

# BODY MORPHOMETRICS, AGE STRUCTURE, AND PARTIAL MIGRATION OF URBAN MERLINS

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**ABSTRACT.**—Saskatoon, Saskatchewan, has both a dense urban breeding population of Merlins (*Falco columbarius*) and a large wintering population. We censused Merlins in the city to determine population size. Individuals were trapped to identify banded birds and to obtain sex, age, and body-measurement data. We collected data during the breeding seasons and winters of 1985 to 1988. The wintering population, which varied from 22 to 38 birds, consisted almost entirely of locally hatched birds; only 4 of 303 Merlins seen during the four winters of this study were confirmed to be unbanded. Males predominated in the winter-trapped sample (32 of 55) but not significantly so. There was a significant difference in the age distribution of the sexes. Most males (29 of 32) were 3 years old or younger, and most females (12 of 23) were 4 years old or older. Body mass of adults trapped in winter was significantly higher (10.0% for males, 5.3% for females) than those of nonmigrants trapped during the breeding season. Yearling males were 7.6% heavier than breeding yearlings. Yearling female masses were significantly lower (8.7%) in winter than during the breeding season. Of 45 birds trapped in winter, 20 subsequently bred in the city. These birds occupied preferred nesting sites (those showing more consistent occupancy) more often than would be expected by chance. Nests involving a nonmigratory male tended to be more productive than those with a presumed migratory male. We suggest that increased familiarity with the breeding area may convey some advantage to nonmigratory males. Recruitment into the breeding population did not vary at a statistically significant level with migrant/nonmigrant behavior. Only 1 of 15 yearling males, and 0 of 9 yearling females, caught in winter obtained a breeding territory the next spring, even though yearlings made up 21% of the breeding population during our study. Wintering Merlins had a much greater tendency to have offspring that also wintered; individuals presumed to be migratory did not. This implies a genetic component to the development of a resident nonmigratory population. Received 10 January 1989, accepted 3 July 1989.

THE north-temperate zone is characterized by wide seasonal variation in climatic and biotic environmental factors. Winters in these regions are thermally stressful periods during which the food resources of most birds are substantially reduced. Consequently, winter populations of resident species may be limited on their breeding grounds (Lack 1954: 243, Fretwell 1972: 166, Jansson et al. 1981, Brittingham and Temple 1988). In response to winter conditions, individuals may either migrate or remain and adapt to the reduced resources and lower temperatures. As a basis for whether or not an individual will migrate, Lack (1954: 244) sug-

gested a cost-benefit model for the evolution of migratory strategies. If the costs of staying in the breeding area are greater than the benefits (measured in survival and reproductive success), selection should favor migration. Conversely, if the costs of migration exceed the benefits of staying, then selection should favor remaining in the breeding area. When the winter climate is constantly and predictably severe, an obligate migratory strategy would be favored. However, where the winter climate is severe only periodically and these periods are unpredictable, partial migration may develop. In *partially migratory* populations, some individuals stay in the breeding area while others migrate (Lack 1944, Gauthreaux 1982).

Four distinct hypotheses have been proposed to account for the patterns in migratory behavior which have developed in partially migra-

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tory populations (see reviews by Gauthreaux 1982, Ketterson and Nolan 1983, Berthold 1984). According to the *body-size hypothesis*, differences in fasting endurance, due to the higher proportion of energy stores in larger individuals, force a greater number of smaller members of the population to migrate than larger individuals (Ketterson and Nolan 1976). With the *dominance hypothesis*, intraspecific competition for resources will force subordinate individuals to migrate in light of either expected or actual contests (Gauthreaux 1978). The *arrival-time hypothesis* predicts that those members of the sex or age class that must compete for breeding-ground resources winter closer to, or on, the breeding grounds, while other classes migrate (Myers 1981). Based on the *genetic hypothesis*, partially migratory populations will consist of both sedentary and migratory individuals that differ in their genetic background for the migratory trait (Lack 1944; Berthold and Querner 1981, 1982).

Saskatoon, Saskatchewan (52°07'N, 106°38'W), has both a dense urban breeding population of Merlins (*Falco columbarius*) and a large wintering population (Oliphant 1974, Oliphant and Haug 1985, James et al. 1987). Since 1970, when the first Merlin nest was found in the city (Houston and Schmidt 1981), the breeding population has grown to 25 pairs in 1988 (unpubl. data). Richardson's Merlin (*F. c. richardsonii*), the subspecies of the North American prairies, formerly wintered in an area bounded by Colorado, Wyoming, and California (AOU 1957). Recently, a partially migratory strategy has developed among individuals of this subspecies. The result has been a northward expansion of the wintering range to include many towns and cities at the northern limit of its breeding range (AOU 1983, James et al. 1987). The earliest records of Richardson's Merlin wintering in Alberta and Saskatchewan were in 1922 (W. Rowan, University of Alberta Archives) and 1948 (Roy 1956), respectively. Analysis of Christmas Bird Count data revealed significant increases in the number of Richardson's Merlins that wintered in the four major cities on the Canadian prairies between 1957 and 1983 (James et al. 1987). Merlins have wintered in substantial numbers in Saskatoon only since the mid- to late 1960s (Oliphant 1974, Houston and Schmidt 1981, James et al. 1987). The sex and age class characteristics of these populations were previously unknown.

We examined the morphometric and age characteristics of the nonmigratory Merlins resident in Saskatoon, and we compared them with those characteristics in the presumed migratory segment of the breeding population. Data on body mass of North American Merlins are limited, except for those collected by Clark (1985) from *F. c. columbarius* migrating past Cape May, New Jersey, and a few scattered reports in the literature (Slipp 1942, Craighead and Craighead 1956, Oliphant 1974, Snyder and Wiley 1976). Published data on body measurements of Richardson's Merlin are restricted to two studies (Friedmann 1950 and Temple 1972). Information on the age structure of raptor populations is rare, and no data are available for that of a Merlin population. We evaluated the four hypotheses explaining partial migration, based on the characteristics of the Saskatoon Merlins.

#### METHODS

Merlins have nested continuously in Saskatoon since 1970, and a program to band nestlings has operated within the city since 1971 (Houston and Schmidt 1981, Oliphant and Haug 1985). Trapping and banding of breeding birds was sporadic until 1985. Since that time only 16 birds from 85 pairs have not been identified individually (1985–1988). Some of the Merlins trapped at nest sites were banded as nestlings in the city, whereas others were banded for the first time as breeders. Thirty-nine birds were caught and identified in more than one year. We used a tethered Great Horned Owl (*Bubo virginianus*) as a lure and mist-netted Merlins at the nest during the breeding season (generally in mid- to late June each year, when females were ending incubation or brooding young). Merlins occur regularly during winter and were recorded on 28 of 31 Christmas Bird Counts from 1957 to 1987. For this study, some initial trapping was done in the winter of 1983–1984. Beginning in November 1984, we traveled an 80-km route through the city by car at least weekly from 1 November to 28 February during the following four winters. The route passed known Merlin nest sites used in previous years and through areas of the city frequented by Merlins in previous winters (based on sightings). On average, it took 4 h to cover the route, but the time varied depending on the number of Merlins seen. The route was driven in two 40-km sections at various times of the day, but >80% of the runs began just after sunrise or within 2–3 h of sunset. We attempted to trap all Merlins seen during the survey using a dho gaza net (0.8 × 2.0 m) modified from the design of Clark (1981) to be freestanding, with two tethered House Sparrows (*Passer domesticus*) used as lures.

Male and female Merlins were easily sexed in the hand because of the high degree of sexual dimor-

TABLE 1. Measurements ( $\bar{x} \pm SE$ ) of male Merlins in Saskatoon, Saskatchewan. Numbers of individuals are in parentheses; \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ .

	Migratory		Nonmigratory		
	Yearling summer	Adult summer <sup>a</sup>	Yearling winter <sup>b</sup>	Adult winter	Adult summer <sup>c</sup>
Weight (g)	167.8 $\pm$ 3.7 (10)	166.9 $\pm$ 2.3 (16)	180.5 $\pm$ 2.2 (15)*	190.1 $\pm$ 3.1 (7)	171.3 $\pm$ 3.4 (8)**
Total length (mm)	272.1 $\pm$ 2.2 (10)	272.9 $\pm$ 1.9 (15)	274.3 $\pm$ 1.8 (15)	276.2 $\pm$ 0.9 (6)	270.4 $\pm$ 2.8 (7)
Tail length (mm)	120.3 $\pm$ 0.8 (10)	121.6 $\pm$ 0.7 (14)	121.7 $\pm$ 0.8 (15)	121.7 $\pm$ 1.3 (7)	121.3 $\pm$ 1.1 (7)
Wing chord (mm)	197.8 $\pm$ 0.8 (10)	199.5 $\pm$ 0.8 (15)	200.7 $\pm$ 1.4 (15)	203.6 $\pm$ 0.7 (7)	198.4 $\pm$ 0.8 (7)***
Culmen (mm)	12.8 $\pm$ 0.1 (10)	12.4 $\pm$ 0.1 (15)***	12.1 $\pm$ 0.1 (15)	12.4 $\pm$ 0.3 (6)	13.3 $\pm$ 0.1 (7)*

<sup>a</sup> Significant differences indicated are between migratory and nonmigratory adults in summer.

<sup>b</sup> Significant differences indicated are between nonmigratory yearlings and adults in winter.

<sup>c</sup> Significant differences indicated are between nonmigratory adults in winter and summer.

phism. Yearling and adult males not banded as chicks were distinguished based on plumage characteristics (Friedmann 1950, Temple 1972). We are not confident in our ability to age females accurately based on the plumage criteria suggested by Temple (1972) because of inconsistencies in the absence or presence of blue-grey feathers on the rumps of yearling and adult females in this population. Therefore, we excluded all females banded after hatch year from age-related data analysis. Body mass was measured to the nearest gram using Pesola scales. We measured tail length (from point of emergence from the skin to tip of the tail), total length (from top of head to tip of the tail), and wing length (chord of the unflattened wing) to the nearest millimeter with metal wing rulers; and we measured culmen length to the nearest 0.1 mm using Vernier calipers (Baldwin et al. 1931). All measurements were taken by one person. Values reported are mean  $\pm$  standard error ( $\bar{x} \pm SE$ ), unless otherwise noted.

All Merlins were banded with USFWS aluminum leg bands. Starting in 1982, nestlings were banded on the opposite leg with year-specific aluminum color bands. We also marked birds caught in winter with individually color-coded plastic leg streamers. This enabled us to identify them in subsequent winter and summer surveys without recapture. The streamer was attached to a bird's leg by a standard falconer's jess attachment (Beebe 1976: 192) over the top of aluminum color bands, or the USFWS numbered band, so that the 8-mm-wide strip of material extended ca. 10 cm from the leg. We replaced the streamers of all birds retrapped in subsequent winter and summer trapping programs. In winter, the location and identifying features (leg streamer, USFWS band, and year-specific color bands) were noted for all Merlins found. Birds marked with a leg streamer could be distinguished from unmarked birds, either when perched or in flight. Positive identification of an individual, based on the color-coded leg streamer, was possible only with binoculars or spotting scope at appropriate

distances. We assumed that birds seen at any time during the study period (1 November to 28 February) spent that entire winter in the city. Population estimates in winter were based on the proportion of marked and unmarked birds seen during the survey runs (weighted mean; Begon 1979).

One possible advantage for Merlins that winter in Saskatoon is access to better quality breeding territories. We defined *nesting area* as an area which may include several alternate nest sites used in different years, and attempted to determine if site selection was random. Although nesting areas were often occupied for many years, Merlins seldom returned to the same nest site within an area. We subjectively assigned nests to nesting areas based on the clumping of locations for previous nestings. All nesting areas occupied in 4 or 5 of the previous 5 yr were considered consistently occupied *high grade* areas, whereas those areas used in  $\leq 3$  yr over the previous 5 yr were considered inconsistently occupied *low grade* areas (following Newton and Marquiss 1976). Productivity was based on the number of young banded in each successful nest. We assumed that birds which had reached an age to allow banding were likely to fledge.

Although it was possible to positively identify nonmigratory birds by trapping, not all Merlins that wintered in the city were trapped. As a result, the *migratory group* includes all those that actually do migrate, as well as some wintering birds.

## RESULTS

*Body morphometrics and age structure.*—When various body parameters were compared (Tables 1 and 2), there were few statistically significant differences between adults and yearlings, or migratory and nonmigratory birds. Adults were heavier than yearlings in winter (two-tailed Student's *t*-test,  $t = 5.91$ ,  $df = 16$ ,  $P < 0.001$  for females;  $t = 2.51$ ,  $df = 20$ ,  $P < 0.05$

TABLE 2. Measurements ( $\bar{x} \pm SE$ ) of female Merlins in Saskatoon, Saskatchewan. Numbers of individuals are in parentheses after values. \* =  $P < 0.05$ ; \*\*\* =  $P < 0.001$ .

	Migratory		Nonmigratory		
	Yearling summer	Adult summer <sup>a</sup>	Yearling winter <sup>b</sup>	Adult winter	Adult summer <sup>c</sup>
Weight (g)	260.6 $\pm$ 3.9 (5)	253.8 $\pm$ 2.0 (29)*	237.9 $\pm$ 6.1 (9)***	279.6 $\pm$ 2.9 (9)	265.5 $\pm$ 4.8 (14)*
Total length (mm)	299.2 $\pm$ 1.5 (5)	300.8 $\pm$ 1.1 (29)	301.2 $\pm$ 2.0 (9)	308.0 $\pm$ 2.7 (8)	306.3 $\pm$ 2.2 (11)
Tail length (mm)	134.2 $\pm$ 1.5 (5)	134.1 $\pm$ 0.6 (29)	136.3 $\pm$ 1.7 (9)	135.8 $\pm$ 0.7 (8)	134.7 $\pm$ 0.7 (11)
Wing chord (mm)	216.4 $\pm$ 1.4 (5)	218.8 $\pm$ 0.9 (29)	218.8 $\pm$ 1.4 (9)	223.5 $\pm$ 1.8 (8)	219.4 $\pm$ 1.1 (11)
Culmen (mm)	15.4 $\pm$ 0.2 (5)	14.8 $\pm$ 0.1 (29)	14.2 $\pm$ 0.1 (9)	14.1 $\pm$ 0.3 (7)	15.2 $\pm$ 0.2 (11)*

<sup>a</sup> Significant differences indicated are between migratory and nonmigratory adults in summer.

<sup>b</sup> Significant differences indicated are between nonmigratory yearlings and adults in winter.

<sup>c</sup> Significant differences indicated are between nonmigratory adults in winter and summer.

for males; comparison b, Tables 1 and 2). Non-migratory females (comparison a, Tables 1 and 2) remained heavier than their migrant counterparts ( $t = 2.68$ ,  $df = 41$ ,  $P < 0.05$ ), but males were not different ( $t = 1.10$ ,  $df = 22$ ,  $P > 0.20$ ). Similar comparisons were not possible for non-migrant yearlings. Although there were yearlings in the breeding population, 0 of the 9 female yearlings trapped during winter in the city was known to breed. Only 1 of the 15 yearling males trapped as a wintering bird bred the following spring in the city. Adults trapped in winter were significantly heavier than the birds of this group in summer (comparison c, Tables 1 and 2; females,  $t = 2.20$ ,  $df = 21$ ,  $P < 0.05$ ; males,  $t = 4.03$ ,  $df = 13$ ,  $P < 0.01$ ). Yearling males showed a similar trend of higher winter mass (7.6% heavier) when compared with those of breeding yearlings ( $t = 3.18$ ,  $df = 23$ ,  $P < 0.01$ ). In contrast, yearling females were significantly lighter (8.1%) in winter when compared with breeding yearlings ( $t = -2.46$ ,  $df = 12$ ,  $P < 0.05$ ).

Although the overall sex ratio among trapped wintering birds (including known-age birds and birds originally banded as adults) did not differ from 1:1 ( $\chi^2 = 0.25$ ,  $df = 1$ ,  $P > 0.10$ ), there were age-related differences apparent in the wintering population. Birds up to 3 yr old were found in the wintering population which had not previously bred. We compared the distribution of birds among age classes ( $\leq 3$  and  $4+$  yr) and sex in a contingency table. The relative distributions were significantly different from that based on chance alone ( $\chi^2 = 12.32$ ,  $df = 1$ ,  $P < 0.001$ ), with more younger males ( $\leq 3$  yr) than younger females, and more older females ( $4+$  yr) than

older males, present during our study (Table 3). The breeding population showed no such differences ( $\chi^2 = 2.31$ ,  $df = 1$ ,  $P > 0.10$ ).

We found proportionately more yearlings in the wintering population than we found to breed in their first summer ( $\chi^2 = 7.92$ ,  $df = 1$ ,  $P < 0.01$ ). However, if compared with the hypothetical population structure present at fledging (which assumes no proportional difference in migratory behavior between age or sex classes, no floaters, and an average of four young produced per successful nest—see Results), the minimum adult to yearling ratio would be ca. 1:2. Instead, we found 2.6 times more adults than expected from this hypothetical situation. Hatch-year birds undoubtedly experience high mortality after fledging. In Eurasian Sparrowhawks (*Accipiter nisus*), Newton et al. (1983) found high mortality during the first 2 months of independent life. Maximum annual mortality for the breeding Merlins in Saskatoon was estimated at 29% (James et al. 1989). If Merlins in the study population have a first-year mortality in the 50–74% range experienced by other falcons (Newton 1979: 368), this alone could explain the high adult-to-yearling ratio without having to invoke either a floater population of such proportions, or differences in migratory behavior between the two age groups. A floating population might have a slight impact on this ratio, but we emphasize that the Saskatoon population is still increasing each year (Oliphant and Haug 1985, unpubl. data), and a large nonbreeding population is unlikely.

*Color-marking and trapping.*—We color-marked 45 Merlins over the five winters; 37 of these birds were of known age, 8 had been banded

TABLE 3. Age structure of population for known-age Merlins breeding and wintering in Saskatoon, Saskatchewan, Canada. Sample sizes are in parentheses.

Years	Summer		Winter	
	Male (64)	Female (45)	Male (32)	Female (23)
1	13	10	15	9
2	25	9	8	1
3	8	7	6	1
4	5	8	2	2
5	5	5	0	4
6+	8	6	1	6

previously as adults, and 9 were seen in more than one winter. The maximum known longevity of a marker not replaced was 2 yr 3 months; 1 bird, retrapped 1 yr 6 months after initial trapping in winter, had lost its streamer. No other birds were known to have lost their leg streamer, and there were no apparent adverse effects from these markers. The majority of the Merlins that winter in Saskatoon appear to be year-round residents. Only 4 of the 303 sightings made over four winters, where the bird's legs could be clearly seen or the bird was color-marked, involved unbanded birds. Of 45 Merlins trapped in winter during the study, 20 appeared at least once in the breeding populations of 1985-1988.

Although trapping in summer was comprehensive, with the vast majority of breeding Merlins caught and identified, we tested for possible bias in the method used for winter trapping. Because the lure was potential prey, there may have been a greater likelihood of capturing yearling birds because of their relative inexperience at hunting when compared with adults. However, a comparison of birds trapped with those subsequently resighted through the remainder of that winter revealed no difference in the ratios of yearlings to adults ( $\chi^2 = 0.23$ ,  $df = 1$ ,  $P > 0.10$ ) or males to females ( $\chi^2 = 0.06$ ,  $df = 1$ ,  $P > 0.10$ ). This suggests that sampling was essentially random. Because the plumage of adult males is distinctive from that of all other age classes, sightings of adult males were used as an additional test for potential trapping bias. There was no significant difference between the proportion of adult males among all birds caught and the proportion of adult males among all birds sighted during population surveys each winter ( $\chi^2 = 0.46$ ,  $df = 1$ ,  $P > 0.10$ ). Further, some birds seen in subse-

TABLE 4. Population estimates of Merlins wintering in Saskatoon, Saskatchewan, based on the marked and unmarked birds seen during surveys. Percentage of yearlings is the percentage of all wintering birds (trapped or identified by markers attached in previous winters) that were yearlings.

Period	Estimated population	Number marked (%)	Estimated no. yearlings (%)	Estimated no. adults
1984-1985	38	12 (32)	22 (58.3)	16
1985-1986	22	11 (50)	3 (18.2)	19
1986-1987	29	17 (59)	9 (29.4)	20
1987-1988	33	16 (48)	17.5 (50.0)	17.5

quent winters were identified simply from the leg streamer and did not need to be retrapped. The use of baited traps to catch birds in winter may also have tended to trap birds in poorer condition than the population in general. It was difficult to test for this possible bias.

Population estimates for the four winter surveys varied from 22 to 38 Merlins in the city (Table 4). There was an apparent association between the number of yearlings present and the population level. Whereas the number of adults marked each winter remained relatively stable, the percentage of all birds marked each winter (either marked in a previous winter and resighted, or actually captured that winter) that were yearlings was directly proportional to the population level (Spearman's correlation coefficient,  $r_s = 1.0$ ,  $P = 0.05$ ).

*Breeding biology of migratory and nonmigratory Merlins.*—During the four breeding seasons concurrent with this wintering study, nonmigratory Merlins nested in high-quality areas at levels (13/20; 65%) significantly higher than found in presumed migratory birds (37/98; 38%) ( $\chi^2 = 3.94$ ,  $df = 1$ ,  $P < 0.05$ ). There was, however, no statistical difference between high- and low-grade areas in productivity, as measured in the number of young per successful nest. Productivity in 36 high-grade areas equaled  $4.1 \pm 0.2$  and that in 51 low-grade areas equaled  $4.1 \pm 0.1$ . The productivity of nests in which the male was nonmigratory and the female was presumed to be migratory ( $4.8 \pm 0.1$ ,  $n = 12$ ) was significantly higher than the productivity of nests in which both birds were presumed to be migratory ( $4.0 \pm 0.1$ ,  $n = 56$ ;  $t = 2.71$ ,  $df = 66$ ,  $P < 0.01$ ), as well as nests in which both birds were nonmigratory ( $4.0 \pm 0.4$ ,  $n = 5$ ;  $t = 2.19$ ,  $df = 15$ ,  $P < 0.05$ ). The relationship between

productivity in nests with a nonmigratory male and a presumed migratory female, and that of nests in which the male was presumed to be migratory and the female was nonmigratory ( $4.3 \pm 0.2$ ,  $n = 14$ ;  $t = 1.77$ ,  $df = 24$ ,  $P < 0.10$ ), was not significantly different. All other comparisons between the various groups (both birds nonmigratory and both presumed migratory, both nonmigratory and pairs in which only the female was nonmigratory) did not differ significantly. Eggs in nests with at least one nonmigrant parent hatched significantly earlier than did those in the nests of migratory birds (day  $160.0 \pm 0.9$ ,  $n = 30$ , and day  $164.0 \pm 1.0$ ,  $n = 54$ , respectively; day 1 = 1 January;  $t = 2.61$ ,  $df = 82$ ,  $P < 0.05$ ).

#### DISCUSSION

*Body morphometrics.*—There are few diurnal raptors for which data on body mass through the year are available. Those of Newton et al. (1983) for body mass of Eurasian Sparrowhawks differ sharply from Merlins in the direction and extent of mass change. We compared masses in the winter (November–February) with values from June when females of both species had finished egg laying, and were near the end of incubating eggs or were brooding young. Sparrowhawk winter masses dropped 12.9% (41.1 g) and 0.7% (1.1 g) from levels in June for females and males, respectively (Newton et al. 1983). While male sparrowhawks showed little mass variation, female body mass fluctuated by as much as 33% through the year (Newton et al. 1983). This difference was attributed to the females' role in breeding and the necessity for the storage of large body reserves before reproduction. Merlins resident in Saskatoon require large energy reserves both to reproduce and to withstand severe winter conditions. Greater mass would enable birds to withstand inclement weather, when hunting is impossible, for longer periods. We found significant changes in the mean seasonal masses of nonmigratory Merlins (comparison c, Tables 1 and 2); adult females were 5.3% (14.1 g), and adult males 10.0% (18.8 g), heavier in winter than in mid- to late June. Yearling males displayed similar trends with an average mass in winter 7.6% (12.7 g) heavier than in the breeding season, but yearling females were 8.7% (22.7 g) lighter in winter than those caught during breeding.

There are apparent parallels between the level of recruitment from the wintering yearling population and body condition, as reflected by the comparison of body mass between the sexes in summer and winter. Whereas yearling males have higher winter masses than breeding yearlings, and 5 of 15 birds caught in winter eventually bred in Saskatoon, female yearlings had lower winter masses than breeding female yearlings, and 0 of the 9 birds caught in winter was found breeding in subsequent years.

Yearling Merlins made up 21% (23 of 109 birds) of the breeding population during this study, but only 4.2% (1 of 24) of the Merlins caught wintering as yearlings bred in their first full summer. This value was not significantly different from the estimated number of presumed migrant Merlins entering the breeding population as yearlings. We do not have values for first-year mortality in this population, but based on a reported average of yearling mortality values for falcons ( $\bar{x} = 62.5\%$ , range 50–74%,  $n = 10$  studies; Newton 1979: 368) and subtracting all known nonmigrant Merlins from the calculation, recruitment from this population of presumed migrants as yearlings was 12.0% (13 of 108; Fisher exact test,  $P = 0.46$ ). Among Merlins available to enter the population as second-year birds, the differences between recruitment of presumed migrants (estimate of recruitment based on an additional second-year mortality of 29%; James et al. 1989; 7 of 53 presumed migrants; 13.2%), and nonmigrant birds (6 of 18; 33.3%) approached statistical significance (Fisher exact test,  $P = 0.08$ ).

The low level of recruitment among wintering yearlings may reflect higher costs of wintering for inexperienced birds at northern latitudes when compared with migratory individuals and, particularly among females, a consequent lower survival rate. But the appearance later of wintering males in the breeding population also suggests that (at least for males) survival of the first winter facilitates future wintering and breeding in the city. The advantages, due to familiarity with the city, for resident birds in future breeding attempts may make up for the costs of wintering in Saskatoon and opportunities lost during the first summer because of insufficient energy reserves for breeding. The lower masses among female yearlings may also explain why proportionally fewer younger females appear to breed than younger males. Perhaps, because of factors such as

the slower development of hunting skills, it is more difficult for yearling female Merlins to survive winters at northern latitudes than for males.

*Partial migration.*—Among falcons which exhibit partial migration (Eurasian Kestrel, *Falco tinnunculus*, Village 1985; Gyrfalcon, *F. rusticolus*, Platt 1976; Peregrine Falcon, *F. peregrinus*, Mearns 1982), males tend to remain on the breeding grounds through winter more often than females, and adults generally outnumber yearlings (Newton 1979: 184). The age structure of the wintering Merlin population in Saskatoon (Table 3) contrasted with this generalization and with data from the only other North American falcon (the Gyrfalcon), which remains on the breeding grounds at higher latitudes. Unlike the Merlin, only adult Gyrfalcons are found in the western Canadian Arctic during winter (Platt 1976). The overall age structure of the winter Merlin population in Saskatoon, with younger males and older females over-represented, did not follow the expected patterns.

Competition for food or some other winter resource is the basis for the *dominance hypothesis* (Gauthreaux 1982); the predicted outcome of competitive interactions among wintering Merlins would be a high proportion of breeding adults in the nonmigratory population with more females than males present (Gauthreaux 1985). The sex ratio and age structure of wintering Merlins in Saskatoon did not support the dominance hypothesis, because only 56% were adults (and 55% of these were males). The reproductive status of a bird, breeding vs. non-breeding, may indicate its dominance in the population. Of the 29 males of 3 yr or less seen in the city in winter, 15 were yearlings who had not yet had the opportunity to breed. In addition, 7 of 8 two-year-olds and 3 of 6 three-year-olds had not been captured previously as breeders in the city. We believe that the majority of birds in this group were socially subordinate.

Because nonmigratory birds tended to be hatched earlier than presumed migrants, they also may have fledged earlier and gained the extra mass which would be advantageous in contesting any resources with other Merlins. Unfortunately, precise dates of fledging were not known. Data on yearling mass in early autumn, before the departure of migrants, are needed also to determine if this short period is

sufficient for the nonmigratory Merlins to develop a size advantage over migrants. Among females specifically, dominance may produce the skewed ratio that favors older birds and leaves fewer young females than expected by chance. More yearling females may be forced out in winter because of their significantly smaller size when compared with nonmigratory adult females, but this interpretation must be qualified by the fact that, among most birds (except the Anatidae), females tend to disperse farther from their natal area than do males (Greenwood and Harvey 1982).

Higher winter mass among birds living in temperate areas is well documented (King and Farner 1966, Newton and Evans 1966). If energy stores are proportional to body size within a species, larger individuals should have greater energy reserves relative to their basal metabolic rate because metabolic rate does not rise proportionately with body size (Calder 1974). Thus the *body-size hypothesis* predicts that female Merlins, with larger bodies to buffer them from the cold, are more likely to remain than males with their higher surface-to-volume ratio. But this leaves unexplained the large number of yearling males, which have the lowest mass among wintering birds. Additionally, this hypothesis predicts that migrant Merlins should be smaller than nonmigrants. But, while presumed migratory adults had lower body mass in females and smaller culmen in males during the breeding season than did their nonmigratory counterparts, there were no other significant morphometric differences (Tables 1 and 2).

Male Merlins have a greater attachment to the breeding site than females. Males return earlier each spring (Newton et al. 1978) and show greater nest-site fidelity than females (James et al. 1989). The *arrival-time hypothesis* predicts that breeding adult males should predominate in the nonmigratory population. This hypothesis was not supported by the age structure data.

Observations and breeding experiments with several European passerines have demonstrated a genetic factor in migratory behavior (Berthold and Querner 1982, Biebach 1983, Schwabl 1983, Berthold 1988), although there is some question as to the exact mechanism by which migratory and nonmigratory behavior might be selected (Lundberg 1987). Genetic influence among wintering Merlins in Saskatoon is suggested by the fact that, of 20 birds trapped in winter whose

parents were known, 19 had at least one parent that had been captured in the city during winter. These values were compared with the parentage of 13 Merlins (hatched in the city) that returned to breed in Saskatoon but had not been caught during winter. Only 31% (4/13) of these presumed migratory birds had at least one known nonmigratory parent. This was significantly different from the parentage of nonmigratory Merlins (Fisher exact test,  $P < 0.001$ ). Further, because some of these presumed migrants with nonmigrant parents may themselves have actually wintered in the city without being detected, this is a conservative estimate of their parentage. Other explanations of this pattern in parentage include the potential of a learned component, in which offspring mimic the behavior of their parents. Two lines of evidence suggest that this is not the primary mechanism governing migratory behavior. First is the lack of any indication in the literature that Merlins migrate in family groups or groups of any nature. The second is the relative absence of breeding adult males in the winter population. The body-size hypothesis also may explain the pattern described above. If body size is a heritable trait, then the body-size hypothesis predicts that nonmigratory birds will be larger than migratory birds. In addition, the offspring of nonmigrants also should be larger and so tend to be nonmigratory as well. As mentioned earlier, there were no indications that nonmigrant Merlins were larger than their migrant counterparts.

The advantages to Merlins of wintering in Saskatoon are unclear in terms of reproductive success. Nonmigratory birds tended to occupy high-grade nesting areas more frequently than migratory birds, but there was no evidence that productivity at these sites was any better than in low-grade nesting areas. Site quality may represent some aspect less easily quantified such as the ease of hunting due to prey availability or abundance. Although their young hatched significantly earlier than those of migratory parents, the biological significance of this 4-day difference was uncertain.

Presumably one advantage of year-round residency was access to preferred nest sites, enabling nonmigratory breeders to acquire better quality nesting areas than migrant birds. Merlins moved from winter home ranges and associated former nesting area into new nesting areas in late winter (February–March), and some

courtship activity by nonmigratory birds was observed as early as the first week of February (Warkentin and Oliphant 1990). Nonmigratory birds probably had a greater familiarity with their home range than migratory birds, which arrived later in spring. Such familiarity would be particularly beneficial to males (considering that they provide most of the prey for the female and nestlings from courtship through the second week after hatch). This could enable them to exploit their home range's resources more efficiently, and subsequently to increase their reproductive output, to increase reproductive success by producing fledglings in better condition, to decrease the energy expended in supplying nestlings, or some combination of these. The significantly greater productivity of nests involving nonmigratory males, when compared with other combinations of parents, suggests that this familiarity leads to increased reproductive output. The lack of an apparent advantage for nests in which both parents were nonmigrant may partly be an artifact of small sample size for this type of pairing ( $n = 5$ ). An additional comparison of productivity in all nests that have nonmigratory males with productivity in those that do not (regardless of female strategy) approaches statistical significance (nonmigratory males,  $4.5 \pm 0.2$ ,  $n = 17$ ; migratory males,  $4.1 \pm 0.1$ ,  $n = 70$ ;  $t = 1.98$ ,  $df = 85$ ,  $0.10 > P > 0.05$ ). Information on the lifetime reproductive output of migrant vs. nonmigrant birds may more accurately reflect the reproductive advantages of wintering in Saskatoon.

Without more extensive information on the migratory portion of this population on their wintering grounds and the problems encountered on migration, it is difficult to discuss the disadvantages of wintering on the breeding grounds. Certainly survival through the winter must be a key element. The age structure (Table 3) may in fact be interpreted (particularly for males) to suggest higher mortality rates among nonmigrants than migrants. However, those that are successful appear more likely to secure a breeding site, as implied by their higher recruitment levels when compared with presumed migrants (see above). The potential exists for high mortality rates among resident birds during especially severe winter weather over prolonged periods, or from sudden changes in food-supply levels. There is a relatively depauperate prey base (in terms of species diversity)



for Merlins wintering in Saskatoon. This means that a sudden dramatic decline in the abundance or availability of House Sparrows (which along with Bohemian Waxwings, *Bombycilla garrulus*, made up 89.5% of all prey observed in a four-winter study; Warkentin and Oliphant 1990) in one winter could lead to heavy mortality. Prey switching would be difficult considering the low abundance of prey other than the Bohemian Waxwing (which itself varies extensively in abundance from year to year). Bohemian Waxwings ranged from 16.5 per party-mile (1983, Christmas Bird Count) to 2.8 birds per party-mile (December 1986).

Merlins wintered consistently in small numbers in the towns and cities of the northern Great Plains for a decade or more before they began to breed in these urban centers in large numbers. This wintering pattern, and the consequent habituation to the urban environment, may have led to the development of extensive urban breeding populations. With the exception of Rowan's 1922 observation of wintering Merlins, there are no extant records of Merlins wintering until the 1940s (W. Rowan, University of Alberta Archives; Roy 1956). Since that time these wintering populations have increased gradually (James et al. 1987). The development of a wintering Merlin population in Saskatoon has occurred slowly over the last 30 yr, at apparently different rates for males and females. Although there is no previous detailed study of this wintering population, it has been possible to detect changes in the sex ratio because of the sexually dimorphic plumage of the Merlin. During the months of November through February for 3 yr beginning in 1974, only 8% (3 of 36) of Merlins seen in the city were adult males (Oliphant unpubl. data). In contrast, adult males made up 20% (99 of 501) of sightings during this study. Because wintering by Merlins in general in the northern Great Plains is a fairly recent phenomenon, a stable pattern may not have developed. The lack of an equilibrium situation may explain why the overall age structure for wintering Merlins did not fit the predictions arising from the body-size, arrival-time, or dominance hypotheses regarding partial migration. If there is a genetic component, as we suggest, it may take some time to build up levels of different age groups—particularly among males, where the tradition to winter in Saskatoon is even more recent than for females. With time, a clearer picture of the

ultimate and proximate causes for partial migration in this population may emerge.

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