Short Communications and Commentaries

The Auk 114(2):288–290, 1997

Age of First Breeding in Merlins (*Falco columbarius*)

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Age of first breeding is an important aspect of the study of population dynamics (Harris et al. 1994). The proportion of individuals that die without breeding increases each year that breeding is delayed, strongly influencing individual lifetime production of young (e.g. Sternberg 1989). Furthermore, the presence of nonbreeding individuals has important implications for the stability and persistence of populations by providing replacements for vacancies created by the loss of established breeders (see Porter and Coulson 1987). Determination of the age of first breeding is made difficult by low return rates of marked fledglings (Court et al. 1989). This problem is especially prevalent in female birds because they tend to exhibit lower natal philopatry than males (Greenwood 1980). Moreover, long-lived species often exhibit prolonged periods of delayed maturity (Newton 1989), which poses special problems by demanding long-term observations (Harris et al. 1994). Thus, accurate estimates of the age of first breeding are difficult to obtain.

Our long-term study of nesting Merlins (*Falco columbarius*) enabled us to examine age of first breeding in both sexes. From 1987 to 1995, we used captures and color-band sightings to determine the age of breeding Merlins that had been banded as nestlings. To our knowledge, these data provide the first description of age of first breeding for this species.

Study area and methods.—Merlins have nested within the city of Saskatoon, Saskatchewan, Canada (52°07′N, 106°38′W) since the late 1960s and have been monitored continuously since 1971 (Oliphant and Haug 1985). The species shows a marked preference for breeding in old American Crow (*Corvus brachyrhynchos*) nests in the numerous spruce (*Picea* spp.) trees scattered throughout the city (Warkentin and James 1988). The high abundance of House Sparrows (*Passer domesticus*), the primary prey species of Merlins in Saskatoon, appears to have contributed to the establishment of Merlins in this urban habitat (Sodhi 1992).

Merlin nestlings have been banded with year-specific combinations of numbered aluminum and color bands each year since 1982 (Warkentin et al. 1990). Beginning in 1985, we attempted to capture all breeding birds each year. Age of first breeding was tabulated from 1987 onwards so that birds breeding for the first time as late as age three could be detected. Based on these banded nestlings, we used two methods to determine age of first breeding. First-time captures of banded breeders were used as an approximation of the age of first breeding (e.g. Newton et al. 1983, Court et al. 1989, Porter 1988). This technique is reliable when capture success is high. In addition, we determined band combinations of breeding birds that were not captured (observed with a spotting scope [22×] or binoculars [10×]) to generate an age distribution of breeders. The number of birds breeding at one, two, and three years was pooled across years to form a life table. This method provided an estimate of age of first breeding without the influence of trapping bias. All yearling breeders obviously were first-time breeders. The number of birds breeding for the first time at ages two and three was calculated by subtracting the number of birds surviving from the previous age class, using an annual survivorship estimate of 69% (James et al. 1989).

Because we trapped adults in mid- to late June (see Warkentin et al. 1990), some birds may have undergone failed nesting attempts before we could catch them. Therefore, our results refer to birds that nested successfully until at least mid-June. An additional bias would have been introduced if nesting failures were dependent on the age of breeders. We tested this by comparing the distribution of nesting failures (five males, seven females) among age classes one, two, and three with the frequency distribution of breeders in each age class. The frequency of nesting failures was independent of the age class of breeders for both sexes (males: $\chi^2 = 0.35$, df = 2, $P = 0.84$; females: $\chi^2 = 1.60$, df = 2, $P = 0.45$).

Results and discussion.—Based on first-time captures, age of first breeding was determined for 52 males and

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TABLE 1. Age of first breeding for 52 male and 20 female Merlins captured in Saskatoon, Saskatchewan.

Age of first breeding (years)	Year of first capture									Total
	1987	1988	1989	1990	1991	1992	1993	1994	1995	
				Males						
1	3	2	2	1	1	4	1			14
2	1	6	3	4	4	3	2	5	1	29
3			1				2	2	3	8
4			1							1
				Females						
1	2	3		3		2	3		3	16
2		1	1		1					3
3									1	1

20 females (Table 1). On average, we caught 57.2 ± SD of 19.4% of males and 84.5 ± 13.7% of females in each year. Given the capture success of females, it would be unlikely that a three-year-old could have bred in our study area undetected by us in the previous two years ($P = 0.024$). However, the probability of missing a male in the previous two years is considerably higher ($P = 0.18$) and could result in an overestimate of the age of first breeding. For all years combined, 27% of males bred for the first time at age one, 56% at age two, 15% at age three, and 2% at age four. On average, male Merlins entered the breeding population at 1.9 ± 0.7 years of age. For females, 80% were recorded breeding for the first time at age one, 15% at age two, and 5% at age three ($\bar{x} = 1.3 \pm 0.6$ years). The ratio of birds entering the breeding population at age one versus age two was significantly lower in males (1:2.1) than in females (5.3:1; Fisher exact test, $P < 0.001$, $n = 62$).

The estimated age distribution of breeding birds was based on observations of 93 males and 35 females (Table 2). On average, we identified 85.4 ± 10.6% of breeding males and 95.2 ± 5.1% of breeding females (with or without capture) in each year. For males, 19 (37%) bred for the first time at age one, 29 (57%) at age two, and 3 (6%) at age three ($\bar{x} = 1.7 \pm 0.6$ years). For females, 17 (81%) bred for the first time at age one, none at age two, and 4 (19%) at age three ($\bar{x} = 1.4 \pm 0.8$ years). These estimates also confirmed that the ratio of birds entering the breeding population at age one versus age two was significantly lower in males (1:1.53) than in females (1:0; Fisher exact test, $P < 0.00001$, $n = 65$).

Estimates of the age of first breeding based on first-time captures did not differ significantly from those based on the age distribution of observed breeders (males: $\chi^2 = 3.03$, df = 2, $P = 0.22$; females: $\chi^2 = 4.81$, df = 2, $P = 0.09$). Therefore, the estimates of age of first breeding based on first-time captures were not seriously affected by the fact that some birds may have been missed in previous years. It is possible that capture success differed among age classes. Based on the number of unsuccessful versus successful capture attempts of banded known-age birds, however, catchability was independent of age class for both sexes (males: $G = 0.006$, df = 2, $P = 0.997$; females: $G = 0.016$, df = 2, $P = 0.992$; Table 2).

A longer delay in the age of first breeding for males compared with females has been reported for many raptors (see Newton 1979), including Gyrfalcons (*Falco rusticolus*; Nielsen 1991) and Peregrine Falcons (*Falco peregrinus*; Mearns and Newton 1984, Heyne and Wegner 1991). The difference in age of first breeding between males and females reported for these species was comparable to that for Merlins.

Some non-raptorial species also show a tendency for male-biased delay in age of first breeding, including Common Murres (*Uria aalge*; Harris et al. 1994), Thick-billed Murres (*Uria lomvia*; Gaston et al. 1994), and Semipalmated Sandpipers (*Calidris pusilla*; Gratto 1988). None of these species exhibited differences in age of first breeding between males and females as pronounced as that observed in Merlins. In contrast to the species noted above, males appear to initiate breeding at younger ages than females in many other species of seabirds (Nelson 1988).

One possible explanation for sex differences in age of first breeding is differential mortality (Wooller and Coulson 1977, Nelson 1988). In such cases, higher mortality in one sex may create a larger number of vacant territories for prospective breeders. Although it is possible that female Merlins initiate breeding earlier because they experience higher mortality, we have no data to support this hypothesis (see James et al. 1989). A more likely explanation is that male Merlins of age

TABLE 2. Number of male and female Merlins observed breeding each year by age class and number captured successfully. Data include birds breeding for the first time as well as experienced breeders captured previously.

	Age of males (years)			Age of females (years)		
	1	2	3	1	2	3
No. observed	19	42	32	17	8	10
No. caught	14	31	23	16	8	10

two and older are competitively superior to yearlings. The major investment in breeding made by male raptors in general, i.e. establishment and defense of territories, attraction of mates, and provisioning of food to mates and nestlings (Newton 1979), suggests that experience is a key component in determining when a male can breed successfully for the first time. In comparison, female Merlins experienced little delay in the age of first breeding, with more than 80% breeding for the first time as yearlings. This suggests that females of age two and older have no competitive advantage over yearlings. Under these conditions, we would expect the number of male territory holders to be one of the main factors limiting the number of breeding pairs.

Acknowledgments.—We thank T. Breen-Smith, B. Hanbridge, E. Labbe, G. Peat, H. Saunders, N. S. Sodhi, and P. Thompson for their assistance in the study and D. M. Becker, C. D. Marti, and R. N. Rosenfield for insightful comments on the manuscript. This study was supported by a Natural Sciences and Engineering Research Council of Canada grant to L.W.O and P.C.J., and by a University of Saskatchewan Graduate Teaching Fellowship to D.J.L.

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Received 12 July 1996, accepted 31 October 1996.
Associate Editor: J. S. Marks