The Condor 94:418–426

ASSORTATIVE MATING IN URBAN-BREEDING MERLINS[1]

IAN G. WARKENTIN
Department of Zoological Research, National Zoological Park,
Smithsonian Institution, Washington, DC 20008

PAUL C. JAMES
Saskatchewan Museum of Natural History, Wascana Park, Regina,
Saskatchewan S4P 3V7, Canada

LYNN W. OLIPHANT
Department of Veterinary Anatomy, University of Saskatchewan,
Saskatoon, Saskatchewan S7N 0W0, Canada

Abstract. We examined assortative mating behavior in 149 pairs of Merlins (*Falco columbarius*) breeding in Saskatoon, Saskatchewan, Canada from 1985 through 1990. Yearlings paired with yearlings and adults (2-plus years old) paired with adults more frequently than expected. Among adult pairs, however, there was no significant assortment by age. The productivity of pairs which included a yearling member was significantly lower than that of pairs with two adult birds. Similarly, pairs with two adults hatched their young on average nine days earlier than pairs with at least one yearling. There was no significant assortment of pairs based on body size with the exception of tail length. Along with differences in the timing of breeding activities, one other possible proximate mechanism promoting the distinction between adults and yearlings when choosing a mate was the difference in plumage between adult and yearling males.

Key words: Merlin; Falco columbarius; *urban; assortative mating; breeding; age; Saskatchewan.*

INTRODUCTION

One means of developing an understanding of the mechanisms of mate choice within a population is to document nonrandom, assortative mating (i.e., the tendency to mate preferentially with individuals having, for example, certain morphological characteristics, territorial possessions, or experience; Searcy 1982). The ultimate reason for making such choices is presumably the attainment of greater fitness by the individual making the selection, either directly through greater assistance with parental care (incubating, brooding, nest defense, and provisioning), and access to superior quality resources, or indirectly through some genetic benefit to the young which may enhance their fitness. For researchers to assess such behavior accurately, it is necessary that the characteristics examined be resistant to cheating and vary sufficiently within a population to permit choice to occur (Searcy 1979).

Elsewhere (Warkentin et al. 1991), we have examined the patterns of mate and site fidelity among Merlins (*Falco columbarius*) in an urban-breeding population. We found that male Merlins are much more likely to return in subsequent years to a nesting territory than are females. Among females, mate fidelity is directly linked to site fidelity; females who change nesting territory are unlikely to have the same mate but those returning to the same site are more likely to have the same mate. However, among males, mate and site fidelity are independent of each other; whether or not males change nesting territory, the probability of retaining the same mate is no better than by chance. We found also that the rate of mate switching between years is very high in this population, although there is no apparent effect on breeding productivity which can be linked to the pattern of mate or site retention. Based on these data, we suggested that little mate choice was likely to occur within this population. To test this further, in this paper we examined the population for evidence of assortative mating on the basis of age, previous breeding experience, location of origin (urban versus presumed rural), and body size.

This population represents one of the highest breeding densities of Merlins reported (Oliphant

---

[1] Received 26 August 1991. Accepted 9 December 1991.

and Haug 1985). Because of the close proximity of birds in the city (density estimates range from 16.4 to 25.4 pairs/100 km^2; Sodhi et al., unpubl. data), the potential for choice to occur is likely greater than would be encountered in most other populations. Therefore, there was a higher probability that patterns of nonrandom mating would be expressed than might be the case in other Merlin populations.

METHODS

As part of a broader study, we examined the mate choice behavior of a color-marked population of Merlins nesting in the city of Saskatoon, Saskatchewan, Canada (52°07′N, 106°38′W) from 1985 through 1990. We identified the majority of nests in the city each year and, on average, annually trapped 78% of breeding males and 93% of breeding females (Warkentin et al. 1991). Males and females were easily distinguished by their size difference and yearling males could be separated from adult (2-plus years old) males based on differences in their plumage (Temple 1972). Unless previously banded as nestlings, however, we could not make the same distinction among females. Nearly 46% of birds breeding in the city during the study were originally banded as nestlings and could be aged precisely, but many entered the breeding population as unbanded birds from outside the city. While males could be aged, or at least classified as adults based on plumage, previously unbanded females were only categorized as adults in a subsequent breeding attempt to avoid misclassifying yearlings as adults or vice versa.

We used standard mist nets to trap breeding Merlins, with a tethered Great Horned Owl (*Bubo virginianus*) as the lure bird (see Warkentin et al. 1990 for details of trapping methods). Breeding birds, not previously marked, were fitted with a United States Fish and Wildlife Service (USFWS) aluminum leg band. Nestlings at each site were banded with a USFWS leg band and a year-specific aluminum color band. All breeding Merlins trapped were measured to determine mass to the nearest 1 g, wing chord, tail length and total body length to the nearest 1 mm, and culmen to the nearest 0.1 mm (see Warkentin et al. 1990 for details on measurements). Trapping and measurement were carried out during the last two weeks of June, which was four to six weeks after females completed egg laying.

The data were derived from the 149 nests identified during the study. Only those nests in which both birds could be identified as either a yearling or an adult were included in the analyses (n = 74), except where noted. Age-related pairing was analyzed on a yearly and combined-years basis using Fisher's exact or the chi-square test. All other comparisons were taken from the six-year pooled data set; thus, some individuals were present for several years in the combined samples. Since unbanded yearling and adult females could not be distinguished, we excluded those pairs which involved unbanded females caught for the first time from any age-related calculations (except where noted). On recapture in subsequent years, these females were considered to be adults and included in the data set. When calculating the correlations of body size characteristics between the members of pairs, we eliminated data from all but the first capture when two birds were paired together more than once. We included all instances when birds were caught more than once but with a different partner. All individuals were included once in the calculation of body morphometric means for the comparison of adults versus yearlings, and locally-hatched versus presumed immigrant birds (see below).

Marzluff and Balda (1988) suggested that pairing within a population is dependent upon the previous choices made by other individuals in the population. They argue (Marzluff and Balda 1988, Johnson and Marzluff 1990) that the pool of potential mates is finite and, consequently, that mate choice lacks the independence necessary for analyses with standard statistical techniques. We suggest that at least three factors influence the dependence/independence of mate choice in a population, acting on a continuum rather than as a rigid dichotomy. (1) Group size—Mate choice will not be independent when occurring in small groups where pool size is finite. However, as the group size increases, the pool of potential mates quickly becomes large enough so that mate choice is essentially independent. The presence of floaters and the movement of migrants through an area during courtship periods also adds to the total pool of potential mates from which the selection is to be made. (2) Behavior—In highly social, tightly knit groups of birds, one could reasonably expect that a rigid structure, such as a dominance hierarchy, might develop to govern the pairing of birds. However, in species which are highly territorial and consequently solitary, mate choice would be more independent in the absence of a strong social structure. (3) Pair bond—When pair bonds are strong, and potentially life long, mate choice would be highly dependent upon the continuation of pairings. Where pair bonds are weak and mates constantly switch partners from year to year, pairs would be more likely to be set up independently of each other.

Marzluff and Balda (1988) and Johnson and Marzluff (1990) based the development of their model for statistical analysis of mate choice on the Pinyon Jay (*Gymnorhinus cyanocephalus*). This is a species which lives in tightly knit, highly social flocks, breeds colonially, and is long lived with life-long pair bonds (Balda and Bateman 1972). In contrast, the Merlin is territorial, with little social interaction between pairs, and high levels of mate switching between years (Warkentin et al. 1991). In the latter case, mate choice is more likely to be independent than in the former; thus, we believe that the analyses suggested by Marzluff and Balda (1988) for examining mate choice would be inappropriate for our data.

Because of the extensive nature of nest searches each year, we assumed that the majority of nest sites were discovered and most young hatched in the city were banded. Nesting Merlins in Saskatoon have been studied continuously since 1972 (Oliphant and Haug 1985, James et al. 1989); consequently, any birds found breeding in the city during the period included in this study which had not been banded as nestlings were probably the product of pairs nesting outside of the city. We assumed also that, with the limited breeding dispersal found among birds in general (Greenwood and Harvey 1982) and specifically among Merlins of this population (James et al. 1989), any breeding birds which were not banded when captured at a nest site were first-time breeders.

Approximately 20% of the Saskatoon Merlin population remains in the city throughout the year (Warkentin et al. 1990), and many of these birds have winter territories which are on or near nesting areas (Warkentin and Oliphant 1990). These circumstances make it difficult to examine and compare the timing of arrival on breeding areas as an index of the timing of breeding activities. Therefore, hatch date was used to indicate the relative timing of breeding for pairs. We estimated the average hatch date for the chicks of each nest based on their age at banding. Ages were determined by comparison with an unpublished aging scheme developed for Merlins from captive-rearing studies and observations of wild birds.

TABLE 1. Age-based pairing patterns of yearling (Ylg) and adult (Ad) Merlins from 1985 through 1990, and for all years combined.

	Number of matings between				
Year	Ylg/Ylg	Ylg male/ Ad female	Ad male/ Ylg female	Ad/Ad	P
1985	0	1	1	8	0.900
1986	0	1	0	10	—
1987	2	0	0	10	0.015
1988	1	0	2	9	0.250
1989	0	0	0	14	—
1990	1	2	2	10	0.516
All years	4	4	5	61	0.004

Productivity was based on the number of young which were banded in each nest, assuming that birds which were old enough to be banded were likely to fledge. All values reported are mean ± standard deviation, except where noted.

RESULTS

A significant relationship existed between the ages of the birds in breeding pairs. More yearling/yearling and adult/adult pairs were found than expected by chance in the population for the combined six-year data set (Table 1; Yate's corrected $\chi^2 = 8.38$, df = 1, $P = 0.004$). However, this trait was more apparent in some years (e.g., 1987) than others where the pair combinations suggested random mating between the two age groups. While mating apparently was not random between yearlings and adults, there was no trend for older adult Merlins to mate with older adults. Among pairs in which both birds were 2-plus years, and the ages of both were known precisely, there was no significant correlation between male and female age ($r_s = -0.1419$, $n = 20$, $P = 0.551$).

We found a significant relationship when we examined the influence of age on the productivity of pairs. The productivity of mixed pairs which consisted of both a yearling and an adult member was substantially reduced (combined mean productivity = 2.6 ± 1.6 young per nest, $n = 9$) when compared with the productivity of pairs consisting of either both adults or both yearlings (Table 2). To obtain a more general picture of the influence of yearlings on the productivity of pairs, we examined the productivity of pairs with

TABLE 2. Age-based comparisons of the number of pairings, hatching date and productivity for urban-breeding yearling (Ylg) and adult (Ad) Merlins.

Type of pairing	n	Hatch date[a,b]	Productivity[b]
Ylg/Ylg	4	172 ± 6 (164–178, 173)	4.3 ± 1.0 (3–5, 4.5)
Ylg male/Ad female	4	168 ± 9 (158–175, 171)[c]	1.3 ± 1.5 (0–3, 1)
Ad male/Ylg female	5	168 ± 6 (161–176, 169)	3.6 ± 0.5 (3–4, 4)
Ad/Ad	61	161 ± 5 (151–176, 160)	4.2 ± 1.2 (0–5, 5)

[a] In Julian days, where day 1 = 1 Jan.
[b] Values presented are: mean ± SD (range, median).
[c] $n = 3$.

at least one yearling (including 15 pairs with females of unknown age; 3.4 ± 1.4, $n = 28$, median = 4, range = 0–5), and found that it was significantly lower than that of pairs which consisted of two adult birds (Table 1; Median test, $\chi^2 = 9.37$, df = 1, $P = 0.002$). Nine of 14 known-age females entered the breeding population as yearlings (unpubl. data). If females immigrating into the Saskatoon population to breed from rural areas had a similar age structure, many of the 15 pairs with a female of unknown age were likely yearling/yearling pairs. The results in Table 2 suggest that including these data would bias the productivity estimate upwards for all pairs with at least one yearling member; this would decrease the difference between the two groups being compared. Since the productivity of pairs with a yearling (including unknown-aged females) is still significantly lower than that of adult pairs, addition of these data appears justified.

The timing of breeding also varied with age. On average, the hatch date of chicks in the nests of two adult birds was seven days earlier than that for mixed pairs involving an adult and a yearling bird, and 11 days earlier than pairs with two yearling birds (Table 2). Again, considering all pairs with at least one yearling member (including those with unknown-age females), the mean hatch date for these pairs (day 170 ± 7, $n = 27$, median = 171, range = 151–179) was significantly later than that of pairs with two adults (Table 2; Median test, $\chi^2 = 19.57$, df = 1, $P < 0.001$).

Birds which were not known to have previously bred were found most often with others which had not bred, and those with breeding experience tended to mate with others having breeding experience at a statistically significant level ($\chi^2 = 6.52$, df = 1, $P = 0.011$). Of 52 pairings which involved inexperienced females, there were 37 instances in which they were paired with inexperienced males, while only 17 of 40 females with previous breeding experience were mated with inexperienced males (Table 3). To examine the ability of females to distinguish between experienced and inexperienced adult males in the absence of potential visual cues such as plumage differences, we removed all known yearlings from the analysis. This changed the number of pairings which involved two inexperienced birds to 19 of 34 cases, while the number of experienced pairs was altered slightly to 23 of 39 pairings (Table 3). The statistical significance of the relationship disappeared with this modification of the data ($\chi^2 = 1.07$, df = 1, $P = 0.318$).

There was no indication that Merlins were choosing mates on the basis of origin (hatched either in Saskatoon, or presumed to be hatched outside of the city). Locally-hatched females were paired with males hatched in the Saskatoon population in 26 of 39 pairings, while presumed immigrant females were paired with locally-hatched males in 57 of 94 instances ($\chi^2 = 0.21$, df = 1, $P = 0.648$). None of the possible combinations of locally-hatched and immigrant males and females produced significantly better than the other (Kruskal-Wallis, H = 0.596, $P = 0.897$). Locally-hatched males were no more productive than presumed immigrant males (4.0 ± 1.2 fledglings, $n = 83$, median = 4; and 3.9 ± 1.4, $n = 49$, median = 4, respectively; Median test, $\chi^2 =$

TABLE 3. The influence of breeding experience on assortative mating of Merlins for A) all pairings, and B) pairings in which known yearlings are eliminated from the sample.

	Female			
	A		B	
	Not bred	Bred previously	Not bred	Bred previously
Male				
Not bred	37	17	19	16
Bred previously	15	23	15	23

0.01, df = 1, $P = 0.931$). Similarly, for females there were no significant differences between the productivity of these two groups (local: 3.9 ± 1.2, $n = 39$, median = 4; immigrant: 4.0 ± 1.3, $n = 93$, median = 4; Median test, $\chi^2 = 0.72$, df = 1, $P = 0.396$).

We examined five components of body size in Merlins for potential body-size selection in mate choice. For wing chord and tail length we found a significant positive correlation ($P < 0.05$; Table 4) between the size characteristics of males and females when all pairs were considered. However, there was assortative mating of yearlings and adults in this population (see above). Since yearlings were significantly smaller than adults in several of the characteristics measured ($P < 0.05$, 2-tailed t-tests; Table 5), we examined the same correlations among pairs of birds in which both were known to be adults (i.e., at least two years old). In this more restricted data set, only tail length was significantly correlated between the members of these adult pairs (Table 4). Similar analyses were carried out to compare the morphological characteristics of presumed rural birds with those of locally-hatched birds. We found no significant differences except among males in wing chord length; locally-hatched individuals were significantly longer (2-tailed t-test, $t = 2.712$, df = 61, $P = 0.009$).

DISCUSSION

EVIDENCE OF ASSORTATIVE MATING

The pairing of similarly-aged birds is not uncommon; assortative mating by age has been found across all age groups in a variety of taxa (e.g., Silver Gulls, *Larus novaehollandiae,* Mills 1973; Great Tits, *Parus major,* Greenwood et al. 1979; Kittiwakes, *Rissa tridactyla,* Coulson and Thomas 1983; Pinyon Jays, Marzluff and Balda 1988), and up to age four in Canada Geese (*Branta canadensis,* Raveling 1981). Among raptors, Newton et al. (1981) found assortative mating between adults and yearlings in Eurasian Sparrowhawks (*Accipiter nisus*), as did Korpimäki (1989) in Tengmalm's Owls (*Aegolius funereus*). We found disproportionately high numbers of yearling/yearling and adult/adult pairs in this population of urban-breeding Merlins (Table 1).

Hypothetically, this age-based relationship may have resulted from pairs forming in their first breeding attempt as yearlings or two-year-old birds and remaining paired for a period of years until one of them died. Annual mortality among adult Merlins averages 29% for this population (James et al. 1989), but only 20% of pairs contain the same mates in two consecutive years when all birds are considered; and among only those pairs which have the potential to re-unite (i.e., no re-pairing due to mortality) the rate of mate switching is 68% (Warkentin et al. 1991). With an average survival rate of about 70% for both sexes, this means that both members of at least half of all pairs will survive from one year to the next. Since only 20% of all pairs re-unite for a second year, a substantial number of birds which are available to do so, are not re-uniting for a subsequent breeding attempt. The longest period that we observed two birds paired together was three years (unpubl. data). Additionally, we found no significant trend among adult birds to pair with progressively older partners over time. With such a low level of mate fidelity from year to year, it is unlikely that the pattern of positive assortment by age described above could be explained by such an hypothesis.

This pattern of assortative mating between age/plumage classes could be related to territory quality and the relative abilities of adult and yearling males to establish and defend better quality nesting areas. Studies in the Eurasian Sparrowhawk (Newton and Marquiss 1982), Red-winged Blackbird (*Agelaius phoeniceus,* Beletsky and Orians 1987), Tengmalm's Owl (Korpimäki 1988), and Eurasian Nuthatch (*Sitta europaea,* Matthysen 1990) have all shown examples of younger, less experienced birds moving from lower to higher quality territories as they get older. This suggests that it may be easier for adult males to establish and maintain ownership of high quality nesting sites. If similar competition for superior quality sites (and males) occurred among female Merlins, then we might expect to find an age-based mating pattern similar to that in Table 1. However, none of the potential parameters of territory quality we examined such as length of occupancy, order of occupancy, date of clutch initiation, or age of occupants correlated with the productivity of a nesting area (unpubl. data).

Another possible explanation for this age-based mating pattern could be the timing of arrival on the breeding grounds by birds of different age classes. Village (1985) presented data indicating support for such a mechanism as one of the controlling factors of assortative mating by age in

TABLE 4. Correlation between members of Merlin pairs (for all pairs and for adult-adult pairs only) in body size represented by body mass, tail length, total length, wing chord, and culmen.

Body component	All pairs			Adult-adult pairs only		
	r	n	P	r	n	P
Body mass	0.1325	90	0.213	0.1776	36	0.301
Tail length	0.4019	89	<0.001	0.4421	36	0.007
Total length	−0.0401	90	0.707	0.0717	36	0.678
Wing chord	0.2757	91	0.008	0.1962	37	0.244
Culmen	0.0538	91	0.613	0.0291	37	0.864

Eurasian Kestrels (*Falco tinnunculus*). We do not know when birds established territories each spring during this study. For migratory individuals, it is quite likely that they follow the arrival pattern displayed by Merlins migrating along the east coast of North America, as demonstrated by Clark (1985): males preceding females. A substantial proportion of the population remains on or near breeding sites in Saskatoon as wintering birds (Warkentin et al. 1990, Warkentin and Oliphant 1990), which would make assessment of such data difficult. However, the nine day difference in mean and 11 day difference in median date of hatch, between adult/adult pairs and those pairs with at least one yearling member, suggest that there is a substantial asynchrony in the timing of breeding activities. This lack of synchrony in timing is one possible proximate explanation for the predominance of yearling/yearling and adult/adult pairs. Adults may establish territories and begin pair formation earlier in the season than yearlings. This would lead to a "passive" form of mate choice (sensu Newton et al. 1981) in which adults pair with adults because yearlings have not yet arrived, or not begun territory establishment and courtship activities. Such differences could also lead to a reduction in the number of mixed yearling/adult pairs, as observed in Table 1.

We found also assortative mating based on experience. However, this criterion appears to be very closely associated with age, and it is likely that there is little or no selection for experience beyond that which is attributable to age. Initial analysis produced a significant assortment of experienced and inexperienced birds mating within their own group. When yearling birds were removed from the analysis there was no longer a significant assortment based on experience (Table 3). This could indicate also that Merlins were unable to distinguish between experienced and inexperienced birds, once the most obvious plumage differences (particularly among males) were removed. In the absence of positive assortment by age or experience beyond the first year, it also suggests that plumage may be one of the signals used by females in selecting an adult mate.

TABLE 5. Morphometrics (mean ± SD, n) of adult and yearling Merlins breeding in Saskatoon, Saskatchewan. Differences were examined using a 2-tailed t-test.

Body component	Adult	Yearling	t	P
Female				
Body mass (g)	255.5 ± 17.1 (25)	254.7 ± 11.7 (9)	0.129	0.898
Tail length (mm)	136.0 ± 3.4 (25)	133.2 ± 4.2 (9)	1.992	0.055
Total length (mm)	302.6 ± 8.1 (25)	297.2 ± 5.6 (9)	1.839	0.075
Wing chord (mm)	221.9 ± 4.0 (25)	214.2 ± 4.8 (9)	4.700	<0.001
Culmen (mm)	14.8 ± 0.6 (25)	15.2 ± 0.5 (9)	−1.784	0.084
Male				
Body mass (g)	166.9 ± 11.1 (46)	163.3 ± 7.0 (16)	1.212	0.230
Tail length (mm)	121.6 ± 2.6 (46)	119.6 ± 1.8 (16)	2.841	0.006
Total length (mm)	271.6 ± 6.8 (47)	269.9 ± 5.5 (16)	0.902	0.371
Wing chord (mm)	199.4 ± 4.0 (47)	196.1 ± 2.0 (16)	3.018	0.004
Culmen (mm)	12.4 ± 0.6 (47)	12.7 ± 0.5 (16)	−1.270	0.209

Morphometric characteristics may have played some role in the choice of a breeding partner, but the evidence from our data suggests that its influence is minimal. At least some of the correlation in body size found between breeding males and females occurred because yearling Merlins (which were significantly smaller than adults in several characteristics, Table 5) tended to mate with each other. Interestingly, for a species with such high reversed sexual size dimorphism, we found no negative assortment overall, and indications of positive assortment in tail length (Table 4). Tail length may not reflect skeletal size of birds, but may indicate individuals which are better hunters of avian prey. Hakkarainen and Korpimäki (in press) proposed that long-tailed male Tengmalm's Owls were more adept than short-tailed males at catching avian prey. If their hypothesis is correct and longer-tailed raptors, in general, are more agile hunters of small birds, this may explain the pattern of positive assortment by tail length that we found between male and female Merlins.

Overall, selection of larger males by female Merlins would be unexpected according to most theories of reversed size dimorphism (e.g., see Safina 1984). Among the few other studies which have looked at mate choice in raptors, both Bowman (1987) for American Kestrels (*F. sparverius*) and Marti (1990) for Barn Owls (*Tyto alba*) found no evidence to suggest that smaller males were chosen preferentially by females. As discussed above, however, Hakkarainen and Korpimäki (in press) have evidence from their study of Tengmalm's Owls which suggests that smaller males may be chosen preferentially under certain circumstances.

EVIDENCE FOR IMPROVED FITNESS

Breeding pairs which involved a yearling bird had significantly lowered nestling productivity, when compared with that of pairs involving two adults. Differences in productivity between the nests of yearling and adult males were not unexpected given the substantial demands placed upon the male when provisioning a nest. From the beginning of the courtship period through until the chicks are half grown, the male provides most, if not all, of the food for himself, his mate, and young in the nest (Lawrence 1949; Temple 1972; Sodhi et al., unpubl. data). A yearling male, relatively inexperienced at foraging when compared to an adult male, may have difficulty supplying the amount of food required to fledge the same number of chicks as an adult male. This trend can be seen in the productivity of mixed yearling/adult pairs (Table 2). Those pairs with a yearling male had substantially fewer fledged young than those with an adult male. This interpretation must be viewed with caution, however, due to the small sample size available. The productivity of yearling/yearling pairs in this population is similar to that of adult/adult pairs and does not fit the general trend described above of lower values for pairs with at least one yearling member. This result is somewhat puzzling and may again simply reflect the small sample size.

Assuming that the higher productivity and earlier average hatch dates we found in adult/adult pairs accurately reflected the superior quality of an adult partner, this also may explain the paucity of mixed yearling/adult pairs, and the relative excess of yearling/yearling and adult/adult pairs among Merlins breeding in Saskatoon. Adults may have selected other adults as mates because of their better quality as partners, while those yearlings capable of establishing a territory, and/or attracting a mate were excluded from doing so (either by active or passive choice) and were more likely to pair with another yearling. Some adults may have elected to mate with a yearling rather than forego breeding for the year if they were unable to find a suitable adult partner. This final point is difficult to document because of our inability to assess the availability of potential mates. The number of extra birds seen at nests during the breeding season (James and Oliphant 1986) suggests that there is a substantial pool of non-breeders, but while most of these were yearling males, it is difficult to determine how representative this is of the non-breeder population as a whole.

FACTORS INFLUENCING ASSORTATIVE MATING IN THE SASKATOON MERLIN POPULATION

Merlins in this population commonly switch mates (Warkentin et al. 1991) providing many opportunities to choose specific partners should there be any selective advantage in doing so. However, the ability of females to assess the quality of males may be hindered by the absence of cues, due to certain attributes of this population, which would normally influence such a process. These properties of the Saskatoon population may make any choice of partners with specific characteristics, beyond choosing an adult over a yearling male as a partner, unimportant to the yearly output of a female. The productivity of Merlins in Saskatoon is high; the population averages 0.5 to 1.6 nestlings per successful nest above that found in rural populations of the northern Great Plains (Warkentin and James 1988). There are few nest failures once egg laying has begun (Warkentin et al. 1991), and hatching and fledging rates are higher than most other populations studied (unpubl. data). In addition, we found that suitable nest sites are not limiting for this population (Warkentin and James 1988), and the primary food source for breeding Merlins in Saskatoon (House Sparrows, *Passer domesticus,* Oliphant and McTaggart 1977) is abundant and available (based on hunting success rates; Sodhi et al., 1991) to males on territories throughout the city. With abundant nest sites and food resources, female assessment of male/territory quality on the basis of such criteria during courtship may be difficult. With little apparent distinction of territories based on quality, switching mates frequently could be a strategy used by females to overcome an inability to distinguish superior males. Although they may also risk losing a good mate, this might increase their chances of obtaining a better quality mate during their reproductive life. It could also explain the low levels of mate and site fidelity we found in females previously (Warkentin et al. 1991), and the absence of choice based strongly on specific traits which we noted in this paper.

ACKNOWLEDGMENTS

We thank Hugh Saunders, Edith Labbé, Barb Hanbidge, Geoff Peat, and Dillon Von Kuster for field assistance. Financial support was provided by a Natural Sciences and Engineering Research Council of Canada (NSERC) Operating Grant to L. W. Oliphant, and a NSERC Postdoctoral Fellowship to I. G. Warkentin. Erkki Korpimäki and John Marzluff provided thoughtful and constructive reviews.

LITERATURE CITED

BALDA, R. P., AND G. C. BATEMAN. 1972. Breeding biology of the Pinon Jay. Living Bird 11:5–42.

BELETSKY, L. D., AND G. H. ORIANS. 1987. Territoriality among male red-winged blackbirds. I. Site fidelity and movement patterns. Behav. Ecol. Sociobiol. 20:21–34.

BOWMAN, R. 1987. Size dimorphism in mated pairs of American Kestrels. Wilson Bull. 99:465–467.

CLARK, W. S. 1985. Migration of the Merlin along the coast of New Jersey. Raptor Res. 19(2/3):85–93.

COULSON, J. C., AND C. S. THOMAS. 1983. Mate choice in the Kittiwake Gull, p. 361–376. *In* P. Bateson [ed.], Mate choice. Cambridge Univ. Press, Cambridge.

GREENWOOD, P. J., AND P. H. HARVEY. 1982. The natal and breeding dispersal of birds. Ann. Rev. Ecol. Syst. 13:1–21.

GREENWOOD, P. J., P. H. HARVEY, AND C. M. PERRINS. 1979. Mate selection in the Great Tit *Parus major* in relation to age, status and natal dispersal. Ornis Fennica 56:75–86.

HAKKARAINEN, H., AND E. KORPIMÄKI. In press. Reversed sexual size dimorphism in Tengmalm's Owl: is small male size adaptive? Oikos.

JAMES, P. C., AND L. W. OLIPHANT. 1986. Extra birds and helpers at the nests of Richardson's Merlin. Condor 88:533–534.

JAMES, P. C., I. G.WARKENTIN, AND L. W. OLIPHANT. 1989. Turnover and dispersal in urban Merlins, *Falco columbarius.* Ibis 131:426–429.

JOHNSON, K., AND J. M. MARZLUFF. 1990. Some problems and approaches in avian mate choice. Auk 107:296–304.

KORPIMÄKI, E. 1988. Effects of territory quality on occupancy, breeding performance and breeding dispersal in Tengmalm's Owl. J. Anim. Ecol. 57: 97–108.

KORPIMÄKI, E. 1989. Mating system and mate choice of Tengmalm's Owls *Aegolius funereus.* Ibis 131: 41–50.

LAWRENCE, L. DE K. 1949. Notes on nesting Pigeon Hawks at Pimisi Bay, Ontario Wilson Bull. 61:15–25.

MARTI, C. D. 1990. Sex and age dimorphism in the Barn Owl and a test of mate choice. Auk 107:246–254.

MARZLUFF, J. M., AND R. P. BALDA. 1988. Pairing patterns and fitness in a free-ranging population of Pinyon Jays: what do they reveal about mate choice? Condor 90:201–213.

MATTHYSEN, E. 1990. Behavioral and ecological correlates of territory quality in the Eurasian Nuthatch (*Sitta europaea*). Auk 107:86–95.

MILLS, J. A. 1973. The influence of age and pair-bond on the breeding biology of the Red-billed Gull (*Larus novaehollandiae scopulinus*). J. Anim. Ecol. 42:147–162.

NEWTON, I., AND M. MARQUISS. 1982. Fidelity to breeding area and mate in Sparrowhawks *Accipiter nisus.* J. Anim. Ecol. 51:327–341.

NEWTON, I., M. MARQUISS, AND D. MOSS. 1981. Age and breeding in Sparrowhawks. J. Anim. Ecol. 50: 839–853.

OLIPHANT, L. W., AND E. A. HAUG. 1985. Productivity, population density and rate of increase of an expanding Merlin population. Raptor Res. 19: 56–59.

OLIPHANT, L. W., AND S. MCTAGGART. 1977. Prey utilized by urban Merlins. Can. Field-Natur. 91: 190–192.

RAVELING, D. G. 1981. Survival, experience, and age in relation to breeding success of Canada Geese. J. Wildl. Manage. 45:817–829.

SAFINA, C. 1984. Selection for reduced male size in raptorial birds: the possible roles of female choice and mate guarding. Oikos 43:159–164.

SEARCY, W. A. 1979. Female choice of mates: a general model for birds and its application to Red-winged Blackbirds (*Agelaius phoeniceus*). Am. Nat. 114:77–100.

SEARCY, W. A. 1982. The evolutionary effects of mate selection. Ann. Rev. Ecol. Syst. 13:57–85.

SODHI, N. S., I. G. WARKENTIN, AND L. W. OLIPHANT. 1991. Hunting techniques and success rates of urban Merlins (*Falco columbarius*). J. Raptor Res. 25:127–131

TEMPLE, S. A. 1972. Sex and age characteristics of North American Merlins. Bird-Banding 43:191–196.

VILLAGE, A. 1985. Spring arrival times and assortative mating of kestrels in south Scotland. J. Anim. Ecol. 54:857–868.

WARKENTIN, I. G., AND P. C. JAMES. 1988. Nest-site selection by urban Merlins. Condor 90:734–738.

WARKENTIN, I. G., P. C. JAMES, AND L. W. OLIPHANT. 1990. Body morphometrics, age structure, and partial migration of urban Merlins. Auk 107:25–34.

WARKENTIN, I. G., P. C. JAMES, AND L. W. OLIPHANT. 1991. Influence of site fidelity on mate switching in Merlins (*Falco columbarius*). Auk 108:294–302.

WARKENTIN, I. G., AND L. W. OLIPHANT. 1990. Habitat use and foraging behaviour of urban Merlins (*Falco columbarius*) in winter. J. Zool. (London) 221:539–563.