

- bill size constraints: a comparative study of the acceptance of cowbird eggs by old hosts. *Evol. Ecol.* 2: 27-36.
- ROTHSTEIN, S. E. 1975. An experimental and teleonomic investigation of avian brood parasitism. *Condor* 77: 250-271.
- . 1976. Experiments on defenses Cedar Waxwings use against cowbird parasitism. *Auk* 93: 675-691.
- . 1977. Cowbird parasitism and egg recognition of the Northern Oriole. *Wilson Bull.* 89: 21-32.
- SPAW, C. D., & S. ROHWER. 1987. A comparative study of eggshell thickness in cowbirds and other passerines. *Condor* 89: 307-318.

Received 31 October 1988, accepted 3 May 1989.

## Early Nest Departure Does Not Improve the Survival of Lapland Longspur Chicks

ROBERT L. MCLAUGHLIN<sup>1</sup> AND ROBERT D. MONTGOMERIE

*Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada*

In birds, the scattering of broods from the nest site before the chicks are independent (i.e. *brood dispersal*) is usually thought to reduce losses due to nest predation (Lack 1968, Ricklefs 1969). A variety of arguments have been presented to support this assumption. First, nest predation is usually identified as the major source of mortality in avian life histories (Lack 1954). Thus, any trait that reduces the amount of time that chicks spend in the nest should increase survival. Second, in almost all bird species, offspring leave the nest before they are fully developed and thus require further parental care. Although in some species further development involves only learning by the young, in most species there is also a period of physical growth after the young leave the nest (Martin 1987 and references therein). Both the premature nest departure and the fact that chicks move well away from the nest site as soon as they are able indicate that the nest may be a relatively dangerous site. Third, in ground-nesting birds, which tend to suffer a higher risk of nest predation than either tree- or hole-nesters (Ricklefs 1969, Best and Stauffer 1980, Loiselle and Hoppes 1983, Wilcove 1985), chicks leave the nest sooner, everything else being equal.

Although the logic of these arguments seems clear, few studies have presented sufficient data that would allow direct comparison of the survival of broods during the periods of parental care before and after nest departure (Nolan 1978, Dhondt 1979, Ebenmann and Karlsson 1984, Sullivan 1989). We examined the survival rates of Lapland Longspur (*Calcarius lapponicus*) chicks both before and after nest departure to test the proposition that brood dispersal improves chick survival. Maher (1964), in particular, argued that the relatively early nest departure in this species was a

consequence of predation pressure. Moreover, Williamson and Emison (1971) felt that the most plausible explanation for a 2-3 day difference in nestling periods in two longspur populations in Alaska was the difference in predation pressure. Also, chicks of the closely related Snow Bunting (*Plectrophenax nivalis*) remain in their nests about 4 days longer than longspurs and are thought to suffer less nest predation because they nest in rock crevices whereas longspurs nest in exposed cups on the open tundra (Lyon and Montgomerie 1987). This interspecific difference in the timing of nest departure is independent of size and developmental rates (Maher 1964) and therefore seems explicable only as a behavioral response to the risk of predation.

We collected data in June and July of 1981 and 1982 at Sarcpa Lake, Melville Peninsula, Northwest Territories, Canada, as part of a study on the effects of brood dispersal on the foraging behavior of parents (McLaughlin and Montgomerie 1989). We observed 7 broods (34 chicks) in 1981 and 10 broods (45 chicks) in 1982. Nests were checked at least once every other day during the 8-9 day nestling period. Nestlings were color-banded at age 6-8 days so that they could be individually identified. After nest departure, we searched for dispersed chicks, and we recorded the location and identity of each one encountered. Because these birds were easy to observe on the open tundra, we were often able to follow parents on their foraging itineraries and locate all of the young that they fed. Soon after nest departure (8-9 days after hatching) parents divided their broods into two separate units (each tended by a single parent) until independence, ca. 23 days after hatching or 14-15 days after nest departure (McLaughlin and Montgomerie 1985). By 18 days after hatching (9-10 days after nest departure), young longspurs began feeding themselves and were more mobile. Because they were increasingly difficult to locate as they became more mobile, we restricted our analyses to chicks  $\leq 17$  days

<sup>1</sup> Present address: Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montréal, Québec H3A 1B1, Canada.

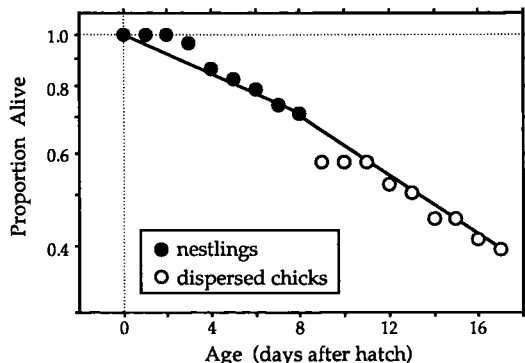


Fig. 1. Proportion of 79 Lapland Longspur chicks (from 17 broods) that survived to different ages during nestling (age 0–8 days) and brood dispersal (age 8–17 days) periods. Slopes of the lines that join the first and last data points in each period give the average daily mortality rate for that period as calculated from equation 3 in Ricklefs (1969).

after hatching (see also McLaughlin and Montgomerie 1989).

Predation accounted for 100% of the chick mortality during the nestling period. We do not know the fate of any chicks that disappeared after nest departure, but we presume that most losses were again due to predation (we have recorded predation on dispersed longspur chicks in other years). A chick was assumed to have died one day after it was last observed alive. Our estimates of survival are conservative because chicks could possibly have survived longer without being seen, especially because inclement weather prevented us from studying each brood every day.

Brood dispersal could have influenced chick survival by increasing either the mean survival rate of chicks or the probability that at least one member of the brood would survive (see Tinbergen 1939, Rubenstein 1982). To assess each of these probabilities, we performed two separate analyses of survival rates: one was on the survival rate of chicks and the other on the survival rate of broods.

We used a life table estimation procedure (Kalbfleisch and Prentice 1980: 15) to calculate *survivorship curves* (i.e. proportion of chicks surviving to different ages) for dependent chicks before and after nest departure. This method of analysis allowed us to include individuals that were removed from the sample partway through the study (i.e. *right-censored*). Data for chicks from 4 broods were right-censored—3 broods (15 chicks) nesting near the edge of our study site moved out of the area shortly after nest departure, and one other chick was only 16 days old when our 1982 field season ended. Such right-censored individuals should be included in survival rate estimates because chicks that live longer are more likely to be censored. Omitting them from the sample is equivalent to treating them as dead and this results

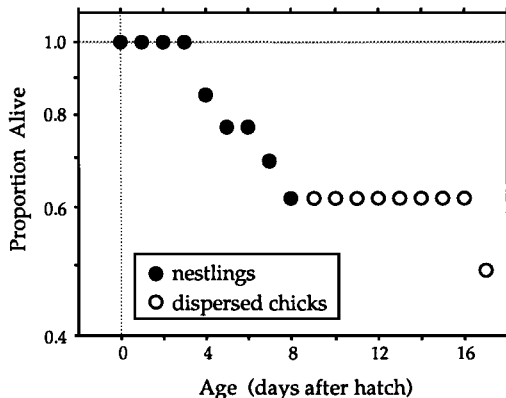


Fig. 2. Proportion of 17 longspur broods with at least one chick alive at different ages after hatching.

in underestimated survival rates. Although preferred, this type of analysis is rarely performed in studies of avian demography because we rarely know whether individuals that disappear from a sample are still alive at that time.

We found that the proportion of chicks alive (log-transformed) declined linearly with age both before and after nest departure (Fig. 1). The average daily mortality rate from hatching to age 17 days was 0.054 (SE = 0.013,  $n = 18$ ) and was independent of age over the entire period ( $r_s = 0.27$ ,  $P > 0.28$ ,  $n = 18$ ). These results are consistent with an exponential model of chick survival, or constant daily mortality rate, through this period (see Ricklefs 1969). Also, the highest daily mortality rate occurred at ages 8 and 9 days when 8 chicks from 6 broods were lost within 24 h of nest departure. This suggests that the immediate consequence of nest departure was increased mortality rates, contrary to our expectation.

To assess the survival rate of broods, we calculated survivorship curves from the proportion of broods with at least one chick alive (log-transformed) at different chick ages. These data were also right-censored when 4 broods were removed from the analysis as described above. During the nestling phase, brood survival (like chick survival) was consistent with an exponential model in that the proportion of whole broods surviving (log-transformed) declined more-or-less linearly with brood age (Fig. 2). After nest departure, however, all broods had at least one chick alive from age 8 to 16 days and brood survival no longer declined exponentially.

To examine whether survival rates changed after nest departure, we compared the survival of chicks in the nestling period with chick survival in the post-nestling period, using a nonparametric Wilcoxon test (Kalbfleisch and Prentice 1980: 146). This method of analysis is distribution-free, compensates for the fact that sample sizes decrease with age (gradually reducing the accuracy of survival rate estimates), and

allows for the analysis of right-censored data. Probabilities for these tests are approximations based on asymptotic distributions, but they can be close to exact probabilities even for sample sizes as small as ours (Kalbfleisch and Prentice 1980).

Differences among broods accounted for 87% of the total variation in chick survival times (days after hatching), differences among chicks from the same brood accounted for only 13% of this variation (one-way ANOVA). (Survival times [in days] were log-transformed to equalize variances across broods.) This difference in the proportion of variance explained was due to the fact that losses during the nestling period involved entire broods at a time, whereas partial brood losses occurred after nest departure. The results of the ANOVA also indicate that the survival of an individual chick is related to the survival of its brood members, hence the survival of chicks within broods cannot be considered independent. To compare chick survival rates, we used mean chick survival for each brood. To compare brood survival rates, we used only the maximum chick survival for each brood to avoid problems with the individual samples from each brood not being independent.

Contrary to expectation, mean chick survival did not increase after nest departure ( $z = -0.70$ ,  $P > 0.70$ ; one-tailed Wilcoxon test). On the other hand, the probability of at least one brood member surviving was significantly higher after nest departure ( $z = 1.74$ ,  $P = 0.04$ ; one-tailed Wilcoxon test). Thus, although the overall rate of chick loss from the population changed little after nest departure (Fig. 1), chick mortalities were distributed more evenly among the remaining broods after chicks became spatially separated (Fig. 2). This occurred because losses during the nestling period involved entire broods at a time, whereas losses after nest departure involved only individual chicks largely independent of other brood members.

Because nest departure does not appear to improve chick survival, we question Williamson and Emison's (1971) assertion that nest predation was most likely responsible for the observed difference in nestling period between two arctic populations of this species. Although they presented limited data, it seems to us that the difference in daylength or food availability between these two sites could have influenced chick growth rate, which alone could have determined the timing of nest departure. We suggest that nest predation should no longer be invoked to explain differences between species or populations without testing reasonable alternatives (see McLaughlin and Montgomerie 1989).

Our analyses also provide the first empirical evidence that brood dispersal can reduce the variance in parental reproductive success, measured here as the number of offspring that reach independence. As some workers have suggested (Tinbergen 1939, Rubenstein 1982), brood dispersal may be advantageous because

it maximizes the probability that at least one offspring from a brood survives, even if mean offspring survival rate is not affected. Bulmer (1984) questioned the logic of these "bet-hedging" arguments and showed that the apparent reduction in the variance of offspring survival is due to selection on mean fitness in populations where survival is density-dependent. From our data and Bulmer's (1984) equation 7, we estimate that the selective advantage (Bulmer's  $s$ ) of having chicks dispersed rather than clumped during the period from nest departure to age 17 days is less than 0.03. Values of this magnitude are thought to be of little evolutionary importance (Bulmer 1984) but "bet-hedging" appears to be adaptive in a variety of contexts (Seger and Brockman 1987) and should probably not be ruled out as a potential advantage for brood dispersal.

Although unexpected, our study was consistent with the limited data available on fledgling survival in other species. In Great Tits (*Parus major*; Dhondt 1979) and Yellow-eyed Juncos (*Junco phaeotus*; Sullivan 1989), chick survival rates were not significantly different after they left the nest, though the survival of Yellow-eyed Juncos did improve once they could fly proficiently and thereby avoid most predators. In Dark-eyed Juncos (*Junco hyemalis*; Wolf et al. 1988) and Prairie Warblers (*Dendroica discolor*; Nolan 1978), the survival rates of chicks before and after nest departure were similar but were not compared statistically. Moreover, Ebenmann and Karlsson (1984) found that daily mortality rates of Eurasian Blackbird (*Turdus merula*) offspring were actually about 70% higher during the first 5 days after nest departure than they were during the nestling period.

In longspurs, a variety of factors may account for the fact that chick mortality rate does not decline after nest departure. First, chicks begin to call after brood dispersal to indicate their location to parents. Their calling and greater mobility may make chicks more conspicuous to predators when they cannot fly well enough to escape easily. Second, because they become widely dispersed and are tended by only a single parent (McLaughlin and Montgomerie 1985), the chances of a chick being lost or abandoned are probably increased. Third, it is not possible for a parent to protect all of the members of its dispersed brood from the rigors of arctic weather and they may be too widely dispersed to bring together quickly. While chicks are considered endothermic by age 7 days (Maher 1964), it is not clear that they can tolerate prolonged cold weather as well as adults. These factors may also account for the high mortality observed immediately following nest departure (Fig. 1; see also Ebenmann and Karlsson 1984).

Our data and analysis are suggestive but do not demonstrate unequivocally that mortality rates do not decline after nest departure. A completely convincing demonstration would require that nestlings be experimentally confined to a nest for a few days after

their usual departure. It is possible, for example, that chicks become increasingly conspicuous as they age and that predation rates on chicks >8 days old would have been much higher than observed if those chicks had not left the nest and dispersed. The fact that mortality rates do not increase systematically during the nestling phase (Fig. 1) makes this unlikely but our sample size may have been too small to detect a slight increase. It is clear, however, that the long-held notion that brood dispersal decreases predation risk must be reexamined.

This study was supported by operating, equipment, and northern supplement grants from the Natural Sciences and Engineering Research Council of Canada and Northern Scientific Training Grants from Indian and Northern Affairs Canada. We are particularly grateful to the Eastern Arctic Scientific Resource Centre at Igloolik for logistic support and for the use of their satellite field station at Sarcpa Lake. Ralph Cartar, Elsie Krebs, Bruce Lyon, and Mary Reid provided field assistance and endless entertainment. Kim Sullivan kindly provided copies of unpublished manuscripts. We thank Jim Mountjoy, Val Nolan Jr., Pat Weatherhead, and an anonymous reviewer for useful comments on the manuscript.

## LITERATURE CITED

- BEST, L. B., & D. F. STAUFFER. 1980. Factors affecting the nesting success in riparian bird communities. *Condor* 82: 149-158.
- BULMER, M. G. 1984. Risk avoidance and nesting strategies. *J. Theor. Biol.* 106: 529-535.
- DHONDT, A. A. 1979. Summer dispersal and survival of juvenile Great Tits in southern Sweden. *Oecologia* 42: 139-158.
- EBENMANN, B., & J. KARLSSON. 1984. Urban blackbirds (*Turdus merula*) from egg to independence. *Ann. Zool. Fennica* 21: 249-251.
- KALBFLEISCH, J. D., & R. L. PRENTICE. 1980. The statistical analysis of failure time data. Toronto, Wiley Press.
- LACK, D. 1954. The natural regulation of animal numbers. London, Oxford Univ. Press.
- . 1968. Ecological adaptations for breeding in birds. London, Chapman and Hall.
- LOISELLE, B. A., & W. G. HOPPES. 1983. Nest predation in insular and mainland lowland forest in Panama. *Condor* 85: 93-95.
- LYON, B. E., & R. D. MONTGOMERIE. 1987. Ecological correlates of incubation feeding: a comparative study of high arctic finches. *Ecology* 68: 713-722.
- MAHER, W. J. 1964. Growth rate and the development of endothermy in the Snow Bunting (*Plectrophenax nivalis*) and the Lapland Longspur (*Calcarius lapponicus*) at Barrow, Alaska. *Ecology* 45: 520-528.
- MARTIN, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. *Annu. Rev. Ecol. Syst.* 18: 453-487.
- MCLAUGHLIN, R. L., & R. D. MONTGOMERIE. 1985. Brood division by Lapland Longspurs. *Auk* 102: 687-695.
- , & ———. 1989. Brood dispersal and multiple central place foraging by Lapland Longspur parents. *Behav. Ecol. Sociobiol.* In press.
- NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler (*Dendroica discolor*). *Ornithol. Monogr.* 26: 1-595.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contrib. Zool.* 9: 1-48.
- RUBENSTEIN, D. I. 1982. Risk, uncertainty, and evolutionary strategies. Pp. 91-111 in *Current problems in sociobiology* (King's College Sociobiology Group, Eds.). Cambridge, Cambridge Univ. Press.
- SEGER, J., & H. J. BROCKMANN. 1987. What is bet-hedging? *Oxford Surv. Evol. Biol.* 4: 182-211.
- SULLIVAN, K. A. 1989. Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaeonotus*). *J. Anim. Ecol.* 58: 275-286.
- TINBERGEN, N. 1939. The behavior of the Snow Bunting in spring. *Trans. Linnaean Soc. New York* 5: 1-95.
- WILCOVE, D. S. 1985. Nest predation in forest tracts and the decline of forest songbirds. *Ecology* 66: 1211-1214.
- WILLIAMSON, F. S. L., & W. B. EMISON. 1971. Variation in the timing of breeding and molt of the Lapland Longspur (*Calcarius lapponicus*) in Alaska, with relation to differences in latitude. *Bioscience* 21: 701-707.
- WOLF, L., E. D. KETTERSON, & V. NOLAN JR. 1988. Parental influence on growth and survival of Dark-eyed Junco young: do parental males benefit? *Anim. Behav.* 36: 1601-1618.