

## EFFECTS OF POPULATION DENSITY ON SURVIVAL IN MERLINS

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**ABSTRACT.**—Accurate estimation of survival probabilities is an important component of population demographics, and it permits a test of the life-history prediction that densities influence population dynamics via suppression of survival rates. As part of a long-term study of urban-nesting Merlins (*Falco columbarius*), we estimated survival rates and tested for the effects of density dependence based on capture histories from 1,354 individuals (43 males and 110 females caught for the first time as adult breeding birds, and 597 males and 604 females caught for the first time as locally produced nestlings). Overall capture probabilities were  $0.55 \pm \text{SD of } 0.039$  per year for adults,  $0.10 \pm 0.075$  per year for juvenile males, and  $0.58 \pm 0.23$  per year for juvenile females. Mean survival rate of adults was  $0.62 \pm 0.11$  per year and did not differ significantly between males and females. Overall juvenile survival rates were  $0.23 \pm 0.032$  for males and  $0.055 \pm 0.012$  for females. Band returns suggest that the discrepancy in survival rates between juvenile males and females resulted from higher natal dispersal of females rather than from lower survival. Survival of adults (but not juveniles) was negatively density dependent, suggesting that density-dependent declines in survival exerted a regulatory effect on population size. Received 27 July 1998, accepted 18 June 1999.

ESTIMATING PARAMETERS that influence the stability and persistence of animal populations is central to the understanding of population dynamics (Eberhardt 1985, Clobert and Lebreton 1991). Survival probability is an important component of population demography (Ricklefs 1972, Lebreton et al. 1992). The importance of estimating survival rates is clear when we consider that the stability of any animal population is at least partially an outcome of the balance between the establishment of new breeders and the mortality of older breeders (Lebreton et al. 1993).

Until recently, survival rates were estimated from capture-recapture studies using life tables. Using this procedure, recaptures or re-sightings of previously marked individuals are used only to confirm that individuals were alive in the previous sampling period (Pollock et al. 1990). Furthermore, survival probabilities

derived from life-table methods really are estimating "return rates" (Loery and Nichols 1985), which are a function of the probability of survival between periods and the probability of capturing or sighting surviving individuals (Pollock et al. 1990, Lebreton et al. 1993). Estimates based solely on return rates commonly underestimate survival probabilities (Lebreton et al. 1993, Newton et al. 1997).

As part of a long-term study of an urban-nesting population of Merlins (*Falco columbarius*), we sought to estimate survival rates and test for the effects of density dependence. In light of the findings of Lebreton et al. (1992), Blums et al. (1996) and Newton (1998), we also considered the likelihood that survival rates are lower in juveniles than in adults. Because density-dependent suppression of juvenile or adult survival is one way that population size can be regulated (Stubbs 1977), we were keenly interested in examining the effects of density dependence on survival. Our goal was to combine the recent advances in capture-recapture methodology with a long-term data set to consider the issue of density-dependent survival more closely.

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## METHODS

*Study population.*—Merlins have nested sporadically in the city of Saskatoon, Saskatchewan (52°07'N, 106°38'W), since the late 1960s (Houston and Schmidt 1981, Oliphant and Haug 1985). Saskatoon is particularly well suited for Merlins because of the high abundance of prey (i.e. House Sparrows [*Passer domesticus*]) and the surplus of old nests of American Crows (*Corvus brachyrhynchos*) and Black-billed Magpies (*Pica pica*) that provide crucial nesting sites for the birds (Houston and Schmidt 1981, Warkentin and James 1988).

*Census and capture methods.*—We conducted a systematic census of the city each spring and summer from 1985 to 1996, during which time we recorded the number and location of breeding pairs. The full-time survey was initiated in early April and conducted until mid- to late May. Sites known to have been used in previous years were searched first, followed by examination of peripheral areas. Although the potential search area was large (122 km<sup>2</sup>), the actual area that contained suitable nest sites was smaller, allowing us to concentrate our efforts in areas known to support nesting pairs. Nevertheless, efforts were made to visit seemingly unsuitable areas each year. Searches of the immediate vicinity of medium- to large-sized spruce trees (*Picea* spp.) were conducted on foot, by bicycle, or by vehicle and involved broadcasting a tape recording of the Merlin's "ki-ki-kee" call (Feldsine and Oliphant 1985). Males are known to respond strongly to these recordings (James et al. 1989). Other cues for the presence of breeding pairs included feces, feathers of Merlins or prey items, partially eaten prey remains, and the activity of pair members. In most years, searches were conducted by the authors themselves, or by a combination of the authors and trained assistants. City residents also volunteered information regarding the location of individual Merlins. Areas of suspected breeding activity were searched to confirm the presence of mated pairs. Because our search effort was consistent and the study area was of fixed size, we argue that changes in Merlin numbers from year-to-year reflected actual changes in density (see Arcese et al. 1992).

Nestlings were banded with standard numbered leg bands throughout the study period; beginning in 1982, nestlings were also banded with year-specific colored leg bands (Warkentin et al. 1990). Breeding birds have been captured throughout the nesting season since 1985 (Warkentin et al. 1990). Therefore, data collected from 1985 to 1996 provided 12 annual capture periods that could be used to estimate survival.

Captured birds fell into one of two groups: those caught for the first time, and those with a previous capture history. Young that hatched on the study area were captured for the first time as nestlings, al-

lowing us to examine first-year survival probabilities for this group. First-time captures of birds that were produced outside the study area and that immigrated into the city to breed were considered adults by definition. For the purposes of survival estimation, birds must have been captured to be incorporated in the analysis, because individual band numbers could be read only when the bird was in hand (with the exception of one male and three females that were marked with plastic leg streamers; Warkentin et al. 1990). All birds captured for the first time were treated as that year's cohort for the survival analysis. Birds were defined as juveniles in the year in which they hatched and as adults in subsequent years (one year and older).

*Statistical methods.*—The Cormack-Jolly-Seber procedure (Cormack 1964, Jolly 1965, Seber 1965) provides a powerful method for estimating survival probabilities from capture-recapture data but makes a number of assumptions that should be examined whenever possible (Begon 1983). The assumptions were described by Seber (1982) and include: (1) all animals have the same probability of capture and survival in a single capture period; (2) marked animals do not lose their markers; and (3) all sampling is instantaneous.

The second assumption is supported by the fact that we have double-banded all nestlings raised in the study area since 1982, and not once have we observed an individual that lost a band. Furthermore, the length of the trapping period (three to four weeks) is so short relative to the length of the period between recaptures (ca. 11 months), that the third assumption is reasonable.

The first assumption, that of equal catchability, is more difficult to evaluate, but goodness-of-fit tests for the Cormack-Jolly-Seber model have been incorporated into program JOLLY (Pollock et al. 1990). This test of the assumptions compares return rates of birds caught for the first time in any given year ( $t$ ), with those caught for the first time in an earlier year. Differences in return rates among the two groups suggest the influence of age or capture history on return probabilities and constitute a violation of the homogeneity assumption. Given the small sample sizes commonly attained in studies of vertebrates and the resulting low power of the statistical tests, results from such tests are of limited usefulness. Furthermore, Carothers (1979) demonstrated that rejection of the homogeneity assumption exerted very little bias on subsequent survival estimates in his study of Northern Fulmars (*Fulmarus glacialis*). Provided that the tests are maintained as little more than a tentative and imperfect test of the model assumptions, we feel that they provide an informative measure of the degree to which heterogeneity pervades capture probabilities. We also used program JOLLY to provide capture-recapture estimates of the number of breeding pairs each year. These estimates were in-

tended only for comparison with estimates obtained by direct counts during the population census and were not used to test for density dependence.

We used SURGE 4.1 (Pradel et al. 1990) to test for the effects of sex, trapping year, age (first year vs. adult), natal origin (local vs. immigrant), and population density on survival. Following Lebreton et al. (1992), we initiated the analysis with a complex model incorporating the effects of all of these factors and proceeded by dropping factors one-by-one in an attempt to build a model that was simple enough to permit powerful tests of density dependence, yet complex enough to provide an adequate representation of the observed capture histories. We emphasize that our goal was to derive biologically sensible and statistically plausible models of survival probabilities for the test of density dependence, not to attempt to exhaustively explore every possible combination of model factors. We preferred hypothesis testing using likelihood ratios, but we also used the Akaike Information Criterion (AIC) as a guide during model selection.

To test for the effect of density on survival probability, we constrained survival to be a function of the number of breeding pairs in the year immediately preceding each interval as a logistic regression (logit transformed). Survival probabilities were represented by

$$\text{logit}(\Phi) = \beta_0 + \beta_1 N_{i-1} \quad (1)$$

where  $\beta_0$  is the  $y$ -intercept, and the slope ( $\beta_1$ ) is a function of the number of breeding pairs in the previous year ( $N_{i-1}$ ). We tested the significance of the relationship using an analysis of deviance in which the deviance attributable to density was the difference between the density-dependent model and the constant-survival model. Similarly, total deviance was the difference between the time-dependent model and the constant-survival model. Unlike the likelihood-ratio comparisons used in previous studies (e.g. Clobert and Lebreton 1985, Newton et al. 1993), analysis of deviance does not treat the sampling unit (years in this case) as infinite.

## RESULTS

*Tests of assumptions.*—During this study, 43 males and 110 females were caught initially as adult, immigrant breeders, whereas 597 males and 604 females were banded as local nestlings (Table 1). No birds (male or female) were recaptured after more than five years (median = three years). Of the birds captured for the first time as adults, 14 males (32.6%) and 50 females (45.4%) were recaptured in a subsequent year. Of the birds banded as nestlings, 61 males

(10.2%) and 24 females (4.0%) were recaptured as adults in later years.

Recapture frequencies were tested among cohorts using program JOLLY. For males recaptured from 1986 to 1996, there was no obvious heterogeneity in capture probabilities ( $\chi^2 = 4.98$ ,  $df = 6$ ,  $P = 0.54$ ). Females exhibited a greater departure from the homogeneity assumption than males ( $\chi^2 = 20.48$ ,  $df = 11$ ,  $P = 0.039$ ). However, the overall test was not significant ( $\chi^2 = 25.46$ ,  $df = 17$ ,  $P = 0.08$ ). Excluding capture histories of four birds marked with plastic leg streamers (see Methods) lowered the heterogeneity of the goodness-of-fit tests for males ( $\chi^2 = 4.37$ ,  $df = 6$ ,  $P = 0.63$ ) and females ( $\chi^2 = 17.89$ ,  $df = 12$ ,  $P = 0.12$ ), resulting in an overall goodness-of-fit test that was not significant ( $\chi^2 = 22.26$ ,  $df = 18$ ,  $P = 0.22$ ). Although including these four individuals acted as an additional source of variation, we felt that the information contained in their capture histories was too valuable to be discarded. Therefore, we accepted a higher degree of heterogeneity to obtain more complete capture-recapture information and a larger sample size.

To evaluate the consistency with which our population census adequately sampled the number of breeding pairs, we compared population estimates based on the census with those estimated by the Jolly-Seber procedure. Across all years, the correlation between estimates from both methods was nearly significant ( $r = 0.59$ ,  $P = 0.072$ ; Fig. 1). However, estimates based on the population census also incorporated pairs that were counted but not captured. In years of particularly low capture success, discrepancies between census estimates and Jolly-Seber estimates will occur. This appears to have happened only in 1992 (Fig. 1), when more pairs were counted during the census than estimated by the Jolly-Seber method. When we excluded 1992, estimates from the two methods were highly correlated ( $r = 0.81$ ,  $P < 0.01$ ). Although the Jolly-Seber estimates are not independent of the population census (both incorporated captured birds in their counts), our data suggest that (1) sampling effort was consistent over the study period; and (2) changes in estimates from the population census represented real changes in population density. Changes in observed numbers were represented most adequately by a quadratic regression model ( $F = 10.42$ ,  $df = 2$  and  $8$ ,  $P =$

TABLE 1. Number of Merlins caught (number first caught as adults/number first caught as nestlings) and released in the study area between 1984 and 1995, and number recaptured as breeding birds in subsequent years.

Released		Year recaptured												Never recaptured
Year	No.	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	
<b>Males</b>														
1984	0/26	—/0	—/4	—/2	—/1	—/1	—/1	—/0	—/0	—/0	—/0	—/0	—/0	—/22
1985	5/36		1/1	0/1	2/0	1/1	1/0	0/0	0/0	0/0	0/0	0/0	0/0	3/33
1986	4/41			3/3	1/7	0/3	0/0	0/1	0/0	0/0	0/0	0/0	0/0	1/32
1987	5/48				2/2	1/3	1/4	0/1	0/1	0/0	0/0	0/0	0/0	2/43
1988	4/57					0/2	0/5	0/1	0/0	0/0	0/0	0/0	0/0	4/51
1989	6/59						0/1	0/4	0/0	0/0	0/0	0/1	0/0	6/54
1990	2/64							1/1	1/3	0/2	0/1	0/2	0/0	1/58
1991	4/69								0/4	0/2	0/4	1/1	0/2	3/61
1992	1/54									0/1	0/5	0/5	0/2	1/45
1993	0/38										—/0	—/1	—/3	—/35
1994	4/51											1/0	1/3	2/48
1995	8/54												2/0	6/54
<b>Females</b>														
1984	0/26	—/1	—/1	—/1	—/0	—/0	—/0	—/0	—/0	—/0	—/0	—/0	—/0	—/25
1985	8/37		3/0	3/0	3/0	2/0	1/0	0/0	0/0	0/0	0/0	0/0	0/0	3/37
1986	9/41			4/2	1/2	2/3	0/1	0/2	0/1	0/0	0/0	0/0	0/0	4/38
1987	7/48				1/3	0/2	0/0	0/0	0/0	0/0	0/0	0/0	0/0	6/44
1988	11/41					4/0	1/0	1/0	0/0	0/0	0/0	0/0	0/0	7/41
1989	14/51						7/3	4/3	3/3	0/0	0/0	0/0	0/0	5/47
1990	12/47							2/0	4/0	1/0	1/0	1/0	0/0	7/47
1991	11/64								3/2	1/1	0/1	0/1	0/0	7/62
1992	8/64									4/3	4/1	2/1	1/2	2/60
1993	4/63										2/0	1/0	0/1	2/62
1994	12/54											6/2	2/0	6/52
1995	14/68												3/3	11/65

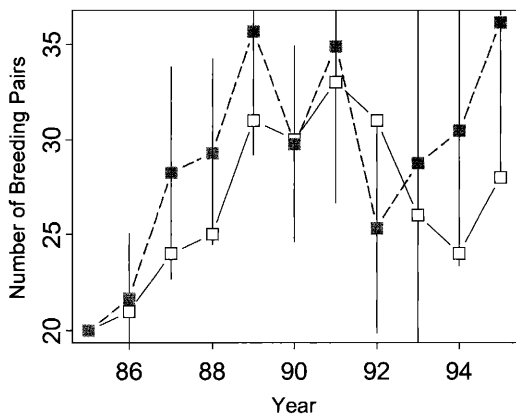


FIG. 1. Comparison of estimates of the number of breeding pairs obtained by direct counts during the population census (open boxes and solid lines), and the Jolly-Seber method (closed boxes and dashed lines). Standard errors for the Jolly-Seber estimates are indicated.

0.006,  $R^2 = 0.72$ ), emphasizing the parabolic shape of the plot (Fig. 1). This pattern of change suggests that breeding numbers were fluctuating around an upper limit.

*Model tests.*—We started by modeling capture rates (Fig. 2). Model 1 represented the fully parameterized model, with the effects of sex, time, age, and natal origin retained. To examine whether the two-age model was necessary, we compared model 2 with model 1. The highly significant increase in deviance ( $\chi^2 = 48.13$ ,  $df = 18$ ,  $P < 0.001$ ) suggested that substantial differences occurred in capture probabilities between first-year birds and adults. We then sought to reduce variation in capture rates by dropping time-specific effects. A comparison of model 3 with model 1 indicated that time effects on capture rates of adults were not statistically significant ( $\chi^2 = 40.66$ ,  $df = 29$ ,  $P = 0.073$ ). In contrast, time effects on capture rates of juveniles were highly significant (model 4 vs. model 3,  $\chi^2 = 70.26$ ,  $df = 24$ ,  $P < 0.001$ ). In subsequent models, we retained time-specificity

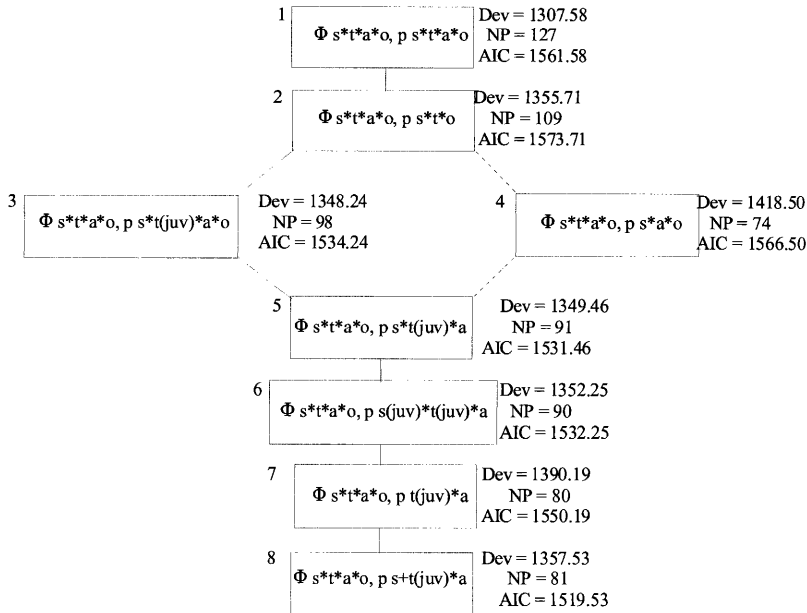


FIG. 2. Progression of model tests (models 1 to 8) on capture rates. In each case, deviance, number of estimable parameters (Np), and the Akaike Information Criterion (AIC) are indicated; s = sex, t = time, a = age, and o = natal origin.

for juvenile capture rates. The effect of natal origin on capture rates was not statistically significant (model 5 vs. model 3,  $\chi^2 = 1.22$ ,  $df = 7$ ,  $P = 0.99$ ). Sex did not exert a substantial influence on capture rates of adults (model 6 vs. model 5,  $\chi^2 = 2.79$ ,  $df = 1$ ,  $P = 0.095$ ) but did strongly influence capture rates of juveniles (model 7 vs. model 6,  $\chi^2 = 37.94$ ,  $df = 10$ ,  $P < 0.001$ ). We hypothesize that juvenile males and females had significantly different capture probabilities from year-to-year, but the pattern of variation was parallel. A comparison of models 8 and 6 confirmed that this assumption was warranted ( $\chi^2 = 5.28$ ,  $df = 9$ ,  $P = 0.81$ ).

We next modeled survival rates in an analogous fashion (Fig. 3). We compared model 9 with model 8 to examine whether age specificity was a significant source of variation. The highly significant result ( $\chi^2 = 88.63$ ,  $df = 21$ ,  $P < 0.001$ ) confirmed that juvenile survival rates were substantially different from those of adults. Time specificity could be disregarded for adult survival rates (model 10 vs. model 8,  $\chi^2 = 37.31$ ,  $df = 39$ ,  $P = 0.55$ ), as well as for juvenile survival rates (model 11 vs. model 10,  $\chi^2 = 25.26$ ,  $df = 22$ ,  $P = 0.28$ ). We also had no reason to suspect that natal origin exerted an

effect on adult survival rates (model 12 vs. model 11,  $\chi^2 = 1.66$ ,  $df = 2$ ,  $P = 0.44$ ). Furthermore, adult survival rates were not significantly different between males and females (model 13 vs. model 12,  $\chi^2 = 1.35$ ,  $df = 1$ ,  $P = 0.25$ ). Survival rates of juvenile males and females were significantly different, however (model 14 vs. model 13,  $\chi^2 = 33.65$ ,  $df = 1$ ,  $P < 0.001$ ). Model 13, being the most biologically plausible model and having the lowest AIC score of the models tested (AIC = 1,457.11; Fig. 3), was the baseline model from which the density-dependent models were derived.

Figure 4 contains models used to test for density dependence in survival rates. For adults, a highly significant proportion of the total variance was attributed to density-dependent effects (analysis of deviance,  $F = 26.7$ ,  $df = 1$  and 9,  $P < 0.001$ ). This density-dependent trend was confirmed by a scatterplot of year-specific adult survival rates against changes in population size (Fig. 5). In addition to explaining a substantial amount of variation in adult survival rates, the density-dependent model (model 16) also exhibited a notably lower AIC value of 1,448.46.

Testing for density dependence in juvenile

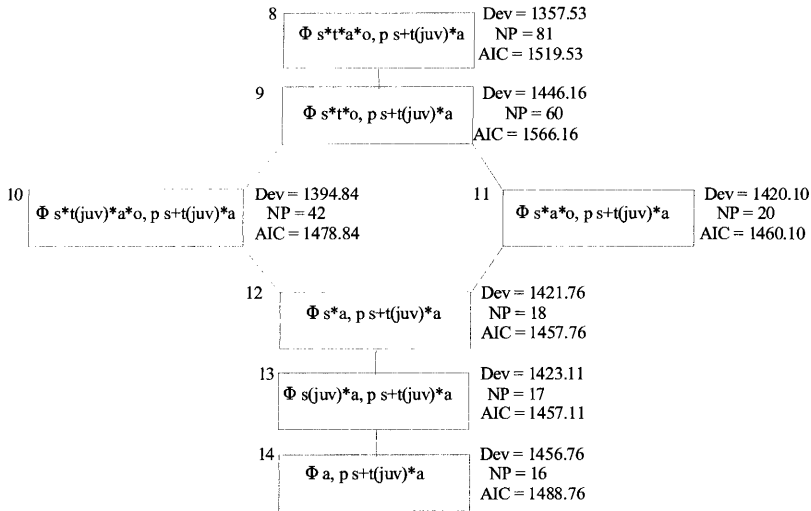


FIG. 3. Progression of model tests (models 8 to 14) on survival rates. See Figure 2 for definitions of labels.

survival rates was somewhat more elaborate. We first tested whether parallelism could be assumed for time and density-specific variation in juvenile males and females. Comparisons of models 18 and 17 ( $\chi^2 = 11.24, df = 11, P = 0.42$ ) and models 20 and 19 ( $\chi^2 = 0.38, df = 1, P = 0.54$ ) confirmed that interactions between time and sex and between density and sex were not significant. Juvenile density-dependent effects also were not significant (analysis of deviance,  $F = 0.21, df = 1$  and  $10, P = 0.66$ ). The absence of density dependence in juvenile survival rates was confirmed by a scatterplot of year-specific juvenile survival rates against changes in population size (Fig. 6).

*Survival and capture estimates.*—Based on the results of the model tests, a final model incorporating density-dependent adult survival rates, but constant sex-specific juvenile survival rates, was accepted. This 18-parameter model had an AIC of 1,448.46 and represented the most biologically plausible and parsimonious representation of the observed capture histories. For adults, mean survival (based on the 12 annual survival estimates from the density-dependent model) was  $0.62 \pm SD 0.11$ . Overall adult capture rates were  $0.55 \pm 0.039$  per year. Average juvenile survival rates were  $0.23 \pm 0.032$  for males and  $0.055 \pm 0.012$  for females, with corresponding mean capture rates of  $0.10 \pm 0.075$  and  $0.58 \pm 0.23$ .

## DISCUSSION

The apparent stability of many animal populations has led to a long-standing debate about the nature and prevalence of density dependence and the role it plays in population dynamics (see Turchin 1995). Interest in factors that could have contributed to the observed stability of their study populations prompted a number of researchers to examine the issue more closely (e.g. Ekman 1984, Newton and Marquiss 1986). Life-history theory suggests that conditions of increasing density can influence population dynamics through the suppression of survival or fecundity (Stubbs 1977, Fowler 1981, Stearns 1992). Although density-dependent effects have been documented in a few species of birds (see Newton 1998), empirical demonstrations of this relationship are uncommon (Sinclair 1989).

Although we did not examine the effects of density on fecundity, we have demonstrated a strongly negative relationship between density and adult survival. Survival rates of juveniles, however, appeared to fluctuate stochastically and independent of density. Thus, the parents, not the young, bore the brunt of density dependence. Other limiting factors, such as food availability or weather conditions, may have played a more important role in influencing juvenile survival.

### Adults

15	$\Phi t(\text{adt}) * s(\text{juv}) * a, p s+t(\text{juv}) * a$	Dev = 1408.87 NP = 27 AIC = 1462.87
16	$\Phi d(\text{adt}) * s(\text{juv}) * a, p s+t(\text{juv}) * a$	Dev = 1412.46 NP = 18 AIC = 1448.46
13	$\Phi s(\text{juv}) * a, p s+t(\text{juv}) * a$	Dev = 1423.11 NP = 17 AIC = 1457.11

### Juveniles

17	$\Phi t(\text{juv}) * s(\text{juv}) * a, p s+t(\text{juv}) * a$	Dev = 1397.96 NP = 39 AIC = 1475.96
18	$\Phi s(\text{juv})+t * a, p s+t(\text{juv}) * a$	Dev = 1409.20 NP = 28 AIC = 1465.20
19	$\Phi s(\text{juv}) * d * a, p s+t(\text{juv}) * a$	Dev = 1422.45 NP = 19 AIC = 1460.45
20	$\Phi s(\text{juv})+d * a, p s+t(\text{juv}) * a$	Dev = 1422.83 NP = 18 AIC = 1458.83

FIG. 4. Models (numbers 15 to 20) used to investigate density dependence. See Figure 2 for definitions of labels.

Although juvenile survival rates were not density dependent, they differed significantly between males and females, with an average of 23% of males and 5.5% of females surviving

their first year. This suggests that juvenile males were more likely to survive and return to breed than were juvenile females. However, permanent emigration is indistinguishable

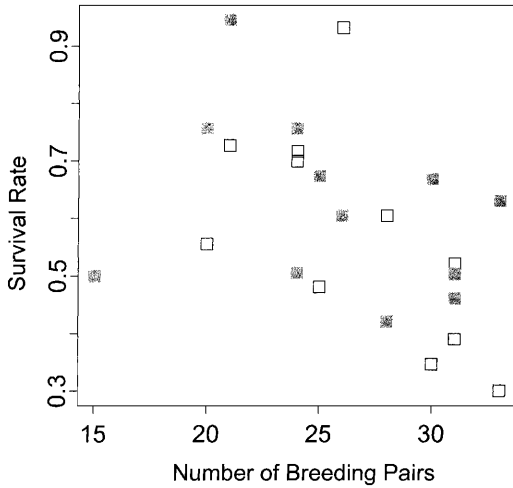


FIG. 5. Yearly survival of adult male (open boxes) and female (filled boxes) Merlins as a function of breeding density.

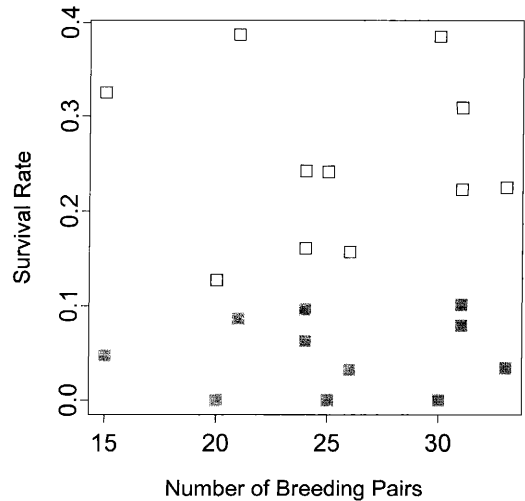


FIG. 6. Yearly survival of juvenile male (open boxes) and female (filled boxes) Merlins as a function of breeding density.

from mortality in standard capture-recapture models such as the ones we used. The discrepancy in survival of juvenile males and females may have resulted from females showing a higher tendency to avoid breeding in their natal area rather than experiencing lower survival. We tested this provisionally by comparing the number of band recoveries of males and females under the assumption that lower female survival would be reflected in a larger number of band returns for females. Of 538 males and 541 females, 27 males (5.0%) and 26 females (4.8%) were recovered dead at or before they had reached one year old. This difference was not statistically significant ( $\chi^2 < 0.001$ ,  $df = 1$ ,  $P = 0.98$ ). We believe that the higher loss of females during their first year represented a greater tendency for females to disperse from the natal area (i.e. lower natal philopatry) rather than lower survival.

Capture rates were also substantially lower for juvenile males than females; only 10% of surviving juvenile males were captured at age one compared with 55% of juvenile females. Males exhibit a significant delay in age at first breeding, with 27 to 37% of males breeding for the first time at age one, but almost all by age two (Lieske et al. 1997). Females, on the other hand, exhibit virtually no delay in first breeding, with 80 to 81% of females breeding for the first time at age one (Lieske et al. 1997). We con-

clude that the lower first-year capture rate for males resulted from their absence from the breeding population, which decreased the probability of capture. After one year, when sex-specific discrepancies in the likelihood of breeding were absent, differences in capture rates disappeared.

Two questions remain with regard to adult survival: (1) how is density dependence mediated, and (2) what role does it play in the dynamics of the population? In answering the first question, we need to consider that this study population has attained one of the highest breeding densities recorded for the species (Sodhi et al. 1992). If density dependence exerts its greatest effect at high densities, as in other "K-selected" species (Fowler 1981), then it is in our study population that we would expect a measurable effect. This was demonstrated by the results of the model tests. According to Milne (1962), competition is the one factor capable of acting in a perfectly density-dependent manner. It seems that the simplest explanation for the observed relationship is that competition for some limiting resource, such as food or space, has increased with density. It may be that nest defense is more energetically costly when there are more potential intruders, or that larger numbers of birds are competing for prey in limited supply (either through exploitation of available prey or interference between foraging birds). In either event, survival



of adults was depressed following years of high breeding densities.

According to Poethke and Kirchberg (1987), any factor suppressing survival in a negatively density-dependent manner can strongly influence the long-term stability and dynamics of populations. The obvious outcome of density-dependent adult survival rates will be that for a given range of population densities, variation in the number of experienced birds returning to breed each year will be reduced relative to a population with random (or unpredictable) fluctuations in survival. In this case, density-dependent regulation of adult survival will act to stabilize variation in population size from year to year, thereby contributing to the long-term persistence of the population (Royama 1977, Murdoch 1994).

The use of self-regulating mechanisms to explain long-term stability has a long history in ecology (Cappuccino 1995) but has been notoriously difficult to demonstrate in practice. Even in taxa that exhibit well-developed territorial behavior, such as birds, detection of self-regulating mechanisms is difficult (Murdoch 1994). Our findings achieve special significance in this context, which we attribute to a number of factors. First, we avoided the statistical pitfalls encountered in studies that focus on time-series analyses to detect density dependence (see Lebreton and Clobert 1991). The detection problems associated with studies conducted at this scale are formidable and largely unresolved (Lebreton and Clobert 1991, Wolda and Dennis 1993, Murdoch 1994). Second, as pointed out by Cappuccino (1995:6): the question is not "is it regulated?" but "how is it regulated?" Sharing this point of view, we looked for evidence of density dependence at the level at which it would most likely be detected, in this case at the level of annual survival of breeding birds.

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#### LITERATURE CITED

- ARCESE, P., J. N. M. SMITH, W. M. HOCHACHKA, C. M. ROGERS, AND D. LUDWIG. 1992. Stability, regulation, and the determination of abundance in an insular Song Sparrow population. *Ecology* 73: 805-822.
- BEGON, M. 1983. Abuses of mathematical techniques in ecology: Applications of Jolly's capture-recapture method. *Oikos* 40:155-158.
- BLUMS, P., A. MEDNIS, I. BAUGA, J. D. NICHOLS, AND J. E. HINES. 1996. Age-specific survival and philopatry in three species of European ducks: A long-term study. *Condor* 98:61-74.
- CAPPUCCINO, N. 1995. Population dynamics: New approaches and synthesis. Pages 1-3 in *Population dynamics: New approaches and synthesis* (N. Cappuccino and P. W. Price, Eds.). Academic Press, San Diego.
- CAROTHERS, A. D. 1979. Quantifying unequal catchability and its effect on survival estimates in an actual population. *Journal of Animal Ecology* 48: 863-869.
- CLOBERT, J., AND J.-D. LEBRETON. 1985. Dependence de facteurs de milieu dans les estimations de taux de survie par capture-recapture. *Biometrics* 41:1031-1037.
- CLOBERT, J., AND J.-D. LEBRETON. 1991. Estimation of demographic parameters in bird populations. Pages 75-104 in *Bird population studies* (C. M. Perrins, J.-D. Lebreton, and G. J. M. Hirons, Eds.). Oxford University Press, Oxford.
- CORMACK, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51:429-438.
- EBERHARDT, L. L. 1985. Assessing the dynamics of wild populations. *Journal of Wildlife Management* 49:997-1012.
- EKMAN, J. 1984. Density-dependent seasonal mortality and population fluctuations of the temperate-zone Willow Tit (*Parus montanus*). *Journal of Animal Ecology* 53:119-134.
- FELDSINE, J. W., AND L. W. OLIPHANT. 1985. Breeding behavior of the Merlin: The courtship period. *Raptor Research* 19:60-67.
- FOWLER, C. W. 1981. Density dependence as related to life history strategy. *Ecology* 62:602-610.
- HOUSTON, C. S., AND A. SCHMIDT. 1981. History of Richardson's Merlin in Saskatchewan. *Blue Jay* 39:30-37.
- JAMES, P. J., I. G. WARKENTIN, AND L. W. OLIPHANT.

1989. Turnover and dispersal in urban Merlins *Falco columbarius*. *Ibis* 131:426–429.
- JOLLY, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52:225–247.
- LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs* 62:67–118.
- LEBRETON, J.-D., AND J. CLOBERT. 1991. Bird population dynamics, management, and conservation: The role of mathematical modeling. Pages 105–125 in *Bird population studies* (C. M. Perrins, J.-D. Lebreton, and J. M. Hiron, Eds). Oxford University Press, Oxford.
- LEBRETON, J.-D., R. PRADEL, AND J. CLOBERT. 1993. The statistical analysis of animal populations. *Trends in Ecology and Evolution* 8:91–95.
- LIESKE, D. J., L. W. OLIPHANT, P. C. JAMES, I. G. WARKENTIN, AND R. H. M. ESPIE. 1997. Age of first breeding in Merlins (*Falco columbarius*). *Auk* 114:288–290.
- LOERY, G., AND J. D. NICHOLS. 1985. Dynamics of a Black-capped Chickadee population, 1958–1983. *Ecology* 66:1195–1203.
- MILNE, A. 1962. On a theory of natural control of insect population. *Journal of Theoretical Biology* 3:19–50.
- MURDOCH, W. W. 1994. Population regulation in theory and practice. *Ecology* 75:271–287.
- NEWTON, I. 1998. *Population limitation in birds*. Academic Press, San Diego.
- NEWTON, I., AND M. MARQUISS. 1986. Population regulation in Sparrowhawks. *Journal of Animal Ecology* 55:463–480.
- NEWTON, I., P. ROTHERY, AND I. WYLLIE. 1997. Age-related survival in female Sparrowhawks *Accipiter nisus*. *Ibis* 139:25–30.
- NEWTON, I., I. WYLLIE, AND P. ROTHERY. 1993. Annual survival of Sparrowhawks *Accipiter nisus* breeding in three areas of Britain. *Ibis* 135:49–60.
- OLIPHANT, L. W., AND E. HAUG. 1985. Productivity, population density and rate of increase of an expanding Merlin population. *Raptor Research* 19:56–59.
- POETHKE, H. J., AND M. KIRCHBERG. 1987. On the stabilizing effect of density-dependent mortality factors. *Oecologia* 74:156–158.
- POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE, AND J. E. HINES. 1990. *Statistical inference for capture-recapture experiments*. Wildlife Monographs No. 107.
- PRADEL, R. J., J. CLOBERT, AND J.-D. LEBRETON. 1990. Recent developments for the analysis of multiple capture-recapture data sets: An example concerning two Blue Tit populations. *Ring* 13:193–204.
- RICKLEFS, R. E. 1972. Fecundity, mortality, and avian demography. Pages 366–435 in *Breeding biology of birds* (D. S. Farner, Ed.). Proceedings of a symposium on breeding behavior and reproductive physiology of birds. National Academy of Sciences, Washington, D. C.
- ROYAMA, T. 1977. Population persistence and density dependence. *Ecological Monographs* 47:1–35.
- SEBER, G. A. F. 1965. A note on the multiple recapture census. *Biometrika* 52:249–259.
- SEBER, G. A. F. 1982. A review of estimating animal abundance. *Biometrics* 42:267–292.
- SINCLAIR, A. R. E. 1989. Population regulation in animals. Pages 197–241 in *Ecological concepts* (J. M. Cherrett, Ed.). Blackwell Scientific Publications.
- SODHI, N. S., P. C. JAMES, I. G. WARKENTIN, AND L. W. OLIPHANT. 1992. Breeding ecology of urban Merlins (*Falco columbarius*). *Canadian Journal of Zoology* 70:1477–1483.
- STEARNS, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford.
- STUBBS, M. 1977. Density dependence in the life-cycles of animals and its importance in *K*- and *r*-strategies. *Journal of Animal Ecology* 46:677–688.
- TURCHIN, P. 1995. Population regulation: Old arguments and new synthesis. Pages 19–40 in *Population dynamics: New approaches and synthesis* (N. Cappuccino and P. W. Price, Eds.). Academic Press, San Diego.
- 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.
- WOLDA, H., AND B. DENNIS. 1993. Density-dependence tests are they? *Oecologia* 95:581–591.

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