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PATTERNS OF HATCHING SUCCESS IN SUBARCTIC BIRDS[1]

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Abstract. Data from a single subarctic locality are used to test Ricklefs' general conclusions regarding patterns of nesting mortality in arctic birds. They provide additional evidence that hatching success is greater among arctic than among Temperate Zone passerines. However, they do not indicate important differences in hatching success between ground-nesting birds with precocial young and those with altricial young, nor do they confirm that predator-induced nesting losses are density dependent in arctic regions. Predation may be a more important cause of nesting failure than Ricklefs acknowledged. Differences in our findings result in part from differences in sampling methods. Future analyses of nesting mortality should combine data from studies of selected species with those from regional studies.

Data on nesting success have now been compiled for a sufficient number of bird species (e.g., Lack 1954, Nice 1957, Ricklefs 1969) that broad studies of reproductive success can be attempted. Recently, Ricklefs (1969: ii) has attempted to analyze nesting mortality "as a feature of the environment and as a selective force in the evolution of reproductive strategies." Several of his conclusions pertain particularly to arctic birds, but because nesting data on arctic species, particularly passerines, are scarce, these conclusions require confirmation. Ricklefs' data were compiled from the studies of many people, in diverse areas, and in different years. In the arctic, year-to-year differences in predator abundance or weather may be pronounced, and these variables can strongly affect breeding success (Jehl and Hussell 1966). Large samples will minimize their effect, but such samples may be available only in years when certain species are particularly abundant or in years of higher-than-average productivity.

By studying nesting success of an entire fauna in one area over a period of years, these biases would be eliminated. The only published studies that approach this goal (Williamson, Thompson, and Hines 1966) were conducted over only two breeding seasons and are insufficient. In this paper I present data gathered at one locality, Churchill, Manitoba, in the summers of 1964–1967. Although the results of this study are strictly applicable only to the Churchill situation, they can be used to test the validity of Ricklefs' conclusions.

METHODS

Churchill, Manitoba, is approximately 5 miles north of the tree line, on the west shore of Hudson Bay. In the course of field studies there in the summers of 1964–1967, I compiled nesting data on all species of birds. Additional data were provided by L. C. Binford, R. M. Evans, D. J. T. Hussell, D. F. Parmelee, C. B. Peake, W. Rees, C. G. Yarbrough. Data on hatching success and on the major sources of egg loss were determined for as many nests as possible, including those destroyed before the clutch was complete as well as those suffering losses during the incubation period. The conventional method of computing hatching success (eggs hatch/eggs laid) was used despite its limitations. Mayfield's (1961) important suggestions for standardizing these calculations could not be employed because data were gathered in various ways by many persons; however, the results are comparable to those of most previous studies.

Assigned categories of egg loss are largely self-explanatory, with the following exceptions. "Infertile" includes only eggs *examined* and found to contain no trace of an embryo. Losses to "weather" include clutches deserted after severe storms and, in the case of Bonaparte's Gulls, eggs blown from the nest in periods of high winds. "Failed to hatch" includes eggs accidentally cracked by the adults or by human observers, eggs containing dead embryos, and, in a few cases, shorebird eggs containing living chicks that failed to hatch with the rest of the clutch and were deserted. Except for White-crowned Sparrows in 1967, the data for all years were combined, as there was no evidence for annual differences in hatching success or sources of egg loss.

As most of my studies were concerned with precocial species, I was unable to gather adequate data on fledging success or causes of chick mortality.

RESULTS AND DISCUSSION

The results of the Churchill study are presented by species in Table 1. Hatching success was generally high, but two species for which there are adequate data were notably less successful: Hudsonian Curlews hatched less than 50% of their eggs, the bulk of their losses coming through pre-

[1] Received April 16, 1970; accepted August 24, 1970.

TABLE 1. Hatching success and sources of egg mortality for birds at Churchill, Manitoba, 1964–1967, by species

Species	Nests	Eggs hatch/eggs laid	Hatching success	Source of egg mortality[a]
Arctic Loon *Gavia arctica*	3	5/6	83%	cracked eggs 1 (1)
Canada Goose *Branta canadensis*	19	84/91	92%	infertile 2 (2) predation 5 (1)
Green-winged Teal *Anas carolinensis*	4	9/32	28%	predation 23 (3)
Shoveler *Spatula clypeata*	6	16/29	55%	deserted 10 (1) failed to hatch 3 (1)
Oldsquaw *Clangula hyemalis*	1	8/8	100%	
Common Eider *Somateria mollisima*	3	12/12	100%	
Pigeon Hawk *Falco columbarius*	1	2/4	50%	failed to hatch 2 (1)
Willow Ptarmigan *Lagopus lagopus*	2	16/17	94%	failed to hatch 1 (1)
Semipalmated Plover *Charadrius semipalmatus*	15	46/55	84%	deserted 4 (1) infertile 3 (3) unknown 2 (2)
Golden Plover *Pluvialis dominica*	8	27/32	84%	deserted 4 (1) failed to hatch 1 (1)
Common Snipe *Gallinago gallinago*	3	2/11	18%	infertile 1 predation 8 (2)
Hudsonian Curlew *Numenius phaeopus*	25	40/82	49%	deserted, human interference? 4 (1) failed to hatch 3 (3) infertile 3 (3) predation 28 (9) weather 4 (1)
Lesser Yellowlegs *Tringa flavipes*	3	8/11	73%	deserted, human interference? 3 (1)
Solitary Sandpiper *Tringa solitaria*	1	0/4	0%	predation 4 (1)
Least Sandpiper *Calidris minutilla*	56	176/219	80%	deserted 4 (1) failed to hatch 3 (3) infertile 11 (5) predation 19 (6) weather 6 (2)
Dunlin *Calidris alpina*	13	50/51	98%	infertile 1 (1)
Short-billed Dowitcher *Limnodromus griseus*	8	30/30	100%	
Stilt Sandpiper *Micropalama himantopus*	43	138/166	83%	disappeared 2 (2) failed to hatch 4 (4) infertile 2 (2) predation 12 (5) unknown 3 (2)
Semipalmated Sandpiper *Calidris pusilla*	8	31/32	97%	failed to hatch 1 (1)
Hudsonian Godwit *Limosa haemastica*	12	39/46	85%	failed to hatch 3 (2) predation 4 (1)
Northern Phalarope *Phalaropus lobatus*	4	12/16	75%	predation 4 (1)
Parasitic Jaeger *Stercorarius parasiticus*	2	4/4	100%	
Bonaparte's Gull *Larus philadelphia*	13	16/38	42%	failed to hatch 1 (1) weather 21 (8)
Flicker *Colaptes auratus*	1	6/6	100%	
Horned Lark *Eremophila alpestris*	2	7/7	100%	
Robin *Turdus migratorius*	3	6/9	67%	predation 3 (1)
Gray-cheeked Thrush *Hylocichla minima*	1	4/4	100%	
Hoary Redpoll *Acanthis hornemanni*	4	15/16	94%	failed to hatch 1 (1)
Common Redpoll *Acanthis flammea*	13	38/49	78%	deserted 4 (1) infertile 1 (1) unknown 1 (1)
Savannah Sparrow *Passerculus sandwichensis*	17	73/81	90%	deserted 5 (1) failed to hatch 2 (2) infertile 1 (1)
Tree Sparrow *Spizella arborea*	13	46/61	75%	failed to hatch 5 (1) predation 4 (1) unknown 1 (1) weather 5 (1)
Harris' Sparrow *Zonotrichia querula*	24	83/93	89%	failed to hatch 1 (1) predation 4 (1) unknown 5 (4)
White-crowned Sparrow, 1964-1966 *Zonotrichia leucophrys*	22	74/90	82%	deserted 5 (1) infertile 2 (2) predation 4 (1) unknown 5 (2)
1967	24	48/87	55%	predation 4 (1) unknown (2) weather 26 (7)
Smith's Longspur *Calcarius pictus*	30	107/114	94%	disappeared 3 (3) failed to hatch 2 (2) infertile 2 (2)
Lapland Longspur *Calcarius lapponicus*	18	65/81	80%	failed to hatch 1 (1) infertile 1 (1) predation 9 (2) unknown 5 (1)

[a]The first figure gives number of eggs lost; the second figure (in parentheses) gives number of nests

TABLE 2. Hatching success and major sources of egg mortality by groups

Group	Eggs hatch/ eggs laid	Hatching success	Major source of egg mortality
Tree-nesting species			
Passerines (redpolls, thrushes)	63/78	81%	failed to hatch 53%
Nonpasserines (Pigeon Hawk, Bonaparte's Gull, Solitary Sandpiper, Flicker)	24/52	46%	weather 75%
Total	87/130	67%	
Ground-nesting species			
Loons and waterfowl	134/178	76%	predation 64%
Shorebirds (except Solitary Sandpiper)	599/751	80%	predation 54%
Passerines (Horned Lark, sparrows, longspurs)	503/614	82%	weather 28% predation 24% unknown 22%
Tunda-nesting Passerines (Horned Lark, Savannah Sparrow longspurs)	252/283	89%	predation 29%
Others (Willow Ptarmigan, Parasitic Jaeger)	20/21	95%	
Total	1256/1564	80%	

dation by Ravens; Bonaparte's Gulls had a hatching success of only 42%, and 96% of their losses were attributable to adverse weather conditions. In 1967, White-crowned Sparrows hatched only 55% of their eggs as compared to 82% in earlier years; nearly all of the losses were due to flooding (W. Rees, pers. comm.). The general results are shown in Table 2 and may be compared with Ricklefs' (1969) findings.

Nesting success of arctic passerines

In her review Nice (1957) found that hatching success for ground-nesting and tree-nesting altricial birds in the North Temperate Zone approximated 60%. Although his data were few, Ricklefs concluded that nesting success averaged higher for arctic passerines than for Temperate Zone species. The Churchill data support his findings, with the hatching success of passerines averaging 80%, which is higher than that listed in any of the studies cited by Nice (1957: 306–307, Table 1). At Cape Thompson, Alaska, the only other arctic locality from which data are available (Williamson et al. 1966: Tables 13, 14), hatching success was also high (74.6%) but the percentage of nests from which one or more young fledged was slightly lower than among Temperate Zone passerines.

Ricklefs also found that field-nesting and marsh-nesting passerines in the Temperate Zone show higher rates of nest mortality than do tree-nesting species. At the treeline at Churchill no marked differences appeared between ground-nesting and tree-nesting species, but the data from tree-nesters are too few to allow definite conclusions.

Precocial birds

Ricklefs suggested that waterbirds and shorebirds with precocial young have higher nesting success than do ground-nesting passerines (altricial young). However, his comparisons included groups that tend to nest in slightly different habitats. At Churchill, hatching success of ground-nesting passerines as well as nonpasserines approximated 80%. A comparison of groups that nest in similar habitats (shorebirds vs. tundra-nesting passerines) indicated that passerines were slightly more successful (80% vs. 89%).

Predation

A more important conclusion involves the effects of predation, which Ricklefs (1969: 23) held "apparently causes negligible mortality in many arctic species." The general applicability of this conclusion is difficult to evaluate because, as D. J. T. Hussell (pers. comm.) has pointed out, some arctic studies were made near settled areas where trapping may have reduced the abundance of certain mammalian predators. Yet, even in the well-settled Churchill area, where avian predators were generally uncommon during my studies and mammalian predators were almost nonexistent, predation remained the major cause of nesting failure among several groups of birds. Among loons and waterfowl, predation accounted for 64%, and among shorebirds 54%, of all egg losses. The proportion of shorebird eggs lost to predators may be inflated, for one-third of the losses were suffered by Hudsonian Curlews, whose nests composed only 14% of the sample. Yet, as 61% of the egg losses of Stilt Sandpipers and 44% of Least Sandpipers resulted from predation, compared to 69% in the Hudsonian Curlew, the importance of predation is probably only slightly exaggerated. Predation did not appear to be an important cause of nesting failure among tree-nesting species, but the sample is small and is heavily biased by losses to weather among Bonaparte's Gulls. In ground-nesting passerines, in general, causes of nesting failure were distributed almost equally among weather, predation, and unknown factors. However, losses to weather occurred almost entirely in one species (White-crowned Sparrow) in 1 year; consequently, the effects of weather may be exaggerated and those of predation minimized. In tundra-nesting passerines losses to predation were the major source of egg mortality and accounted for 29% of egg loss.

At Cape Thompson, Alaska, where much of the data cited by Ricklefs were compiled, predation and weather were the major causes of nest losses, with predation accounting for most of the losses (F. S. L. Williamson, pers. comm.). Similarly, on Devon Island, Canada, (Barrett, Hussell, and Whillans 1969; Barr et al. 1967) predation was a major cause of nesting failure. These data suggest that losses to predators are more important at high latitudes than Ricklefs allowed. I suspect that Ricklefs' data, limited to studies of 50 or more nests, were biased toward years of high productivity and low predation. The costs of arctic research are high, and when predators are abundant observers are not likely to undertake studies of species that may be adversely affected; and if such studies are attempted, their important "negative results" are likely to remain unreported. Since many arctic species nest on cliffs (some gulls, hawks, ravens), on small islands (certain waterfowl), under rock piles (Snow Buntings), and in other generally inaccessible places, predation pressure would appear to exert a strong selection force in the evolution of nest-site preferences.

Additional data will be needed to test Ricklefs' suggestion that predation is a relatively less important cause of nesting failure in arctic than in temperate or tropical regions.

TABLE 3. Hatching success in shorebirds and ground-nesting passerines at Churchill, Manitoba

Species	Hatching success
Shorebirds[a]	
Semipalmated Sandpiper	97%
Golden Plover	84%
Hudsonian Godwit	85%
Short-billed Dowitcher	100%
Stilt Sandpiper	83%
Hudsonian Curlew	49%
Semipalmated Plover	84%
Dunlin	98%
Least Sandpiper	80%
Ground-nesting passerines[a]	
Harris' Sparrow	89%
Lapland Longspur	80%
Smith's Longspur	94%
White-crowned Sparrow[b]	82%
Tree Sparrow	75%
Savannah Sparrow	90%

[a]In each group species are arranged in order of increasing abundance. Only species for which five or more nests were available were included. Data from Table 1.
[b]Data for 1964-1966 only.

Density-dependent mortality

At Churchill (Table 3) I found no apparent relationship between hatching success and abundance, either in shorebirds or in ground-nesting passerines for which samples of five or more nests were available. (Estimates of relative abundance were made on the basis of my field experience; quantitative data on nesting density are unavailable for most species.) However, on the basis of data from only one locality, Cape Thompson, Alaska, Ricklefs (1969: 25–26, Table 12) concluded that nesting losses through predation were density-dependent in arctic regions. At Cape Thompson, Common Redpolls nested at high densities and showed high mortality rates; Lapland Longspurs, White-crowned Sparrows, Savannah Sparrows, and Yellow Wagtails nested less densely, respectively, and showed progressively lower rates of nesting mortality.

Unfortunately, the Alaskan data cannot be used to test Ricklefs' idea because the causes of nesting mortality are unspecified; the problem can only be tested by using data from nests at which predation caused nesting failure. Ricklefs attributed most mortality to predation. However, Williamson et al. (1966: 473), though noting that predation had a "substantial influence," also stated that "periods of unseasonably cold weather . . . caused heavy mortality." Another complication is that data from two of the five species are of negligible value in this context. The wagtail data comprise only four nests and are too scanty for consideration. The redpoll data are numerically adequate, but they cannot be compared meaningfully with data from the other species. Redpolls nest above the ground, usually in areas of dense vegetation, whereas longspurs, sparrows, and wagtails nest on the ground in relatively open areas. Factors affecting nesting success in these situations are not identical (Table 2), and one may not assume that differences in mortality rates in different habitats result solely from differences in nesting density. Ricklefs argued (1969: 25) that because these species "nest at the same time, unusually bad weather should have affected all species to the same extent." Yet, Williamson et al. (1966: 463) pointed out that redpolls nested in "substantial numbers and over a longer period of time than did other passerine birds." Therefore, since neither nesting period, habitat, or weather conditions—all of which affect nesting success—were common to redpolls and the ground-nesting species, the redpoll data must be excluded from the analysis. The data for the remaining species, which may be comparable, tend to suggest that predator-induced nesting mortality may be density-dependent, but many studies that include information on causes of mortality will be needed before that conclusion can be accepted.

Conclusions

Although the Churchill data confirm Ricklefs' findings that hatching success is greater among arctic than among temperate zone passerines, they do not support several of his other conclusions regarding patterns of nesting mortality among arctic birds. Our different findings concerning hatching success of precocial vs. altricial birds and especially regarding the effects of predation on nesting success may result largely from differences in sampling methods. However, Ricklefs' conclusion that predator-induced nesting mortality is density dependent in arctic birds is unsupported by his data; and the Churchill data show no such relationship either.

Although regional studies are less subject to certain sampling errors than are studies of selected species, conclusions derived from them may be applicable to only a small geographic area. Therefore, it is evident that future analyses of nesting mortality will be more useful if they combine data from both types of studies. Until such analyses are made, firm conclusions should be postponed.

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