may reflect a shortage of suitable nesting habitat (Haig and Oring 1988). Although we did not measure nesting area availability, evidence from this study and previous work implies that abundant nesting

sites were available to Merlins in Saskatoon. The population continued to grow throughout the study (see Table 1), which indicates that nest sites were not limiting the population and also that substantial choice of nesting areas was available. In addition, discriminant function analysis of nest-site selection by Merlins in the city of Saskatoon misclassified more than half of 60 randomly chosen, unoccupied corvid nests in the city as fitting the description of occupied nest sites (Warkentin and James 1988). This suggested that there were a large number of suitable nest sites available to Merlins, and that site fidelity was linked to some favorable aspect of the site, which benefited returning individuals through their familiarity with the area.

Greenwood (1980, 1983) hypothesized that sex-biased return rates would occur among monogamous, territorial birds when resources were defended by one sex. Therefore, greater site fidelity was expected among male Merlins because they provide nearly all food for their partner, the nestlings, and themselves from the courtship period until about the second week of the nestling stage. Previously, we reported that male Merlins showed a higher rate of return to the Saskatoon study area (natal philopatry) than females (James et al. 1989). In this study, we demonstrate that males also exhibit breeding-site fidelity significantly more often than females (Table 2). Previous experience in, and familiarity with, an area would be a considerable advantage for males in terms of awareness of spatial and within-season changes in prey abundance and availability. This would make it easier for a breeding male to exploit local resources and either to maintain or to increase his productivity over that of birds with no experience in the area.

Such patterns of male-biased breeding-site fidelity are widespread among passerines (Darley et al. 1977, Greenwood and Harvey 1982, Shields 1984) and are commonly found in birds of prey (Newton 1979) and shorebirds (Thompson and Hale 1989); although some monogamous sandpipers (Oring and Lank 1982, Gratto et al. 1985) and Piping Plovers (Haig and Oring 1988) do not show strong male-biased site fidelity. Hodson (1975) also found that male Merlins were more likely than females to retain their territory in successive years. Of 12 males recaptured a second year on study areas in Alberta, 9 (75%) were on the same territory, but only 2 of 10

(20%) females retrapped during Hodson's study were on the territory where they had bred the previous year.

Mate fidelity.—Variation between the sexes in breeding-site fidelity is just one of the constraints that may influence the extent of mate fidelity in a migratory species. Another is the timing of arrival on the breeding grounds. The possibility of reuniting with a former mate is lessened by difficulties in the timing of return from the wintering grounds to the breeding site (Wickler and Seibt 1983). Although we have no information for this population, Clark (1985) found that, among Merlins migrating along the east coast of North America in spring, males preceded females. Differential mortality between the sexes may also affect whether or not courtship is delayed until the return of last year's partner. We estimated maximum annual mortality rates of 29% for females and 31% for males in this population (James et al. 1989).

For the Saskatoon Merlin population, there are additional considerations because of the partially migratory nature of this population (Warkentin et al. 1990). In all pairs, but perhaps especially in mixed pairs composed of one migrant and one nonmigrant partner, a choice must be made in terms of whether or not the benefits of reuniting with a previous mate outweigh the potential costs of awaiting the return of an individual who may be dead or not returning to breed in the same area. Among those birds that do winter in Saskatoon, it appears rare that a strong pair bond is maintained through the winter. Males retain or return to establish a territory (on the same nesting area >60% of the time; see Table 2), and females pair with their old mate only if both return to the same area (with only one exception). Eight pairs have been observed on adjacent or overlapping home ranges through the winter months, but no pair was known to breed the following summer (Warkentin and Oliphant 1990). It appears that, at present, nonmigratory behavior does not influence mate fidelity in this population.

Although we found a noticeable trend in our data towards more mate-switching among known nonmigratory birds than presumed migrants, even if the values were tripled in each cell of the comparison, there was still no statistical significance to the relationship. Based on theories stated above regarding site and mate fidelity, we would have predicted that pairs with

nonmigratory birds would be more likely than pairs with migrant members to retain their breeding site (particularly nonmigrant males) and, especially where both were nonmigratory, maintain pair bonds between years. At present we are unable to explain why a pattern in which there is an apparently greater tendency to switch mates among nonmigrant than migrant birds might develop.

Few unsuccessful birds retain the same mate for breeding in subsequent years (Brooke 1978, Oring and Lank 1982, Shields 1984, Thompson and Hale 1989). It is generally presumed, provided the nest is successful in one year, that birds will retain the same mate and have higher productivity than those pairs that changed mates from year to year. Among shorebirds, many reunite when both birds are available (Soikkeli 1967, Hale and Ashcroft 1982, Oring and Lank 1982, Gratto et al. 1985, Warriner et al. 1986, but see Haig and Oring 1988). In fact, the generally low rate of mate switching found among seabirds (e.g. Ollason and Dunnet 1978) and shorebirds (Gratto et al. 1985) implies that retaining the same mate, territory, or both, may be advantageous. Eurasian Sparrowhawk pairs that reunited had better productivity than those in which the partners were new to each other or to their territory (Newton and Marquiss 1982), as was the case for several species of seabirds (Rowley 1983). Experience and familiarity between mates allows the pair to establish a nest site and time the events of breeding so that the maximal amount of energy is channeled towards producing young. Newly formed pairs must spend time and energy to establish the pair bond and, where both are new to a territory, to defend a new nesting area. This may lessen the overall amount of energy expended on producing offspring. However, there are instances, such as in Snow Geese (*Chen caerulescens*; Cooke et al. 1981) and Semipalmated Sandpipers (*Calidris pusilla*; Gratto et al. 1985), where mate change between breeding seasons had little or no impact on success. Given the relatively confined area occupied by Merlins breeding in Saskatoon compared with rural populations of similar size, one might expect that former mates would be easier to find; and if mate fidelity was advantageous, it would be enhanced in this population. Yet, in contrast to what we predicted, there was little mate fidelity among Merlins breeding in Saskatoon (Table 2).

Factors influencing mate switching in Merlins.—Several authors (Delius 1965, Soikkeli 1967, Darley et al. 1977, Lessells 1984, Shields 1984, Gratto et al. 1985) suggested that site fidelity is very important in promoting mate fidelity and is closely related to mate fidelity. Harvey et al. (1979a) related site faithfulness to the ecology of different species and suggested that site fidelity occurred most often in stable environments. They found that Great Tits (*Parus major*), which breed in relatively stable deciduous woodlands, have much lower breeding dispersal than species that breed in unpredictable habitat, such as the Eurasian Skylark (*Alauda arvensis*; Delius 1965) and European Greenfinch (*Carduelis chloris*; Greenwood and Harvey 1977). Eurasian Skylarks appear primarily mate faithful and secondarily site tenacious (Delius 1965). Coulson (1966) suggested that mate fidelity was a trait of long-lived species. As we predicted, maintenance of the pair bond in Merlins appeared to be largely the result of site fidelity. We found that Merlins had relatively low mate fidelity and, where they changed nesting area, the probability of having the same mate as the previous year was no better than chance (Table 3). Although we have yet to address the question of mate choice in this population and how this may affect mate and site fidelity, we believe that mate switching in Merlins is largely a function of site fidelity.

Where female Merlins return to the same site, it is often with the same mate (Table 3). However, in this population mate switching was more common than reuniting when both members of a pair returned to the study area the next year. The factors that motivate mate switching in birds, as well as which member of the pair initiates the separation, are poorly understood (Harvey et al. 1979a, Rowley 1983, Gratto et al. 1985). Harvey et al. (1979a) suggested that, where males are the territory holder, females are more likely than males to choose to switch mates and move to a new area and mate. Males presumably have a greater investment in holding their territory, because familiarity with surrounding foraging areas and with their conspecific neighbors is advantageous. Changing nesting areas would not be to a male Merlin's benefit unless conditions on that nesting area deteriorated. In studies that documented decreases in territory quality, several species were shown to change territories and seek areas of similar or better

quality (Baeyens 1981, Newton and Marquiss 1982, Weatherhead and Boak 1986). During our study, many nesting areas were occupied throughout the entire 5-yr period. Additionally, few nesting areas were abandoned, many new ones were established, and except for a small decrease in 1989, productivity remained stable (Table 1). These points suggest that deteriorating territory quality was not likely to be a factor for moving from one nesting area to another.

Whereas site fidelity and mate fidelity have been shown to make a difference in some species, we found no evidence over the short term for a beneficial influence of experience (within the pair-bond) on productivity. Birds that had been paired for ≥ 2 yr had average productivity that was marginally higher, but not significantly so. Likewise, previous experience on a nesting area did not significantly improve an individual's productivity. This may be related to the food source used by Merlins. House Sparrows (*Passer domesticus*) are the predominate prey of urban Merlin populations that breed on the Great Plains (Oliphant and McTaggart 1977, James and Smith 1987). Sparrows occur at high density in the city compared with rural populations, and urban sparrows are often concentrated around central food sources (such as grain elevators, seed mills, and rail yards). The relatively low levels of territoriality found in Saskatoon Merlins (nests as close as 100 m; unpubl. data) may be a consequence of high prey density. The Merlin's food is available in abundance, but not in defendable quantities or locations. Thus, the abundance and accessibility of food may negate any advantage (for foraging purposes) of returning to and holding a specific site to breed. For this population, productivity is relatively high and apparently independent of breeding site or mate retention. Between 0.5 and 1.6 additional nestlings are produced per successful attempt in Saskatoon as compared with rural Merlin populations in the prairie region of North America (see Warkentin and James 1988).

Although mate fidelity was not as high as might be expected from Merlin longevity when compared with other species (particularly passerines), site fidelity was male-biased as predicted from the hypotheses of Greenwood (1980). Despite apparent advantages in other species, productivity was not better for pairs of

Merlins remaining together for >1 yr, nor did the migratory behavior of the pair appear to influence the chance of reuniting in subsequent years. The rate of mate switching between years was quite high in this population, and selection did not appear to strongly favor mate retention. Mate fidelity was largely dependent upon the degree of site fidelity; most birds changed partners when they changed nesting areas.

We could find no obvious advantages for high mate fidelity within this population. There may be advantages to mate switching that we have not measured or that will become evident as lifetime reproductive success data are available for a larger number of individuals in this population. However, with no clear disadvantages within this population to changing mates from year to year, switching mates may be a form of bet-hedging among females, which increases the chances of obtaining a better quality mate the next year. Further analysis of the link between mate and site fidelity would benefit from knowledge of the mate choice that is occurring in this population. A series of controlled removals to test the impact of mate loss would allow more detailed assessment of questions regarding the importance of site retention to mate fidelity.

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LITERATURE CITED

- BAEYENS, G. 1981. Functional aspects of serial monogamy: the magpie pair-bond in relation to its territorial system. *Ardea* 69: 145-166.
- BROOKE, M. DE L. 1978. Some factors affecting the laying date, incubation and breeding success of the Manx Shearwater *Puffinus puffinus*. *J. Anim. Ecol.* 47: 477-495.
- CLARK, W. S. 1985. Migration of the Merlin along the coast of New Jersey. *Raptor Res.* 19: 85-93.
- COOKE, F., M. A. BOUSFIELD, & A. SADURA. 1981. Mate change and reproductive success in the Lesser Snow Goose. *Condor* 83: 322-327.
- COULSON, J. C. 1966. The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull, *Rissa tridactyla*. *J. Anim. Ecol.* 35: 269-279.
- CRAMP, S., & K. E. L. SIMMONS. 1980. Handbook of the birds of Europe, the Middle East and north Africa, vol. II. Oxford, Oxford Univ. Press.
- DARLEY, J. A., D. M. SCOTT, & N. K. TAYLOR. 1977. Effects of age, sex and breeding success on the site fidelity of Gray Catbirds. *Bird-banding* 48: 145-151.
- DELIUS, J. D. 1965. A population study of Skylarks, *Alauda arvensis*. *Ibis* 107: 466-492.
- DOBSON, F. S., & W. T. JONES. 1986. Multiple causes of dispersal. *Am. Nat.* 126: 855-858.
- GRATTO, C. L., R. I. G. MORRISON, & F. COOKE. 1985. Philopatry, site tenacity, and mate fidelity in the Semipalmated Sandpiper. *Auk* 102: 16-24.
- GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28: 1140-1162.
- . 1983. Mating systems and the evolutionary consequences of dispersal. Pp. 116-131 in *The ecology of animal movement* (I. R. Swingland and P. J. Greenwood, Eds.). Oxford, Clarendon Press.
- , & P. H. HARVEY. 1977. Feeding strategies and dispersal of territorial passerines: a comparative study of the Blackbird *Turdus merula* and the Greenfinch *Carduelis chloris*. *Ibis* 119: 528-531.
- , & ———. 1982. The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Syst.* 13: 1-21.
- HAIG, S. M., & L. W. ORING. 1988. Mate, site, and territory fidelity in Piping Plovers. *Auk* 105: 268-277.
- HALE, W. C., & R. P. ASHCROFT. 1982. Pair formation and pair maintenance in the Redshank *Tringa totanus*. *Ibis* 124: 471-490.
- HARVEY, P. H., P. J. GREENWOOD, & C. M. PERRINS. 1979a. Breeding area fidelity of Great Tits (*Parus major*). *J. Anim. Ecol.* 48: 305-313.
- , ———, ———, & A. MARTIN. 1979b. Breeding success of Great Tits in relation to age of male and female parent. *Ibis* 121: 186-200.
- HODSON, K. 1975. Some aspects of the nesting ecology of Richardson's Merlin (*Falco columbarius richardsonii*) on the Canadian prairies. Univ. British Columbia, Vancouver, M.S. thesis.
- HOUSTON, C. S., & A. SCHMIDT. 1981. History of Richardson's Merlin in Saskatchewan. *Blue Jay* 39: 30-37.
- JAMES, P. C., & A. R. SMITH. 1987. Food habits of urban-breeding Merlins, *Falco columbarius*, in Edmonton and Fort Saskatchewan, Alberta. *Can. Field-Nat.* 101: 592-594.
- , ———, L. W. OLIPHANT, & I. G. WARKENTIN.

1987. Northward expansion of the wintering range of Richardson's Merlin. *J. Field Ornithol.* 58: 112-117.
- , I. G. WARKENTIN, & L. W. OLIPHANT. 1989. Turnover and dispersal in urban Merlins, *Falco columbarius*. *Ibis* 131: 426-429.
- LESSELLS, C. M. 1984. The mating system of Kentish Plovers (*Charadrius alexandrius*). *Ibis* 126: 474-483.
- MARTIN, S. G. 1974. Adaptations for polygynous breeding in the Bobolink, *Dolichonyx oryzivorus*. *Am. Zool.* 14: 109-119.
- MOORE, J., & R. ALI. 1984. Are dispersal and inbreeding avoidance related? *Anim. Behav.* 32: 94-112.
- NEWTON, I. 1979. Population ecology of raptors. Berkhamstead, U.K., T. & A. D. Poyser.
- . 1986. The sparrowhawk. Calton, U.K., T. & A. D. Poyser.
- , & M. MARQUISS. 1982. Fidelity to breeding area and mate in sparrowhawks *Accipiter nisus*. *J. Anim. Ecol.* 51: 327-341.
- OLIPHANT, L. W. 1974. Merlins—the Saskatoon falcons. *Blue Jay* 32: 140-147.
- , & E. A. HAUG. 1985. Productivity, population density and rate of increase of an expanding Merlin population. *Raptor Res.* 19: 56-59.
- , & S. MCTAGGART. 1977. Prey utilized by urban Merlins. *Can. Field-Nat.* 91: 190-192.
- , & W. J. P. THOMPSON. 1978. Recent breeding success of Richardson's Merlin in Saskatchewan. *Raptor Res.* 12(1/2): 35-39.
- OLLASON, J. C., & G. M. DUNNET. 1978. Age, experience, and other factors affecting the breeding success of the Fulmar, *Fulmaris glacialis*, in Orkney. *J. Anim. Ecol.* 47: 961-976.
- ORING, L. W., & D. B. LANK. 1982. Sexual selection, arrival times, philopatry and site fidelity in the polyandrous Spotted Sandpiper. *Behav. Ecol. Sociobiol.* 10: 185-191.
- , ———, & S. J. MAXSON. 1983. Population studies of the polyandrous Spotted Sandpiper. *Auk* 100: 272-285.
- PALMER, R. S. 1988. Handbook of North American birds, vol. 5. New Haven, Connecticut, Yale Univ. Press.
- ROWLEY, I. 1983. Re-mating in birds. Pp. 331-360 in *Mate choice* (P. Bateson, Ed.). London, Cambridge Univ. Press.
- SHIELDS, W. M. 1984. Factors affecting nest and site fidelity in Adirondack Barn Swallows (*Hirundo rustica*). *Auk* 101: 780-789.
- SOIKKELI, M. 1967. Breeding cycle and population dynamics in the Dunlin (*Calidris alpina*). *Ann. Zool. Fennici* 4: 158-198.
- TEMPLE, S. A. 1972. Sex and age characteristics of North American Merlins. *Bird-banding* 43: 191-196.
- THOMPSON, P. S., & W. G. HALE. 1989. Breeding site fidelity and natal philopatry in the Redshank *Tringa totanus*. *Ibis* 131: 214-224.
- WARKENTIN, I. G., & P. C. JAMES. 1988. Nest-site selection by urban Merlins. *Condor* 90: 734-738.
- , ———, & L. W. OLIPHANT. 1990. Body morphometrics, age structure, and partial migration of urban merlins. *Auk* 107: 25-34.
- , & L. W. OLIPHANT. 1990. Habitat use and foraging behaviour of urban Merlins (*Falco columbarius*) in winter. *J. Zool. (London)* 221: 539-563.
- WARRINER, J. S., J. C. WARRINER, G. W. PAGE, & L. E. STENZEL. 1986. Mating system and reproductive success of a small population of polygamous Snowy Plovers. *Wilson Bull.* 98: 15-37.
- WEATHERHEAD, P. J., & K. A. BOAK. 1986. Site infidelity in Song Sparrows. *Anim. Behav.* 34: 1299-1310.
- WICKLER, W., & U. SEIBT. 1983. Monogamy: an ambiguous concept. Pp. 33-50 in *Mate choice* (P. Bateson, Ed.). London, Cambridge Univ. Press.