

AGE-DEPENDENT BREEDING PERFORMANCE IN MERLINS (*FALCO COLUMBARIUS*)

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Abstract. We examined the effect of age on breeding performance in male and female Merlins (*Falco columbarius*) from a natural population using a long-term data set. In the analysis, we examined whether differences in chick hatch date and brood size associated with parents of different ages arose due to selection of superior individuals (differential mortality hypothesis) or to changes within individuals over time (inadequate experience hypothesis). In addition, we examined the effect of longevity on production of recruits and lifetime reproductive success (LRS). In both sexes, breeding performance improved with age. In females, this was mainly the result of disproportionate mortality of inferior breeders, with less evidence to support performance changes within individuals. Among males, changes in breeding performance with age were largely the result of improvements within individuals early in their life (between age 1 and 2+). Production of recruits was not dependent on parental age at the time of breeding for either sex. Recruit production and LRS were both influenced by longevity, so that longer-lived birds produced more offspring over their lifetimes and thereby had a greater probability of producing recruits. The differences between the sexes in terms of age-dependent breeding performance are likely a consequence of the differing roles the two parents play in reproduction. Male Merlins provide most of the food for the pair and their young during the breeding season, and changes in hunting skill with age may account for individual improvements in breeding performance.

Key words: age-dependent; breeding performance; differential mortality hypothesis; *Falco columbarius*; inadequate experience hypothesis; lifetime reproductive success; Merlin; recruitment; Saskatchewan.

INTRODUCTION

An understanding of age-dependent reproduction is acknowledged as an integral component for several subdisciplines of evolutionary ecology, such as life history theory and population dynamics. Most iteroparous animal species exhibit age-specific patterns of breeding performance (Forslund and Pärt 1995) and often breeding performance is higher among older individuals (Clutton-Brock 1988, Newton 1989*a, b*, Sæther 1990). Studies of birds over the past 30 yrs have shown significant relationships between age and clutch size (Klomp 1970, Ross 1980, Forslund and Larsson 1992), time of breeding (review in Perdeck and Cavé 1992), and the number of young fledged (Perrins and Moss 1974, Bryant 1979, Reese and Kadlec 1985). The general pattern is that breeding performance increases with age during early reproductive years to reach a high

point at midlife and then sometimes is followed by a decline in old age. Degenerative senescence in later life has been suggested in a number of bird studies (Coulson and Horobin 1976, Perrins 1979, Korpimäki 1988, Newton and Rothery 1997). Nevertheless, studies of lifetime reproductive success (LRS) in birds have shown that longevity is typically the most important contributor to an individual's lifetime reproductive output (reviewed in Newton 1989*a*).

In an excellent review, Forslund and Pärt (1995) describe three primary hypotheses to explain the general pattern of age-dependent reproduction: (1) the differential mortality hypothesis, (2) the constraint or breeding experience hypothesis, and (3) the restraint hypothesis. The differential mortality hypothesis predicts that individuals of different phenotypic quality differ in age of first reproduction or survival probability. This leads to a progressive appearance or disappearance of phenotypes as a cohort ages. The constraint hypothesis predicts that the breeding performance of young birds improves as they get older because they acquire or improve certain skills that positively affect reproduction. Under the restraint hypothesis, younger individuals abstain from or put less effort into breeding be-

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cause reproductive effort increases mortality (Williams 1966, Pugesek and Diem 1990). As birds age they invest more effort into current reproduction, presumably because future reproductive potential is shrinking. The constraint and restraint hypotheses both act within the individual, and most (if not all) studies have not been able to distinguish between them (Wooller et al. 1990, Forslund and Pärt 1995). Because it is so difficult to distinguish between constraint and restraint, we decided to encompass both within a new hypothesis we call the inadequate experience hypothesis.

In actuality, any of the hypotheses describing the relationship between age and breeding performance in birds can operate simultaneously within a population. Therefore, the central question regarding age-dependent breeding performance in birds remains as how much of the age-related trends observed in a population arise due to within-individual changes (inadequate experience) compared to between-individual differences (differential mortality).

The principal objective of this paper was to test the two major hypotheses concerning age and breeding performance in male and female Merlins (*Falco columbarius*). The Merlin is a small, monogamous, single-brooded raptorial bird that occurs in North America, Europe, and Asia (Sodhi et al. 1992, 1993). Merlins, like other raptors, are unusual among birds in that males appear to invest substantially more energy in offspring than do females (Wijnandts 1984, Masman et al. 1988). During the incubation period, female Merlins are largely inactive, leaving the nest for only brief periods to feed. In contrast, males are very active, providing the majority of food for the female as well as for themselves. Males also provide most (Temple 1972), if not all, of the food during the nestling period (Sodhi et al. 1992). Perhaps as a consequence of this, most male Merlins exhibit delayed breeding by starting at 2 yrs of age, while most females show no delay and begin breeding at age 1 (Lieske et al. 1997). Given these life history traits, Merlins are attractive subjects for testing hypotheses concerning age-specific differences in breeding performance. Little is known on the effects of age on breeding performance in birds of prey compared to other bird groups. In particular, male raptors have been less studied than females (due mostly to the difficulties involved in their capture), despite their obvious importance in the reproductive effort. In this study, we used a combination of cross-sectional and longitudinal data to test the two main hypotheses concerning age and breeding performance in male and female Merlins.

As a second objective we examined the relationship between longevity and lifetime reproductive success, and also production of recruits for both male and female Merlins. Here we attempt to relate observed trends in these measures to the cross-sectional data and to address the hypotheses concerning age-dependent breeding performance in Merlins.

METHODS

As part of a 13-yr population study, breeding Merlins were live-trapped during the nestling period (June to early July) in Saskatoon, Saskatchewan, Canada (52°07' N, 106°38' W) from 1985 to 1997. To reduce the possibility of including birds still alive at the end of the study, all birds captured in 1996 or 1997 were excluded in these data analyses and the calculations of LRS. A few individuals breeding near the end of the study period may have evaded capture; however, this group was probably very small, based on our level of capture success (Lieske et al. 1997), and the fact that we allowed two additional years for recapture. We captured an average of 57.2% of males and 84.5% of females in each year (Lieske et al. 1997). Therefore, the reported values must be considered estimates.

Merlins in Saskatoon show a marked preference for breeding in old American Crow (*Corvus brachyrhynchos*) nests in the numerous spruce trees (*Picea* spp.) that have been planted in residential areas (Warkentin and James 1988). For a detailed description of the trapping methods and the study area, see James et al. (1989) and Warkentin and James (1988). An abundance of House Sparrows (*Passer domesticus*) serves as the primary prey for Merlins in Saskatoon (Sodhi and Oliphant 1993). Reproductive data were derived from 378 captures of 129 individual females and 101 individual males. Breeding males could be aged precisely if they had been banded as nestling birds or if they were initially caught in their first year when they are separable from adult males (age 2+) based on plumage features (Temple 1972). The age of females could be determined only if they had been banded as nestlings. Adult males (age 2+) unbanded at the time of first capture were assigned a minimum age of two.

We measured four parameters to assess changes of breeding performance with age in Merlins: (1) Brood size—the number of chicks (at the time of banding) produced by an individual male or female in each year it was captured. (2) Hatch date—calculated by back-dating from the age of the chicks at the time of banding. Ages were determined by comparison with an unpublished aging scheme developed for Merlins by us from captive rearing studies and observations of wild birds. (3) Lifetime reproductive success—the total number of fledglings produced over an individual's life-span (Newton 1989a). (4) Recruits produced—the number of offspring produced by individuals breeding in our study area that survived and bred within our study area and were captured in some subsequent year. Any measure of recruitment is, of course, affected by natal dispersal. For our Merlin population philopatry is relatively high (compared to other raptors) and 10.4% of males and 4.1% of females returned to breed in a subsequent year (Lieske et al. 2000).

An ideal measure of LRS would require data from complete life cycles. Because of postnatal dispersal in

many species (including most birds), these data are difficult to obtain (Barrowclough and Rockwell 1993). It has been reasoned, therefore, that lifetime production of fledglings may provide a reasonable approximation in most circumstances (Newton 1989a). Even so, the number of young resulting from extra-pair fertilizations could bias estimates of LRS (Weatherhead and Boag 1997). In our population of Merlins, although the behavior of extra-pair copulations has been observed (Sodhi 1991), DNA fingerprinting from 20 broods has revealed no cases of extra-pair fertilizations (Warkentin et al. 1994). Breeding dispersal (i.e., movement between birds' successive breeding attempts) is quite low in this population, and the density of nesting Merlins is much lower outside the city than within (Sodhi et al. 1992). Relocated females in Saskatoon moved an average of 2.3 ± 1.83 km, while males moved an average of just 1.1 ± 0.90 km (± 1 SD) between successive breeding attempts (James et al. 1989). We allowed two years at the end of the study to reduce the possibility that some birds in the data set were still alive.

Analyses and hypothesis testing

We analyzed the data for males and females separately because we were most concerned with how age-dependent breeding performance in each sex related to the proposed hypotheses. For both male and female Merlins, brood size, LRS, and number of recruits were not normally distributed ($P < 0.01$, Kolmogorov-Smirnov tests) a condition that did not change when these data were transformed ($\log_{10}[x + 1]$). Therefore, for all analyses of these variables, we used a combination of nonparametric tests (Zar 1984, Siegel and Castellan 1988) and randomization techniques (Crowley 1992, Adams and Anthony 1996). Hatch date was a normally distributed variable ($P > 0.05$, Kolmogorov-Smirnov tests), so analyses of this variable employed parametric tests (Zar 1984). However, when $0.05 < P < 0.25$, we calculated 95% confidence intervals (Johnson 1999) to help determine trends, and employed randomization methods to determine the probability value, as this maximized power and reduced the chance of committing a Type II error (Crowley 1992, Adams and Anthony 1996).

To assess the relationships between age and hatch date, age and brood size, longevity and LRS, and longevity and recruit production we used Kendall's tau correlation (Zar 1984, Siegel and Castellan 1988). One drawback to using Kendall's tau is that it did not allow for the detection of nonlinear relationships. However, follow-up analyses were not constrained in this way. For hatch date and brood size, we also attempted to determine whether any observed general trends with age occurred within individuals (inadequate experience hypothesis), or if they were the result of differential mortality, or both. To test for within-individual trends, we examined data for breeding birds that were captured

as yearlings and again as adults (age 2+). In addition, we used paired t tests (Zar 1984) to determine if there were any differences in breeding performance in birds captured at any time from ages 1–3 (inclusive) and again at any time from ages 4–6 (inclusive). We assigned age 3 as the midlife cutoff because only one Merlin in our sample (a female) lived past age 6. In our analyses of individuals captured before and after midlife, we used the breeding performance values that were separated by the greatest number of years. For example, if we caught a bird when aged 1, 2, and 5, we only used its breeding performance measures from ages 1 and 5 in the paired t tests. We did this to maximize our likelihood of detecting trends within individuals. In order to conduct a further test of the inadequate experience hypothesis, we compared hatch dates and brood sizes of yearling males that bred once to those of 2-yr-old males that bred once. We were interested in these two groups because we wanted to know whether waiting a year would improve LRS for male Merlins making only one breeding attempt. We used a t test to compare hatch dates and a Mann-Whitney U test to compare brood sizes (Zar 1984, Siegel and Castellan 1988). In addition to the above tests, we tested for a relationship between brood size and hatch date using linear regression (Zar 1984).

To test the differential mortality hypothesis, we separated the birds in each age class into two categories. Birds of any age could be divided into those that bred again in a later year ("lived") and those that did not ("died"). Birds were assumed to have died if they were never recaptured between 1985 and 1997. We used "died" and "lived" as two categories of the fixed effect factor in a randomized block analysis of variance (ANOVA) with age as the blocking factor (Zar 1984). This allowed us to examine within each age group whether any relationship existed between breeding success at a given age and survival to the next age class, or in other words, whether poorly performing birds were more likely to die than more highly performing ones. We used mean values of hatch date and brood size in each cell of the block design. We did this because the design was unbalanced (i.e., very unequal sample sizes within each category). Thus, we judged that the best approach to testing the differential mortality hypothesis was to use the mean values for brood size and hatch date for each cell in the analyses. We could not assess any interaction because each cell contained only a single value. Only birds up to age 5 were included in these analyses because our sample contained only one female and no male Merlins older than age 6.

The mean number of young produced by those birds living past a particular age and those that died appeared to follow different patterns before and after midlife in both sexes. Because of the obvious change in the patterns, we split the data at midlife for analyses. Splitting the data at midlife did create a problem when testing

the differential mortality hypothesis. If we used “died” and “lived” as two categories of the fixed effect factor in a randomized block analysis of variance (ANOVA) with age as the blocking factor (and keeping the sexes separate), it precluded finding statistically significant differences between the two categories because there were not enough possible permutations of the data to achieve $P_r < 0.05$ (based on randomization methods three “pairs” of data give eight permutations). Non-parametric methods would have suffered a similar fate. Therefore, in this one instance, we combined data for males and females in order to perform analyses with a potentially falsifiable H_0 . For birds aged 1–3, we used randomized block ANOVA (probability values calculated by randomization) and for birds aged 4–5, we used Friedman’s ANOVA (Zar 1984). In both analyses, males and females constituted separate blocks.

To determine if recruitment of offspring was dependent upon the age of the parent, we compared the observed vs. expected recruitment values for each age category in a contingency table for male and female Merlins using log-likelihood ratio analyses. We used log-likelihood ratio analyses rather than chi-squared analyses because $>20\%$ of the expected frequencies were <5.0 (Zar 1984).

All tests were two-tailed and considered significant when $P < 0.05$. Parametric and nonparametric statistical tests were computed using Statistica for Windows (Version 5.1) (StatSoft 1995). Randomization tests were conducted using the computer program RT (Version 2.1) (Manly 1997). If the number of permutations for reshuffling and sampling the data were small (<2000), we used exact permutation to calculate probability values. If the number of permutations was large, we performed 5000 replications and used the frequency distribution of possible outcomes to calculate probability values (see Crowley 1992, Adams and Anthony 1996). Probability values calculated from randomization techniques are denoted as P_r . Means are reported ± 1 SD.

RESULTS

Of the 225 female Merlin captures, 53 cases were of known age; 105 of the 153 male captures were of known age (Fig. 1). The mean life-span for females was 3.15 ± 1.91 yr; for known-aged males, the mean life-span was 2.67 ± 1.51 yr (Fig. 1). For male Merlins of estimated age, the mean life-span was 2.58 ± 1.18 yr. Parallel analyses run for males of known- vs. estimated-age (in terms of age effects on breeding performance) resulted in qualitatively identical results. Thus we pooled the data for the two groups of males.

Hatch date became earlier with age for both females ($\tau = -0.462$, $n = 52$, $P < 0.001$) and males ($\tau = -0.344$, $n = 150$, $P < 0.001$; Fig. 2). Within individuals, hatch date did not change for females (mean difference = 2.43 ± 13.67 d, paired $t = 0.47$, $n = 7$, $P_r = 0.65$), but came to be substantially earlier for older

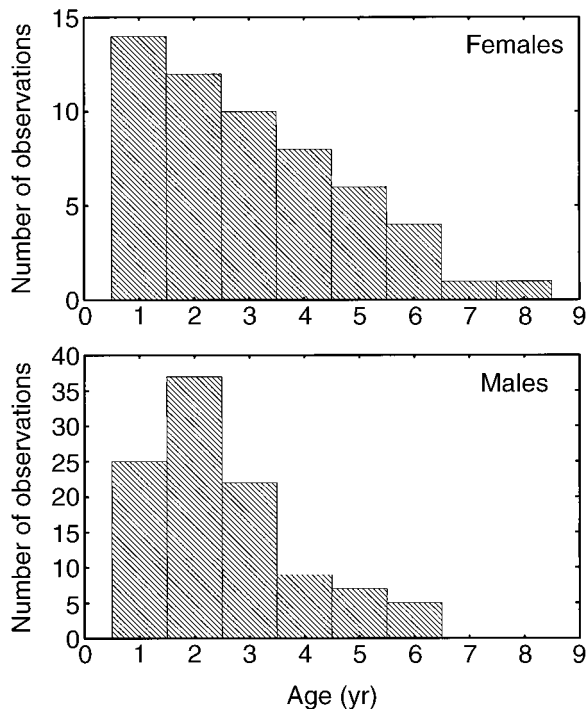


FIG. 1. Age distributions of breeding female and male Merlins captured in Saskatoon, Saskatchewan (1985–1995). Only known-age birds are shown.

males (mean difference = 10.70 ± 5.46 d, paired $t = 6.20$, $n = 10$, $P < 0.001$). For individuals captured before and after midlife, there was a tendency for hatch date to become earlier in older females (mean difference = 4.00 ± 7.53 d, paired $t = 1.06$, $n = 4$, $P_r = 0.25$, 95% CI = $-7.98, 15.98$), but for males, the trend was more apparent (mean difference = 2.41 ± 5.77 d, paired $t = 1.72$, $n = 17$, $P_r = 0.0498$). Using analysis of variance blocked by age, we found that birds surviving past each age category tended to have earlier hatch dates for females ($F = 3.77$, $df = 1,4$, $P = 0.124$, mean difference 95% CI = $-0.63, 3.53$; Fig. 3). This trend was not apparent in males past age 1 and there was no difference in hatch date between those males that survived past each age class and those that did not ($F = 0.001$, $df = 1,4$, $P = 0.98$; Fig. 3). Males that bred for the first time at age 2 (mean = 12 June, $n = 45$) had chick hatch dates that were earlier than yearling male breeders (mean = 22 June, $n = 14$, $t = 6.70$, $P < 0.001$). Males that initially bred at age 2 also produced larger broods (median = 5, $n = 46$) than yearling males only breeding once (median = 4, $n = 15$, $U = 208.5$, $P = 0.015$). Birds having earlier hatching chicks also had significantly larger broods for both females ($\tau = -0.194$, $n = 218$, $P < 0.001$) and males ($\tau = -0.243$, $n = 150$, $P < 0.001$).

The general trend for males was for brood size to increase with age ($\tau = 0.117$, $n = 153$, $P = 0.033$). Among females, brood size was not as strongly cor-

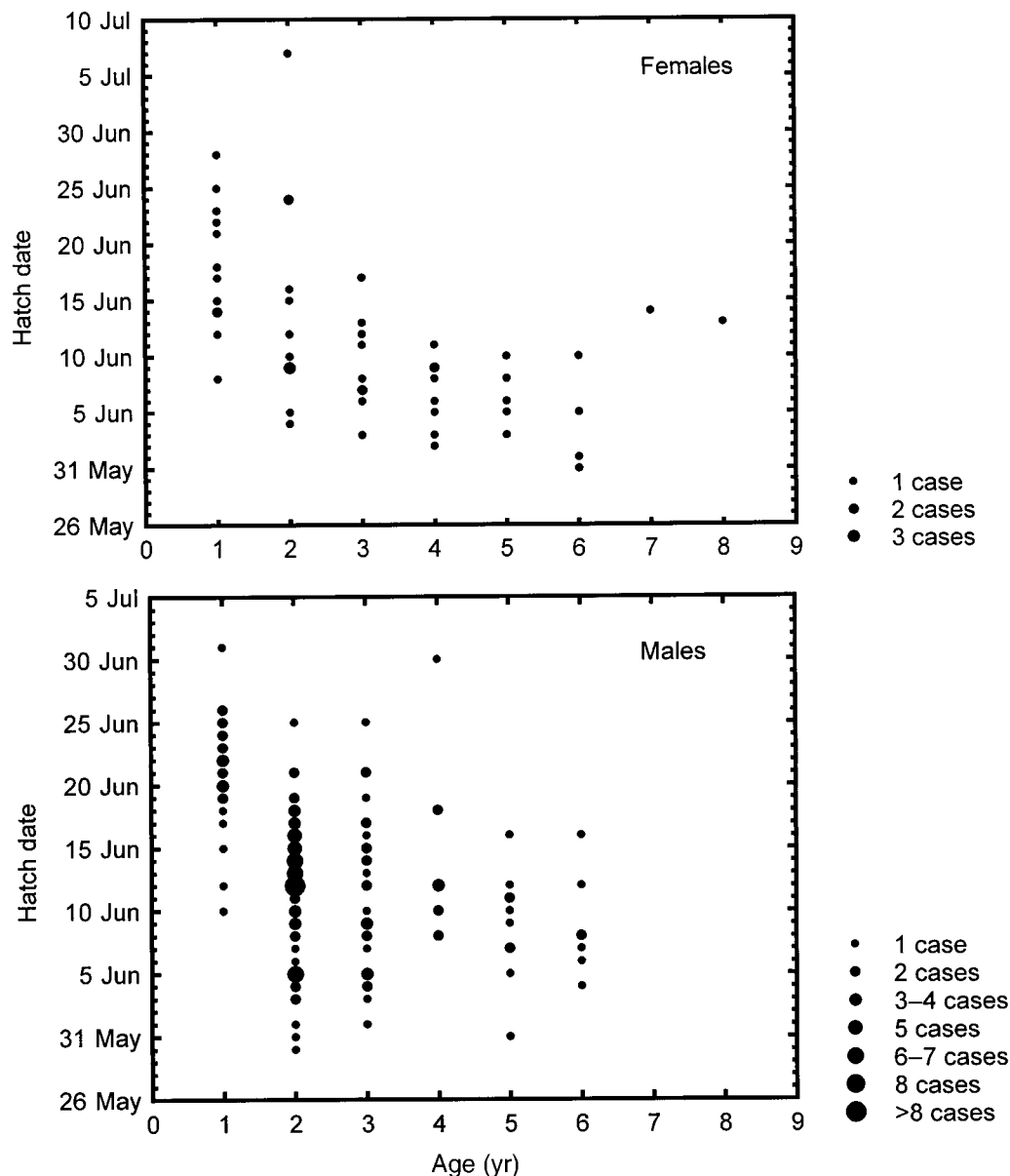


FIG. 2. Scatter diagram of parent age and chick hatch date for female and male Merlins in Saskatoon, Saskatchewan. All captures for each individual are shown. There is a significant reduction in chick hatch date with age for both sexes.

related with age but the trend appeared to be positive ($r = 0.188$, $n = 56$, $P_r = 0.174$, correlation coefficient 95% CI = $-0.079, 0.429$). For yearling breeders that were captured again as adults (age 2+), brood size tended to increase within individual females (mean difference = 0.96 ± 1.31 chicks, paired $t = 1.95$, $n = 7$, $P_r = 0.094$, 95% CI = $-0.25, 2.17$), but not as distinctly as it did within males (mean difference = 0.55 ± 0.72 chicks, paired $t = 2.40$, $n = 10$, $P_r = 0.031$). Brood size tended to increase slightly within individual females (mean difference = 0.50 ± 0.58 chicks, paired $t = 0.234$, $n = 4$, $P_r = 0.25$, 95% CI = $-0.42, 1.42$) and males (mean difference = 0.29

± 1.45 chicks, paired $t = 0.84$, $n = 17$, $P_r = 0.25$, 95% CI = $-0.46, 1.04$) when comparing before and after midlife.

Younger breeders (aged 1–3 yr) of both sexes that were not just about to die tended to have larger broods than those that were just about to die ($F = 6.49$, $df = 1, 5$, $P_r = 0.0625$, mean difference 95% CI = $-0.004, 0.86$; Fig. 4). However, older breeders (aged 4–5 yr) of both sexes reversed this pattern, producing very large broods just before dying (Friedman's ANOVA, $\chi^2 = 4.0$, $df = 1$, $n = 4$, $P = 0.046$, Fig. 4).

As expected, there was a positive correlation between age (i.e., longevity) and lifetime reproductive

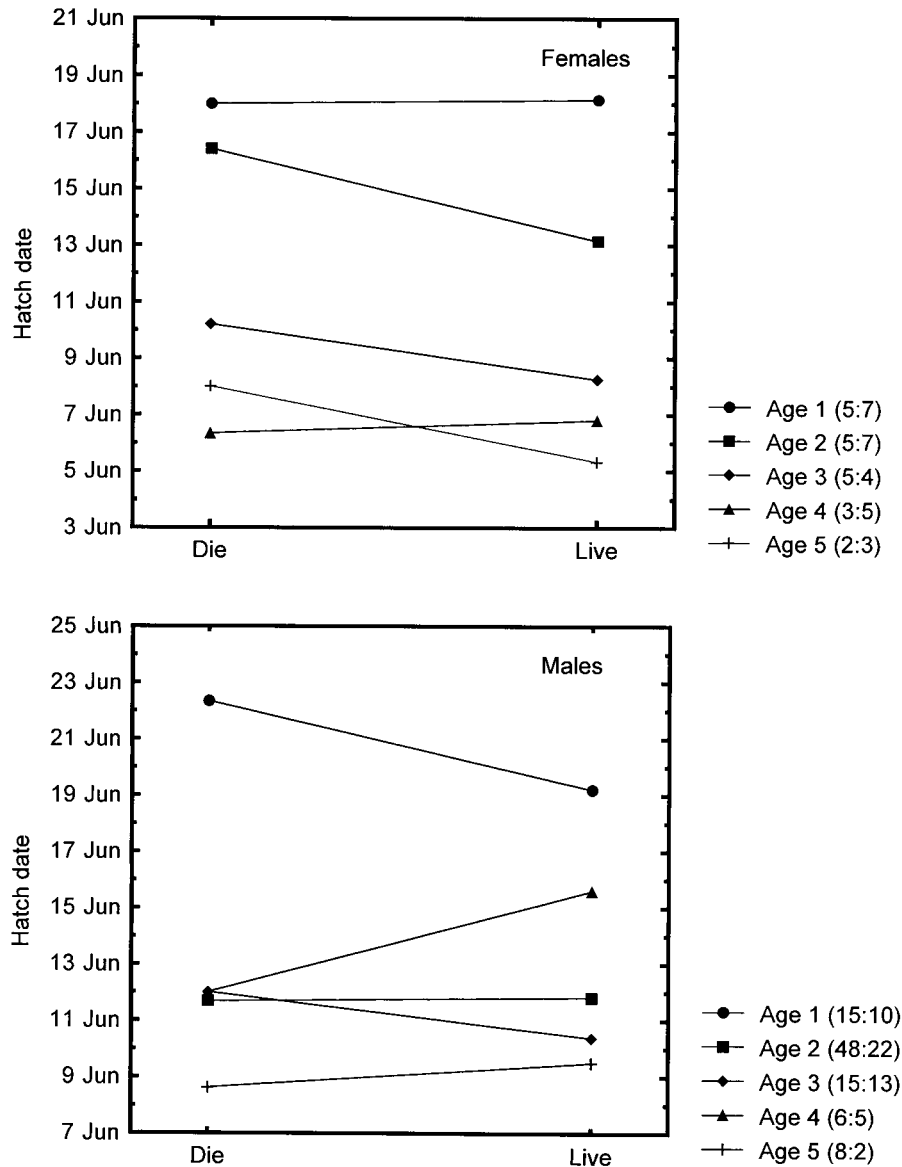


FIG. 3. Mean chick hatch dates for Merlin parents in Saskatoon that survived past or died at a particular age. Two-factor randomized block ANOVA tests (blocked for age effects) revealed a difference in the chick hatch date for surviving vs. dead females, but not for males. Connecting lines are used to illustrate equal-aged birds. Numbers in parentheses in the keys indicate sample sizes for each category (die:live).

success for both male ($\tau = 0.662, n = 102, P < 0.001$) and female Merlins ($\tau = 0.725, n = 26, P < 0.001$; Fig. 5). Females produced a mean of 9.1 ± 6.2 fledglings in their lifetimes, whereas males produced a mean of 7.4 ± 5.9 fledglings in their lifetimes. The maximum number of fledglings produced by a male was 32 and for a female, 24.

The number of recruits produced by Merlins of each age class did not differ from the number expected by chance alone (Table 1). Thus, older birds produced more recruits over their lifetimes in both females ($\tau = 0.455, n = 26, P < 0.01$) and males ($\tau = 0.252, n = 102, P < 0.001$) simply because they lived longer and

bred more times. Even so, the oldest female Merlin in our sample (age 8) did not produce any recruits to our population.

DISCUSSION

Life history theory is based on the assumption that there are trade-offs between different life history traits (Stearns 1992). Lack (1947) was among the first to point out the existence of negative relationships among life history variables by showing that increased investment in one component may result in decreased investment in another. Other studies have suggested that patterns of age-dependent variation in breeding

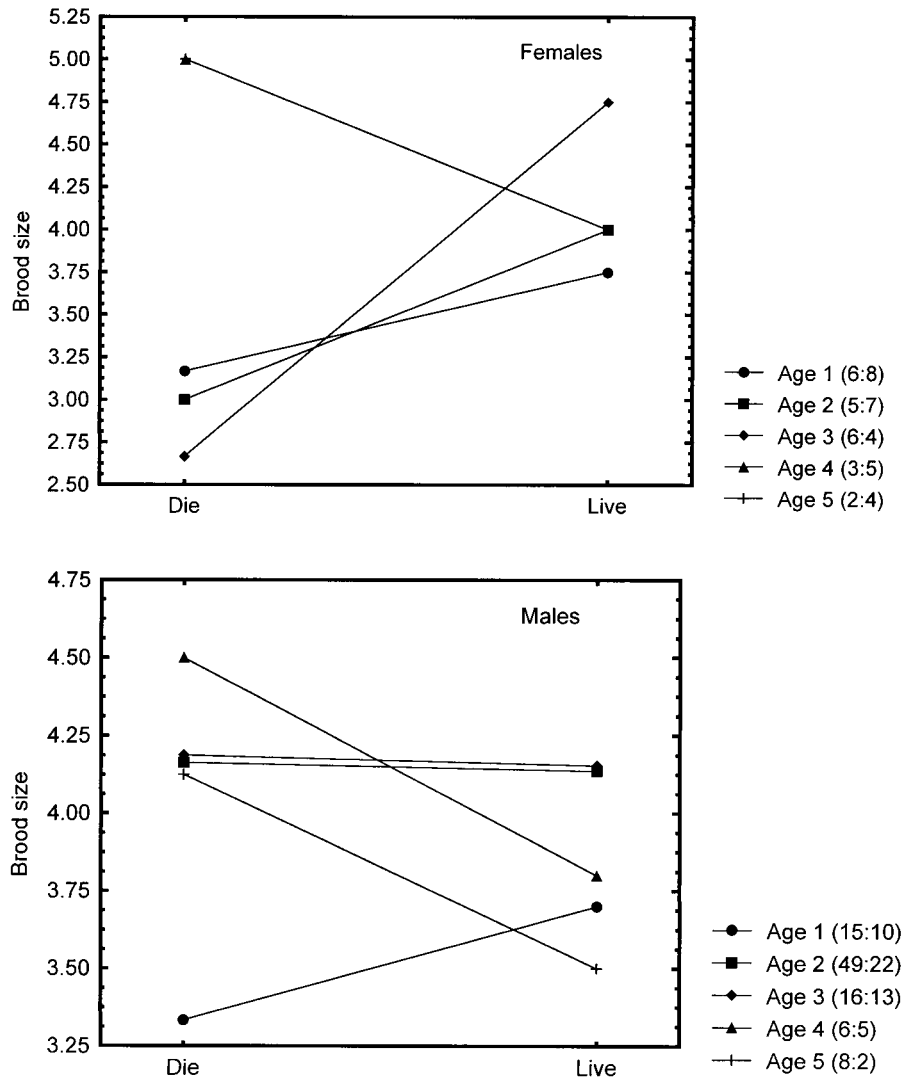


FIG. 4. Mean brood sizes for Merlin parents in Saskatoon that survived past or died at a particular age. Note that, for females, birds aged 4 and 5 produced the same mean number of chicks for both categories. Connecting lines are used to illustrate equal-aged birds. Numbers in parentheses in the keys indicate sample sizes for each category (die:live).

performance should be related both to chances for future survival and to reproduction (Hamilton 1966, Emlen 1970, Charlesworth 1980). In several experimental studies, a cost of reproduction has been shown for several bird species (reviewed by Nur 1988; see also Gustafsson and Sutherland 1988, Gustafsson and Pärt 1990, Jacobsen et al. 1995, Wiehn and Korpimäki 1997). Individual performance in our male and female Merlins also provides clear evidence of age-dependent changes in reproduction for a natural population.

Between-individual trends

In general, our results for both male and female Merlins provide some support for the differential mortality hypothesis based on our analyses of hatch dates. For different-aged male Merlins, the evidence for the dif-

ferential mortality hypothesis was less strong than for females. Nevertheless, among yearling males, the data suggest, at least qualitatively, that higher quality individuals survived better. For females, however, birds surviving past each age category tended to have earlier chick hatch dates than their counterparts that died. Because most female Merlins begin breeding when they are yearlings (Lieske et al. 1997), the observed age-related trends were largely the result of the progressive disappearance at each stage of poor reproductive performers. Seasonal declines in reproductive success have been well documented in birds (e.g., Lack 1950, Perrins 1970, Newton and Marquiss 1984, Daan et al. 1988, Verhulst et al. 1995). Nonetheless, the question arises: Could earlier-breeding Merlins have some advantage over their later-breeding counterparts? There

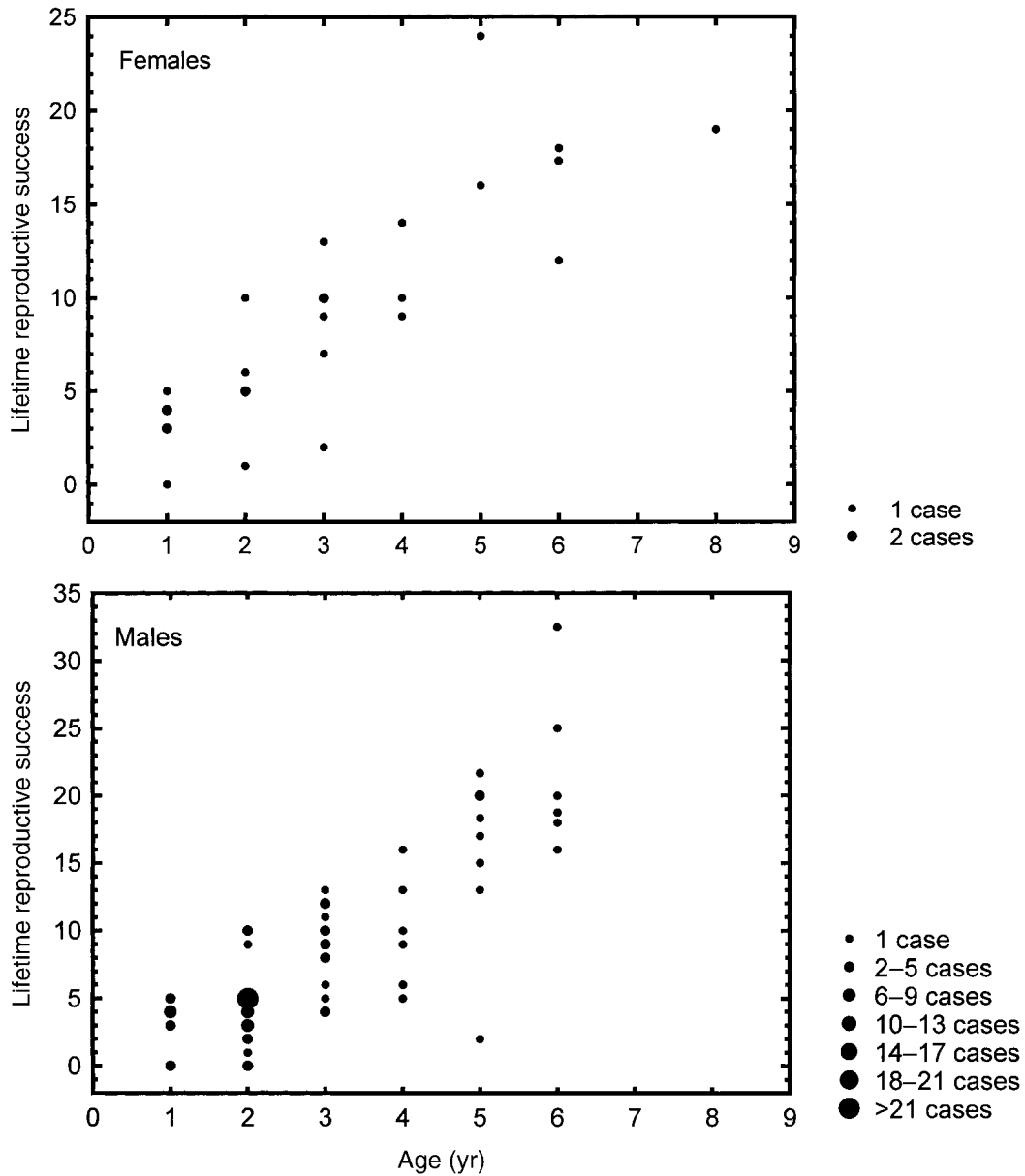


FIG. 5. Scatter diagram of final age attained and lifetime reproductive success for female and male Merlins found breeding in Saskatoon (1985–1995). All known breedings producing no chicks are also included.

is strong evidence to support the idea that Merlins whose offspring have an earlier hatch date were superior breeders. First, Merlins of both sexes showed a seasonal decline in brood size. This seasonal decline in success could have been causally related to the timing of breeding, but could also be caused by variation in the quality of early and late breeders (Verhulst et al. 1995). Timing of breeding in relation to the phenology of other organisms may be important when breeding is synchronized with seasonal fluctuations in the population of prey (van Balen 1973). Previous work has shown that Merlins in Saskatoon time their breeding so that the fledging phase falls during the period of

peak production of juvenile House Sparrows (Sodhi and Oliphant 1993). Other workers have reported increased predation on juvenile prey individuals as the Merlin breeding season progresses (Newton et al. 1984). Second, the timing of molt is of fundamental importance for Merlins, as they renew their feathers at the same time as raising offspring (Espie et al. 1996), two expensive activities that must be accomplished before fall migration. Third, early hatching may be adaptive for Merlin chicks because they would have more time available for practicing hunting and for accumulating body reserves before winter as has been shown for other raptors (e.g., Tengmalm's Owl, *Ae-*

TABLE 1. Total number of young and recruits produced and the expected number of recruits for individual breeding attempts by female and male Merlins of different ages.

Age (yr)	Females			Males		
	No. young	Recruits produced	Recruits expected	No. young	Recruits produced	Recruits expected
1	49	2	2.9	87	5	6.6
2	43	1	2.5	295	24	22.4
3	35	4	2.0	121	11	9.2
4	35	1	2.0	46	2	3.5
5	26	3	1.5	40	3	3.0
6	17	1	1.0	30	2	2.3
Total	205	12	...	619	47	...

Note: For females $G = 5.0$, $df = 5$, $P = 0.42$; for males $G = 1.67$, $df = 5$, $P = 0.89$.

golius funereus; Korpimäki 1987). These lines of evidence, in association with the data from this study, suggest to us that timing of breeding is important for both Merlin parents and their offspring. Mean hatch date for our Merlin population became earlier during the study period (R. H. M. Espie, unpublished data). However, we are unable to say for certain whether Merlins were responding to some environmental trend (e.g., weather, change in House Sparrow breeding chronology, etc.) or if this decrease in hatch date over the study period was due to selection of superior breeders, or both.

Different strategies for optimal brood size were apparent as a function of age in both sexes. Before midlife, adults destined to survive and breed again had larger broods than those soon to die and this pattern was especially clear for females. After midlife, the relationship reversed for both sexes; individuals having smaller broods were more likely to breed again. This suggests that past midlife, higher fecundity reduced future survival in both sexes (i.e., cost of reproduction, Williams 1966). However, it must be noted that the cost of reproduction can only truly be investigated by experimentally manipulating the reproductive effort in individuals and determining how this influences their future reproduction and survival.

For a number of other birds, the differential mortality hypothesis has received limited support (reviews in Forslund and Pärt 1995, Martin 1995), coming from Song Sparrows, *Melospiza melodia* (Nol and Smith 1987); Screech Owls, *Otus asio* (Gehlbach 1989); Short-tailed Shearwaters, *Puffinus tenuirostris* (Wooler et al. 1990); and Kittiwakes, *Rissa tridactyla* (Coulson and Porter 1985, Aebischer and Coulson 1990). Some of the observed trends in hatch date and brood size in male and female Merlins were likely due to the disappearance of inferior individuals, but some changes in breeding performance did occur within individuals, particularly for males.

Within-individual trends

In general, any effects of inadequate experience acting within the individual could give rise to the same general trends explained by differential mortality.

However, our analyses revealed no change in chick hatch date within individual female Merlins (comparing yearlings with adults), but chick hatch date shifted within male Merlins to become earlier as they aged (comparing yearlings to adults). For individuals captured before and after midlife, there was a weak trend for hatch date to become earlier for older birds of both sexes (but stronger in males). Brood size increased with the age of male Merlins (most noticeably early in life), but less so with the age of females. These findings make sense when placed within the context of the ecology of birds of prey. Experimental and observational evidence strongly suggests that in raptors, food limits breeding performance (Newton 1986, Daan et al. 1988, Wiehn and Korpimäki 1997). Because male Merlins provide almost all the food consumed by themselves, their mates, and their offspring during the breeding season (Sodhi et al. 1992), one would expect their ability to provide food to be the primary determinant of breeding success. Improved foraging skills have frequently been suggested as an explanation for increased reproductive success with age early in life (Lack 1968, Burger 1988, Newton 1989a, Pyle et al. 1991, Desrochers 1992, Forslund and Pärt 1995). According to life history theory, individuals should begin breeding when the benefits are greater than any benefits gained from a delay of reproduction (Promislow and Harvey 1990, Stearns 1992). A longer delay in age of first breeding for males compared to females has been reported for many raptors (see Newton 1979, Mearns and Newton 1984, Heyne and Wegner 1991). Most female Merlins in Saskatoon begin breeding at age 1, whereas most males begin to breed at age 2 (Lieske et al. 1997). The simplest explanation for this observation is the different roles the two sexes play in reproduction, which may preclude many inexperienced yearling male Merlins from breeding. Indeed, a 1-yr delay for male Merlins that only bred once as adults significantly improved their LRS over their counterparts that only bred once as yearlings. In this instance, LRS may provide a reasonable estimate of Darwinian fitness, in terms of the number of offspring "on average" that two given designs (yearling breeders vs. delayed breeders) will produce. However, early breeding (even with slightly

reduced fecundity) would be advantageous in terms of production of more distant descendants (e.g., great-grand-offspring) in a stable or increasing population, all else being equal. From our field study it was impossible for us to determine exactly how much of the observed change in male performance between yearlings and adults was due to a change in competence or reproductive effort. Intelligent experimentation in this area may prove useful in determining the influence of these two factors early in life for raptors and other birds. The idea that young breeders show reproductive restraint in order to increase subsequent performance has received little empirical support (Newton 1989a, Forslund and Pärt 1995, but see Pugsek 1981, Pugsek and Diem 1990, Weimerskirch 1992).

LRS and recruitment

Lifetime reproductive success for Merlins of both sexes was highly correlated with age, a pattern that is consistent with most animals studied thus far (reviews in Clutton-Brock 1988, Newton 1989a); longevity is the single most important factor accounting for variance in LRS measures. Despite its value as a measure of breeding performance, however, LRS does not allow for the detection of trade-offs between reproduction and survival or perhaps even signs of senescence (i.e., innate deterioration in probability of survival or breeding performance with increasing age). For example, elderly Merlins (4 and 5 yr olds of both sexes) surviving past these age classes tended to produce fewer offspring than those not surviving. This did not show up in our measures of overall LRS because these birds had done so well in previous breeding attempts that it masked any later reduction in breeding performance. Therefore, the longest lived birds having the highest LRS in our study were not always the best performers at each age. In fact, for Merlins to maximize their LRS, it appeared better to slightly reduce brood size (when past midlife) in a given breeding attempt in order to increase the probability of surviving to breed again. A deterioration in performance in later life, despite the accumulation of experience, is likely attributable to degenerative senescence (sensu Abrams 1991, Newton and Rothery 1997, 1998). Medawar (1952) and Williams (1966) proposed that the evolution of senescence could be understood in terms of age-specific gene action whereby a mutation increases fitness early in life at the expense of reducing it later on. Another explanation is that there may be an accumulation of harmful mutations that reduce fitness in later life (Medawar 1952, Partridge and Barton 1993). Although deterioration in breeding performance has obvious negative consequences, a slight reduction in breeding performance at later ages may not be entirely negative if there is some trade-off between survival and reproduction.

Recruitment of Merlins (in this case limited to locally produced offspring that subsequently returned to breed) was not directly related to the parent's age at

the time of production. Thus, different-aged Merlins did not produce offspring that were more or less likely to be recruited. The total number of recruits produced in a bird's life depended on how long the bird lived. This was because these same birds tended to produce more chicks over their lifetimes and thus, by sheer numbers and probability alone, were able to produce more recruits. Newton (1989b) reported a similar finding for female Sparrowhawks. Therefore, anything that increased LRS should in turn have affected recruitment. However, the fact that so few offspring returned (compared to the number produced) to our study area to breed, probably limits our ability to draw conclusions from the recruitment data. A recent review of 22 long-term studies of birds suggests that individuals that disperse can differ from those that stay (or return), and thus using recruitment of breeding offspring to the local study plot in order to identify individual adaptations may be misleading (Lambrechts et al. 1999).

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