ROBERT E. RICKLEFS

An Analysis of
Nesting Mortality
in Birds

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ABSTRACT

Ricklefs, Robert E. An Analysis of Nesting Mortality in Birds. *Smithsonian Contributions to Zoology*, 9:1–48. 1969.—This study was initiated to evaluate nesting mortality of birds as a feature of the environment and as a selective force in the evolution of reproductive strategies. Representative nesting-success data from the literature for most groups of birds were transformed into daily mortality rates to eliminate differences among species in the length of the nest cycle. These data are presented by taxonomic groupings and for passerines by geographical region and nest construction and placement.

The strength and pattern of various mortality factors are described in detail. Predation, starvation, desertion, hatching failure, and adverse weather are the most prevalent factors, but nestsite competition, brood parasitism, and arthropod infestation may be important in some species. It is demonstrated that the various mortality factors can be identified by characteristic patterns of nesting losses involving differences in mortality rates between the egg and nestling periods and the within-nest component of mortality rates.

Among Temperate Zone passerines, field-nesting and marsh-nesting species have the highest mortality rates while those species nesting in trees, especially in cavities, enjoy higher success. Starvation is prevalent in marsh and field species but desertion is more restricted to tree-nesting species. In general, arctic species have lower mortality rates and tropical species higher rates, although there is a similar gradient from arid to humid regions within the tropics. The relative abundance of a species is related directly to its mortality rate in arctic regions, but is not in temperate and tropical regions.

Birds of prey generally have low mortality rates although starvation is often a major factor. Nesting losses in seabirds are caused primarily by crowded conditions in colonies and loss of eggs due to inadequate nest construction. Chick deaths come about primarily through their wandering away from parental care which is most common in the semiprecocial Charadriiformes. Precocial shorebirds and water birds enjoy higher egg success than ground-nesting passerines but game birds exhibit similar mortality rates. Little is known of the survival of precocial chicks after hatching except that mortality rates may be initially quite high and decrease with age. The fate of altricial birds after fledging is also poorly documented.

It is postulated that interspecific differences in mortality rates are determined by evolutionarily acceptable levels of adult risk to lower mortality rates of offspring through parental care, adult adaptations of morphology and behavior for foraging which result in limitations on nesting adaptations, environmental unpredictability which reduces the effectiveness of adaptations, and—most import—the diversity of predators to which a species must adapt.

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Robert E. Ricklefs # An Analysis of Nesting Mortality in Birds

Introduction

Nesting success of birds has often been treated in relation to reproductive rates to determine population parameters of species (Lack, 1954; Nice, 1957). The purpose of this report is to evaluate mortality as a feature of the environment and as a selective force in the evolution of reproductive strategies.

Mortality rates are evolved characteristics of species just as body size and plumage coloration, and thus they indicate the limits to which evolution may reduce losses through adaptation. These limits vary with species and habitat. Furthermore, that portion of mortality which is due to predation or parasitism represents the balance between two adapted systems: those of the predator and those of the prey. The outcome of this interaction also varies with the environment and provides an insight into community organization.

The emphasis of this study is placed upon the strength of environmental mortality factors as selective forces rather than upon survival as a specific population parameter. It is not possible, however, to completely separate the species from its environment because specific adaptations of the breeding cycle partly determine the schedule of mortality rates. We may ask to what extent nesting mortality is controlled by the external environment and conversely by specific adaptation to modify or restrict this environment. For example, hole-nesting and open-nesting species of birds in the same forest are confronted with markedly diverse "environments" because each presents different problems to predators and affords varying protection from inclement weather. Nest parasites and nest-site competitors play a significant role in the activities of some

species but not others, depending on nest-type and the size and behavior of the adults. Adaptations such as these clearly limit those portions of the environment which are directly relevant to nesting success whether they were evolved in direct response to mortality during the nest period or not. Many aspects of adult morphology and behavior which bear upon nesting success are adaptations primarily for foraging rather than for breeding. On the other hand, such diverse habitats as deserts, arctic tundra, and tropical rain forests differ greatly in the availability of nesting sites and the kinds and abundance of predators as well as in climate. We must, therefore, relate mortality rates to both general habitat and specific adaptations.

The following analysis is divided into three major sections. First, mortality factors are identified, characterized, and quantified for Temperate Zone altricial land birds in detail. Secondly, there is a comparative study of nesting mortality of passerine birds in three other geographical areas: arctic North America, humid tropical areas of Central America and northern South America, and an arid tropical area in South America. Finally, nesting mortality in other groups is surveyed and the relative effects of mortality factors are compared with passerine species. In the discussion, the results of these analyses are brought together into a general statement on the factors influencing the outcome of reproductive efforts of birds. Concluding remarks are offered on the limits to which mortality may be reduced through adaptation.

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Materials

Reviews of nesting success generally have centered around statistical measures of the outcome of nesting attempts (Williams and Marshall, 1938; Kalmback, 1939; Kendeigh, 1942; McCabe and Hawkins, 1946; Lack, 1954; Hickey, 1955; Nice, 1957; Skutch, 1966). Most data have been compiled as parts of life history studies of species, although nesting success also has been analyzed in relation to the structure of the nest (Lack, 1954; Nice, 1957), time of the year (Laskey, 1940; Snow, 1962; Nolan, 1963; and several European studies), brood parasitism (Nice, 1937; Norris, 1947; Smith, 1968), abundance of food (Lack and Lack, 1951; Owen, 1960; Orians, 1966; Wilson, 1966), interspecific competition (Weins, 1965), and nest placement (Goddard and Board, 1967). The quality and completeness of this material varies widely. In general, only studies which contain more than fifty nests are used here, although less desirable data are included if they are of comparative interest. I have made no attempt to present a thorough survey of the literature. European species are by and large ignored, and their nesting success is similar to North American equivalents (see Lack, 1954).

Because of yearly variation in nesting success, studies continued over long periods should provide the most valid estimates of average nesting success. The stage at which nests are found, biases incurred in locating nests, the frequency of visits to nests, and the investigator's criteria for nesting failures are additional sources of variability. Further discussion of sampling problems may be found in Lack (1954), Mayfield (1961), and Skutch (1966).

The amount of disturbance to the study area is also an important consideration because in comparative studies of breeding biology one is most interested in the ecological conditions under which the breeding strategy evolved. For this reason, data from highly developed areas are disregarded. As Lack (1965) has pointed out, however, it is unlikely that any temperate area has not been grossly changed through the activities of man. This would apply equally to most tropical areas as well.

To obtain high numbers of species for comparative purposes, all data from undeveloped areas and some from rural and parklike areas are treated identically. Differences in field methods correlated with groups of species or habitats will introduce some biases. Most of the studies however, represent species whose nests are readily found, which should result in a degree of uniformity of sampling.

Overall nest success and the percent of eggs hatched and fledged are most commonly presented in literature accounts. Further breakdown of nest success into the egg and nestling periods adds significantly to the value of the data. Peterson and Young (1950) and Young (1955, 1963) constructed survivorship graphs for the duration of the nest period which permit more detailed analysis of changes in mortality rates during the nest cycle.

Methods

For the analysis of selective forces, mortality is most meaningfully treated in terms of instantaneous rates rather than as percent losses over a given period of time. Rates are independent of the duration of development stages and may be considered as primarily environmental features rather than as attributes of the species.

Percentage survival data may be converted to mortality rates by considering survivorship as a decaying exponential function of time. Exluding "event-related" losses, the probability of success of a nesting attempt is determined by mortality rates during the nest period. If one divides this period into equal segments there is a probability, s_x, that a nest or individual will survive through any given segment, x, of the nest period. The expectation, $E(S)$, that a nest or individual will survive the duration of the nest period is the product of the survival probabilities for each segment ($s_1 s_2 \ldots s_n$, where n is the total number of segments). If mortality rates are independent of age, that is, if they are constant during the nest period, the product ($s_1 s_2 \ldots s_n$) is s^n. As one makes the segments arbitrarily small (and their number arbitrarily large) the relationship

$$E(S) = s^n \qquad \text{[Equation 1]}$$

may be written

$$E(S) = e^{-mt} \qquad \text{[Equation 2]}.$$

where m is the instantaneous mortality rate and t is measured in any suitable units of time (in this study, days).

Equation 2 may be rearranged for computing average daily mortality rates from field data on nesting success. Given the proportion, P, of nests or individuals which survive any given portion of the nest period, the mortality rate, m, can be calculated by the equation

$$m = -(log_e P)/t \qquad \text{[Equation 3]}.$$

The value m is strictly accurate only if mortality rates are constant during the nest period. When this is not the case, however, errors will be quite small and the calculated value, m, will be very close to the average daily mortality rate.

A more serious source of error is that, while mortality rates are calculated for the entire nest period including egg laying, nests often are not found until the nest period is partly over (Mayfield, 1961). In many species, nests are found readily during construction and they do not present a problem. Also, some authors (e.g. Skutch, 1966) are aware of this source of error and present their data accordingly. For the remaining studies there is no possible way to compensate for such differences in the data and they are treated as if nests were found before the initiation of laying. Thus, calculated mortality rates in some species will be lower than actual rates, especially during the egg period.

Several stages of the breeding cycle are distinguished in this study for the purpose of calculating mortality rates. The "egg period" extends from the initiation of laying until the eggs have hatched, which includes the "laying period" and the "incubation period." Because most species form one egg per day, the laying period is usually one day less than the number of eggs in the clutch. The incubation period refers to the time between the laying of the last egg and the hatching of the last young in the nest (Heinroth, 1922; Nice, 1954). Nidicolous young remain in the nest for part of their postnatal development, the "nestling period." Nidifugous young are capable of moving about and gathering food at, or shortly after, hatching and thus do not exhibit a lengthy nestling period. Several species of semiprecocial seabirds do not remain in well-defined nests after hatching but stay in restricted areas and may be censused for long periods. For convenience, the term "nestling period" also will be used for these species.

After leaving the nest, or nest area, the young remain dependent on their parents during varying and poorly defined periods. Young may be refered to as "fledglings" until they are self-feeding, as "juveniles" until they are independent of parental care, and as "immatures" until all adult characteristics have been acquired. Unfortunately, few survival data have been gathered for these stages.

Mortality Factors

Mortality factors may be referred to two broad classes: (1) those associated with events such as fertilization, egg laying, hatching, and fledging, and (2) those which may occur at any time and whose expectation increases with time. The term "mortality rate" is not strictly applicable to the first class because the duration of critical events is meaningless. The survival of young during the development period may be likened to the outcome of a race which is continuously, but not necessarily equally dangerous along its length, and has several high hurdles placed along the way. The hurdles require special skills, other than swiftness, for their passage.

For species that raise more than one young, we may distinguish also between mortality factors which cause the loss of whole broods and those which result in the death of individual eggs or young within broods. In nidicolous species certain factors are characterized by acting more strongly during either the egg or the nestling period. Mortality rates decrease with the increasing self-sufficiency of nidifugous chicks after hatching, and of altricial young following fledging, until adult characteristics are attained.

The relative contribution of different factors to overall mortality during the nest period of nidicolous birds may be inferred from difference between within-brood and whole-brood losses, and between egg and nestling losses.

Mortality factors are difficult to distinguish in field studies without considerable care and observation time. In a few studies, summarized in Table 1, causes of death are listed in detail and these will be considered in conjunction with the following discussion of mortality factors. The species include three open-nesting blackbirds and grackles (Family Icteridae), a hole-nesting warbler (Parulidae), a hole-nesting thrush (Turdidae) and an open-nesting finch (Fringillidae). These are illustrative of small passerine birds but should not be taken as being widely representative. Raptorial,

TABLE 1.—*Causes of mortality in six passerine species* [a]

| Causes of mortality | Species [a] | | | | | | | | | Total | Percent of individuals | Percent of losses |
	1	2a	2b	3	4a	4b	4c	5	6			
Eggs laid	220	413	163	369	563	577	1632	288	854	5131		
Losses due to:												
Hatching failure	24	34	13	15	31	27	49	18	49	260	5. 1	12. 0
Cowbird parasitism				1			5		46	52	1. 0	2. 4
Nest-site competition		[c] 90								90	1. 8	4. 2
Adult death [b]	17		5		15	9			29	75	1. 5	3. 5
Desertion	10	24	18	16	8	5	59	6		146	2. 8	6. 7
Predation		79	24	102	87	120	583	[f] 37	156	1188	23. 3	54. 9
Weather		29		18	4	8	50		25	134	2. 6	6. 2
Other	1	2	3	[d] 42		3	[e] 112	18	39	220	4. 3	10. 2
Total losses	52	258	63	194	145	172	858	79	344	2165	42. 2	100. 1
Young hatched	220	155	100	175	418	405	774	209	510	2966	57. 8	
Losses due to:												
Cowbird parasitism									4	4	0. 1	0. 4
Nest-site competition		[c] 11								11	0. 4	1. 1
Desertion							4	17		21	0. 7	2. 1
Starvation				13	1	1	23		26	64	2. 2	6. 3
Predation	25	34		21	71	57	284	[f] 23	156	671	22. 6	65. 8
Weather	17	3			8	1	21	20		70	2. 4	6. 9
Other	6	1		[d] 22	2	4	[e] 112	14	18	179	6. 0	17. 5
Total losses	48	49	0	56	82	63	444	74	204	1020	34. 4	100. 1
Young fledged	172	106	100	119	336	342	330	135	306	1946	[g] 65. 6	

[a] Species and sources are: 1. Eastern bluebird, *Sialia sialis* (Thomas, 1946). 2. Prothonotary warbler, *Protonotaria citrea* (Walkinshaw, 1953), in Michigan (a) and Tennessee (b). 3. Yellow-headed blackbird, *Xanthocephalus xanthocephalus* (Young, 1963). 4. Red-winged blackbird, *Agelaius phoeniceus* (Smith, 1943, two colonies, and Young, 1963). 5. Purple grackle, *Quiscalus quiscula* (Peterson and Young, 1950). 6. Song sparrow, *Melospiza melodia* (Nice, 1937).

[b] Losses during the egg and nestling periods are not distinguished.

[c] Nest-site competition from the house wren, *Troglodytes aedon*.

[d] Disappeared from nests.

[e] Ninety-two eggs and 107 nestlings disappeared from nests; 20 eggs and 5 young lost wing to tipping of nests.

[f] Mostly by young boys.

[g] This represents 37.9 percent of eggs laid,

precocial, and seabirds will be considered separately.

Mortality factors are treated in arbitrary order. In some respects the categories are subjective and could be further broken down, but hopefully they correspond to those factors which can be differentiated in the field and which produce recognizably diverse patterns of nesting losses.

Hatching failure, due to infertility, death of the embryo, or death during hatching, may be attributed to eggs which remain in the nest longer than the incubation period. This factor can be ascertained with high reliability because eggs usually are not removed from the nest after others have hatched. Of 5,131 eggs which

were laid in the nests of those species whose losses are tabulated in Table 1, 260 (5.1 percent) failed to hatch. Many of the eggs, however, which were taken by predators and lost to other factors would also not have hatched had they survived the egg period. Thus 8.1 percent of 3,226 eggs which were remaining in nests at the end of the incubation period failed to hatch. Among the three studies involving hole-nesting species, hatching failure in successful nests was 9.8, 11.2, and 18.0 percent. The high value for the prothonotary warbler (18.0 percent) was due to disturbance by house wrens during incubation. Although hatching failure among the hole-nesting species is higher than

among the open-nesting species in Table 1 (6.0–8.8 percent for six studies), other data for open-nesting species are comparable: 10.9 percent of 129 eggs in the traill flycatcher (Berger, 1957), 10.3 percent of 175 eggs in the robin (Howell, 1942), 11.2 percent of 135 eggs in the yellow warbler (Schrantz, 1943), 11.1 percent of 353 eggs in the yellow-headed blackbird (Fautin, 1941), and 5.1 percent of 195 eggs in the chipping sparrow (Walkinshaw, 1952).

Brood parasitism by cowbirds and cuckoos occurs during the egg-laying period of the nesting cycle although its effects on nesting success may appear at anytime during the nest period through loss of eggs, desertion, or starvation of the young. Among the species listed in Table 1, brood parasitism accounted for the loss of only 52 individuals (1.0 percent of the total, 2.4 percent of losses) but its incidence is often much higher, depending on the species and locality. Norris (1947) observed that 73 of 237 nests (30.8 percent) of 14 species were parasitized by brown-headed cowbirds in central Pennsylvania. Of the 73 nests, 21 were deserted during early stages of the nest cycle (28.8 percent), 27 were destroyed (37.0 percent) and 25 produced fledglings (34.2 percent). Successful parasitized nests raised about one fewer host young than successful nonparasitized nests. Of 129 nests of 10 host species found by King (1954) in eastern Washington, 17 (13.2 percent) were parasitized by brown-headed cowbirds. Of 500 nests of 20 host species found by Berger (1951) in Michigan, 112 (22.4 percent, contained 204 cowbird eggs. Several species, such as the song sparrow, yellow warbler, and cardinal were especially susceptable, 40–60 percent of all nests being parasitized. In tropical regions, host-parasite relations are often very complex and parasitized nests may produce more host young than nonparasitized broods in some situations (Smith, 1968).

Nest infestation by arthropod parasites may play a significant role in swallows and other hole-nesting species which reuse nests from year to year (Stoner, 1945; W. Moss, personal communication). Evaluation of the effects of infestation is difficult as desertion or losses occurring after fledging could be due to the weakened condition of the young resulting from infestation. None of the losses in Table 1 were attributed to this factor. The effects of other bird parasites, such as fly larvae and ticks, are poorly known, but it is not likely that these constitute a major mortality factor for many species. It has been shown, however, that bot

flies exert a significant influence on the nesting success of oropendulas in Panama (Smith, 1968). For a more detailed discussion of insect parasites, one should consult Lack (1954:78).

Competition for nest sites may cause substantial nest losses, as in the prothonotary warbler in Michigan (Walkinshaw, 1953). Mortality due to this factor occured primarily during the early stages of the nesting cycle. Ninety of 413 eggs (21.8 percent) compared to only 11 of 155 nestlings (7.1 percent), were lost owing to the destruction of nests by house wrens. An additional 24 eggs (5.8 percent) were deserted and hatching failure was also high (18.0 percent of eggs surviving the egg period). Thus, loss of eggs was three to four times greater than loss of young, which may have resulted either from increasing difficulty of evicting young from nests as they grow, or increased parental tenacity and defense of the nests as the cycle progressed.

Adult mortality is difficult to ascertain unless adults are marked and searched for in the field. The death of one parent may result in starvation of some of the nestlings or desertion of the young by the surviving parent (e.g. Thomas, 1946). In Table 1, 75 losses (1.5 percent of all individuals, 3.5 percent of all losses) are attributed to this factor.

Desertion is a heterogeneous category resulting from many kinds of disturbances which cause a pair to abandon a nesting attempt. In Table 1, the loss of 146 eggs (3.4 percent of all eggs, 8.0 percent of egg losses) and 21 nestlings (0.8 percent of all young, 2.6 percent of nestling losses) resulted from desertion. Again, it is evident either that the factors whose disturbance causes desertion predominately affect the early stages of the nest period or that adults develop a stronger nest tenacity as the nesting cycle progresses.

Starvation is restricted to the nestling period, especially when the young are fully grown and require large quantities of energy, and presumably to the period after fledging until the acquisition of self-feeding capacities. Survivorship graphs of several species of marsh-nesting icterids (Peterson and Young, 1950; Young, 1963) demonstrate that when starvation is a strong factor the mortality rate increases continuously during the nestling period. Presumably this results from the increasing difficulty for the parents to meet the energy demands of the growing young, although Peterson and Young do not cite starvation as a major factor. They attribute the increased mortality in older birds to nest crowding and enhanced attraction to predators. More recent

studies by Orians (1966) and Willson (1966) have shown that this interpretation may be largely erroneous although Horn (1968) observed that predation rates on Brewer blackbird nests increased with age of the young.

Starvation appears to be of varying importance in different species. Of those in Table 1, only the icterids studied by Young (1963) and the song sparrow (Nice, 1937), exhibited any degree of starvation. Young found that 23 (3.0 percent) of 774 nestling red-winged blackbirds were dead in the nest, apparently due to starvation, and that 107 nestlings (13.8 percent) disappeared from nests which were not totally destroyed. Many of these may have been starved young which were removed from the nest by the parents. Thus, as many as 130 of the 444 losses of nestlings (29.3 percent, 16.8 percent of all young hatched) may have been attributable to starvation. Similarly, as many as 35 of the 56 nestling yellowheaded blackbirds lost (63.5 percent, 20.0 percent of all nestlings) may have starved. Orians (1966, and personal communication) and Willson (1966) suggest that starvation may be the greatest single mortality factor in marsh-nesting icterids. It is impossible to estimate losses due to starvation among fledglings, but they may be relatively high if energy requirements of the young are increased because of activity and temperature regulation, as suggested by Royama (1966). Starvation has been cited as a significant cause of death in a variety of species: for example, the common swift (Lack and Lack, 1951), English blackbird (Snow, 1958), and curvebilled thrasher (Ricklefs, 1965).

Predation and inclement weather usually have the same effeect of destroying whole broods, and are important factors during the entire course of the nesting cycle. Both factors are identified readily in the field, and the former constitutes the major cause of mortality. In Table 1, predation accounted for the loss of 1188 eggs (23.3 percent of the total, 54.9 percent of losses) and 671 young (23.3 percent of all young, 65.8 percent of the losses). Lack (1954:77) estimated that three-fourths of the losses of open-nesting birds in England are due to predation. Similarly, inclement weather accounted for 134 egg losses (2.6 percent of the total, 6.2 percent of losses) and 70 deaths of nestlings (2.9 percent of the young, 8.6 percent of losses), but particularly heavy storms may take a much heavier toll (e.g. Fautin, 1941). These data indicate that the effects of predation and inclement weather are distributed evenly between the egg and nestling periods. There are, however, several situations which may result in heavier losses during the egg or nestling period. Skutch (1949) has suggested that the presence of young in the nest and increased activity of the parents during the nestling period may attract the attention of predators, but little evidence to support this hypothesis could be found in this study (cf., Horn, 1968). A second possibility is that there may be marked differences in the location of nests which would result in differences in mortality rates. Nests that are easy to find would be destroyed more rapidly, and toward the end of the nest period the remaining nests would be predominately more difficult to locate and thus would suffer less predation. This appears to have occured in the marsh wren (Kale, 1965). Over a four-year period, 56.0 percent of all eggs were lost to predators but only 30.7 percent of all nestlings. During the last year of the study, when rice rats (Oryzomys) were extremely abundant, 75.8 percent of eggs, but only 25.5 percent of young fell victim to predators.

Thirdly, the development of the young may progressively restrict the variety of animals which prey upon them. This could be especially important in large species whose eggs are relatively small, among raptorial birds which are endowed with formidable defense capabilities and, of course, among precocial species which attain mature physical characteristics at a relatively early age. Also, increasing size enhances homeostatic capabilities and enables the young to withstand exposure to a greater degree.

MORTALITY FACTORS AS SELECTIVE FORCES.—All mortality factors must select for adaptations which reduce mortality rates. In addition, many also favor decreased duration of exposure of the eggs and young through increased developmental rates. This distinction is important in evaluating the relationship between selective forces and the breeding strategy. An empirical method for calculating that component of mortality which would be reduced by decreasing the development period is presented in Appendix 1.

Hatching failure is determined primarily at fertilization or at later events such as hatching, and thus probably would not be reduced by decreasing the length of the egg period. Egg failure due to genetic causes will act to reduce the frequency of deleterious alleles. To the extent that hatching failure is the result of poor incubation, selection may also favor closer sitting.

Brood parasites (cuckoos and cowbirds) generally

observe nest-building activities of their prospective hosts before parasitizing the nest (Hann, 1937; Norris, 1947). This factor should exert selection for more secretive nest building and increased tenacity during the egg-laying stage, shortened nest-building periods, and discrimination and destruction of parasite eggs. The presence of brood parasites may favor more rapid development rates to increase the ability of the host young to compete for food. Early hatching and speeded growth would seem to provide an advantage in this situation. The parasite is always in a competitive environment as a nestling and it may be significant that, for its size, the brownheaded cowbird has the most rapid growth rate of temperate passerine birds (Ricklefs, 1968b).

Arthropod parasitism is probably a significant factor only during the nestling period when the young are poorly feathered and incapable of grooming themselves. When parasites remain in nests which are used over each season, as in swallows, time is required for the population to build up during each nesting cycle (Stoner, 1936) and thus the level of infestation as well as the total effects must increase with time. The effects of parasitic flies and other insects which actively seek host nests must also increase with the length of exposure. Thus, nest infestation and insect parasitism should favor the construction of new nests for each attempt, increased parental attention to the young, shortened nestling periods, and perhaps more precocious development of grooming activity. These selection pressures, however, are probably quite weak in most species.

Among small land birds, nest-site competition probably is found only among hole-nesting species, but it can be a strong selective force. This factor must favor increased nest defense, and reduced nest building and egg periods. For example, the prothonotary warbler requires 3.3 days on the average to build its nest in Michigan where house wrens cause the loss of almost a quarter of all eggs. In Tennessee, where nest-site competition is not a factor, nest building occupies an average of 8.8 days (Walkinshaw, 1953). Losses of young due to nest-site competition are not as great as losses of eggs and thus this factor will have a smaller effect on the length of the nestling period.

Adult mortality will select for early breeding and decreased periods of dependency of the young. One could also postulate an advantage to reducing the breeding effort on the part of the parents by reducing

brood size, but this would be strongly opposed by decreased productivity. Adult death is generally weak compared to other selective forces (in Table 1, 1.5 percent of all eggs laid were lost to this cause) and probably assumes little significance in the breeding behavior of birds.

Desertion is a behavioral response to a variety of disturbances and thus must itself be classified as an adaptation rather than as a selective mortality factor, even though it is treated as a mortality factor in empirical analyses of nesting losses.

Starvation has been shown to be an important selective factor affecting clutch size and breeding season (Lack, 1954), and other behavioral patterns such as asynchronous hatching and brood reduction (Ricklefs, 1965). Fluctuations in food availability which result in occasional suboptimal conditions for feeding would favor reduced periods of dependence on the parents for food. If nestlings require less food than fledglings, however, as suggested by Royama (1966) and the observations of Morehouse and Brewer (1968), an effect of starvation may be to favor lengthened nestling periods. On the other hand, sibling competition during periods of food shortage would favor increased development rates and perhaps shortened nestling periods.

The overall effects of predation and inclement weather are decreased considerably by reducing the length of any stage of the development period, chosing cryptic or well-protected nest sites and adopting anti-predator and protective behavior on the part of the adults. Predation is the most important mortality factor during the nesting cycles of small land birds, although its selective strength varies considerably from species to species (Table 1).

These conclusions on the action of mortality factors are based on accounts of nesting success in passerines only, but should apply more widely. In some groups, however, the relative stength of the factors may vary greatly. Large raptorial birds are subject to little predation, but starvation may assume considerable importance (Lack, 1954). In colonially nesting seabirds, losses may be brought about by crowding (Stonehouse, 1962), and adults often peck unattended checks to death (Nelson, 1966). Waterfowl nesting success may frequently be reduced by extensive flooding of breeding areas. In very hot and very cold regions, exposure may be quite important. These factors will be discussed in further detail where they are relevant.

IDENTIFICATION OF MORTALITY FACTORS.—It is possible to predict how each mortality factor will affect the relationship between mortality during the egg and nestling periods and between individual and nest mortality (Table 2). When the difference between mortality rates during the egg and nestling periods (vertical component) is graphed against within-nest, or partial mortality (the difference between individual and whole nest mortality), the resultant vector indicates the predominate mortality factors in the sample (Figure 1). Losses due to adult death, predation, and weather are well balanced between the egg and nestling periods (Table 1) and produce negligible within-nest loss. Therefore, the vectors for these factors are quite small. Cowbird parasitism is typically characterized by high mortality during the egg period caused by loss of eggs from within clutches and desertion, and high within-brood losses caused by partial loss of eggs and possibly starvation. Hatching failure results in a small, but consistently present vector in the same direction. If egg mortality is high but within-brood losses are low, desertion and nest-site competition are probably significant factors, although it has been shown above that under some circumstances, predation may produce this result.

Starvation differs from these factors in that its vector includes a large within-brood component and is limited to the nestling period. Analysis of nesting losses presented below indicates that starvation also may result in a large number of whole brood losses, perhaps through desertion or increased susceptibility to pre-

TABLE 2.—*Nesting loss patterns of mortality factors*

Relationship between mortality during the egg and nestling periods	Loss of individuals within nests	
	Low	*High*
Greater during the egg period	Nest-site competition	Hatching failure *
	Desertion	Brood parasitism *
Equally weighted	Adult death Predation Weather	
Greater during the nestling period		Infestation Starvation

* These factors are event related but are included in calculated mortality rates.
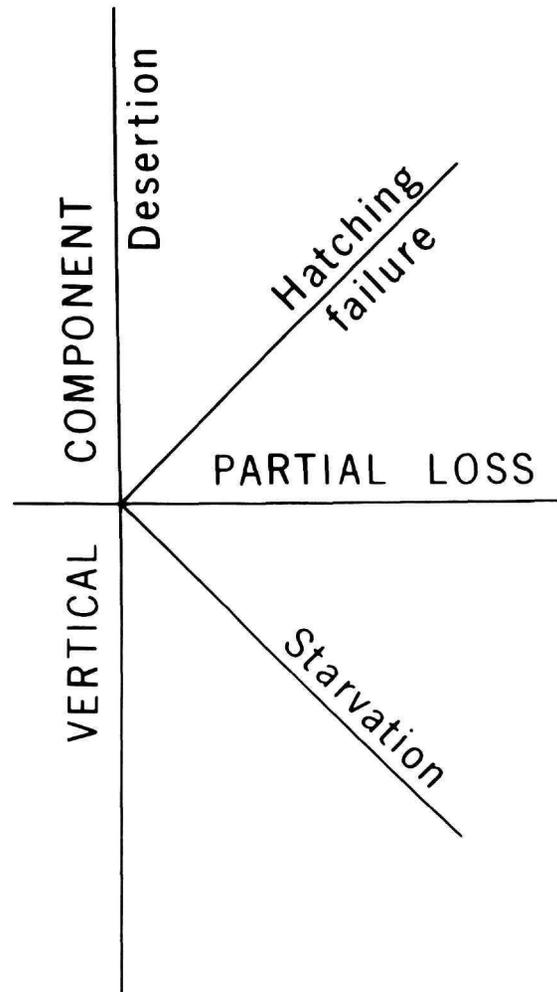
FIGURE 1.—Postulated vectors for major mortality factors during the nest period. The vertical component is the difference between mortality rates during the egg and nestling periods. Partial losses represent the within-nest component of mortality rates. Brood parasitism resembles hatching failure and infestation resembles starvation in mortality pattern.

dation and death from exposure or inclement weather. The action of several mortality factors together will produce intermediate vectors which are more difficult to identify.

Mortality Rates

TEMPERATE ZONE SPECIES.—Fifty studies of nesting success in small altricial Temperate Zone land

birds are summarized in Table 3a. Many of these have been discussed by Lack (1954) and Nice (1957) and the reader will find their comments valuable. Daily mortality rates, calculated from Equation 3 for nests and individuals, and egg and nestling periods where possible are presented in Table 3b for each of these studies. Differences between individual and nest mortality rates $(m - M)$ are related to the magnitude of within-nest loss. Similarly, the difference between individual mortality rates during the egg and nestling periods $(m_e - m_n)$ also are presented. Positive values indicate that rates of egg loss were greater than nestling

TABLE 3a.—*Nesting success of small Temperate Zone altricial land birds*

Species and study designation number	Length of study (years)	Nests (number)	Eggs (number)	Nest success (percent)			Egg success (percent)			Source and locality
				Egg	Nestling	Total	Egg	Nestling	Total	
Costa hummingbird										
(*Calypte costa*)										
1		29	58	65. 6	63. 2	41. 4	58. 7	55. 9	32. 8	Woods, 1923, California
Mourning dove										
(*Zenaidura marcoura*)										
2	6	4273	8018			47. 7	54. 6	85. 2	46. 6	McClure, 1946a, Iowa
3	8	249	500			52. 2			42. 6	Nice, 1931, Oklahoma
4	3	592				52. 3				Pearson and Moore, 1939, Alabama
5	9	235				51. 9				Monk, 1949, Tennessee
6	4	204	398			69. 7	77. 9	88. 4	68. 9	Cowan, 1952, California
Traill flycatcher										
(*Empidonax traillii*)										
7	2	47				76. 6				Berger, 1957, Michigan
Eastern and Say phoebes										
(*Sayornis phoebe, S. sayus*)										
8	2	99				77. 5				McClure, 1946b, Nebraska
Rough-winged Swallow										
(*Stelgidopteryx ruficollis*)										
9	4	66	403	78. 8	82. 7	65. 2	81. 1	84. 2	68. 3	Lunk, 1962, Michigan
9a. Six or fewer eggs	4	39	222	79. 3	74. 2	59. 0	79. 3	74. 4	59. 0	Do.
9b. More than six eggs	4	23	165	91. 3	95. 3	87. 0	91. 4	95. 3	87. 3	Do.
Tree swallow										
(*Iridoprocne bicolor*)										
10	9	219	1123				83. 4	73. 2	61. 0	Chapman, 1939
11	3	352	1759				81. 0	60. 2	48. 7	Low, 1934
12	3	80	430				72. 1	97. 7	70. 5	Kuerzi, 1941
13	2	37	184				88. 6	75. 5	66. 8	Shelley, 1937
14	8	60	363				98. 6	95. 0	93. 7	Weydemeyer, 1935, Montana
15 Average	25						84. 7	80. 3	68. 1	
Horned lark										
(*Eremophila alpestris*)										
16	2	30	102			60. 0	77. 4	58. 2	45. 1	Pickwell, 1931
Black-capped chickadee										
(*Parus atricapillus*)										
17	1	10	74						71. 6	Odum, 1941, New York
Long-billed marsh wren										
(*Telmatodytes palustris*)										
18	4	269	1111				29. 3	66. 6	19. 5	Kale, 1965, Georgia
18a Best year	1	46	178				51. 7	80. 5	41. 6	Do.
18b Worst year	1	62	235				11. 1	61. 6	6. 8	Do.

See footnotes at end of table.

TABLE 3a.—*Nesting success of small Temperate Zone altricial land birds*—Continued

Species and study designation number	Length of study (years)	Nests (number)	Eggs (number)	Nest success (percent)			Egg success (percent)			Source and locality
				Egg	Nest-ling	Total	Egg	Nest-ling	Total	
House wren										
(*Troglodytes aedon*)										
19	19	1056	6773				82. 3	94. 0	79. 0	Kendeigh, 1942, Illinois
20	21	64	333				59. 7	80. 9	48. 3	Walkinshaw, 1941, Michigan
21		104	581			82. 8	73. 1	91. 8	67. 2	Balwin and Bowen, 1928, Ohio
Cactus wren										
(*Campylorhynchus brunnei-capillus*)										
22	12	55		79. 9	85. 0	67. 8				Anderson and Anderson, 1960, Arizona
American robin										
(*Turdus migratorius*)										
23	2	136	259	64. 7	83. 7	57. 4	60. 7	83. 5	50. 7	Howell, 1942, New York
24	3	176	548			48. 7	57. 7	77. 9	44. 8	Young, 1955
Eastern bluebird										
(*Sialia sialis*)										
25	11	1401	6260				63. 0	70. 6	44. 5	Laskey, 1943, Tennessee
26	2	86	377				80. 1	90. 7	72. 7	Low, 1933
27	9	67	272	80. 6	87. 0	70. 2	78. 3	80. 6	63. 3	Thomas, 1946, Arkansas
Cedar waxwing										
(*Bombycilla cedrorum*)										
28	6	60	245	80. 1	95. 8	76. 7	77. 1	90. 4	69. 8	Putnam, 1949, Ohio
Starling										
(*Sturnus vulgaris*)										
29	3		801				91. 2	84. 2	76. 8	Dunnet, 1955, Scotland
Prothonotary warbler										
(*Protonotaria citrea*)										
30 Michigan	4	121	413			23. 1	38. 5	66. 7	25. 7	Walkinshaw, 1953
31 Tennessee	2	36	163			69. 5	61. 3	100. 0	61. 3	Do.
Yellow warbler										
(*Dendroica aestiva*)										
32	2	41	168				70. 8	76. 5	54. 2	Schrantz, 1943
Ovenbird										
(*Seiurus aurocapillus*)										
33	2	24	161				63. 3	68. 7	43. 5	Hann, 1937, Michigan
Orchard oriole										
(*Icterus spurius*)										
34	1	50	157				83. 5	96. 2	80. 3	Dennis, 1948, Louisiana
Yellow-headed blackbird										
(*Xanthocephalus xanthocephalus*)										
35	2	116	369			41. 0	45. 2	67. 0	30. 0	Young, 1963, Wisconsin
Red-winged blackbird										
(*Agelaius phoeniceus*)										
36	1	91	325	85. 7	73. 1	62. 6	79. 4	65. 9	52. 3	Beer and Tibbitts, 1950, Wisconsin
37a	1		563				74. 3	80. 4	59. 7	Smith, 1943, Illinois
37b	1		577				70. 3	84. 5	59. 4	Do.
Combined	[a]1		1140				72. 3	82. 5	59. 5	Do.

See footnotes at end of table.

TABLE 3a.—*Nesting success of small Temperate Zone altricial land birds*—Continued

Species and study designation number	Length of study (years)	Nests (number)	Eggs (number)	Nest success (percent)			Egg success (percent)			Source and locality
				Egg	Nest-ling	Total	Egg	Nest-ling	Total	
Red-winged blackbird—Con.										
38a	1	62	221	82.3	74.5	61.3	76.0	64.9	49.4	Weins, 1965, Wisconsin
38b	1	76	255	68.3	69.2	47.4	63.6	56.8	36.1	Do.
Combined	2	138	476	74.7	71.8	53.7	69.3	60.9	42.3	Do.
39a	1	238	730			34.9	53.8	51.9	28.0	Young, 1963, Wisconsin
39b	1	280	902			23.9	44.6	40.3	18.0	Do.
Combined	2	518	1632			29.0	48.7	45.5	22.5	Do.
40		67	214				77.6	63.3	49.1	Williams, 1940, Ohio
41	1	243	821			26.7	40.2	59.6	23.9	Goddard and Board, 1967, Oklahoma
Brewer blackbird (*Euphagus cyanocephalus*)										
42	1	107	521			49.5	62.7	62.7	39.3	La Rivers, 1944, Nevada
Common grackle (*Quiscalus quiscula*)										
43	3	62	288			54.8	72.6	64.7	46.9	Peterson and Young, 1950, Wisconsin
44	2	33	146	81.8	74.1	60.7	80.1	65.8	52.8	Weins, 1965, Wisconsin
Common goldfinch (*Spinus tristis*)										
45a	1	56	170				63.5	58.3	37.1	Stokes, 1950, Wisconsin
45b	1	81	206				57.8	77.3	44.7	Do.
45c	1	102	320				71.3	80.3	57.2	Do.
Combined	3	239	696				65.4	74.3	48.6	Do.
Chipping sparrow (*Spizella passerina*)										
46	25	50	152	66.0	93.9	62.0	68.5	89.4	61.2	Walkinshaw, 1952, Michigan
Field sparrow (*Spizella pusilla*)										
47	10	593	1738			38.1	51.1	69.8	35.7	Walkinshaw, 1952, Michigan
Song sparrow (*Melospiza melodia*)										
48a	[b] 3	147	585				66.5	62.5	41.5	Nice, 1937, Ohio
48b	[c] 3	76	321				45.8	54.4	24.9	Do.
Combined	6	211	854	69.6	68.0	47.4	59.7	60.0	35.8	Do.
House finch (*Carpodacus mexicanus*)										
49	5		110				72.8	71.3	51.8	Evenden, 1957, California
McCown longspur (*Rhynchophanes mccowni*)										
50	3	45	153			60.0	60.2	77.7	46.4	Mickey, 1943, Wyoming.

[a] Combined data represent two colonies.

[b] First three years when the environment was favorable.

[c] Last three years when the environment was badly disturbed.

TABLE 3b.—*Mortality rates of small Temperate Zone altricial land birds*

Species study number [a]	Length of nesting cycle (days)				Daily mortality rate of nests (percent)			Daily mortality rate of eggs (percent)			Partial loss (percent) $m-M$	Vertical component (percent) m_e-m_n
	Laying	Incubation	Nestling	Total	Egg M_e	Nestling M_n	Total M	Egg m_e	Nestling m_n	Total m		
1	1	16	22	39	2.48	2.09	2.26	3.14	2.65	2.86	0.60	0.49
2	1	15	13½	29½			2.51	3.79	1.18	2.59	0.08	2.61
3							2.20			2.90	0.70	
4							2.20					
5							2.23					
6							1.22	1.56	0.92	1.26	0.04	0.64
7	2½	12	14	28½			0.94					
8	3	16	16	35			0.73					
9	5	15	20	40	1.19	0.94	1.07	1.05	0.85	0.96	-0.12	0.20
15	4	15	19	38				0.88	1.16	1.01		-0.28
16	3	11	10	24			2.13	1.83	5.28	3.32	1.19	-3.49
17	6	13	18	37			0.90					
18	3	13	14	30				7.68	2.87	5.46		4.81
19	5	13	16	34½				1.08	0.37	0.68		0.71
20								2.87	1.28	2.11		1.59
21							0.55	1.74	0.52	1.15	0.60	1.22
22	3	16	20	39	1.25	0.81	1.00					
23	2½	13	13	28½	2.81	0.93	1.89	3.22	1.38	2.38	0.49	1.78
24							2.52	3.55	1.77	2.82	0.30	1.78
25	3	14	17½	34½				2.72	2.03	2.35		0.69
26								1.31	0.56	0.92		0.75
27					1.27	0.80	1.03	1.44	1.23	1.33	0.30	0.21
28	3½	11½	15½	30½	1.48	0.28	0.87	1.74	0.65	1.18	0.31	1.09
29	4	14	21	39				0.51	0.82	0.68		-0.31
30	3½	12½	11	27			5.43	5.97	3.68	5.04	-0.39	2.29
31							1.35	3.06	0.00	1.82	0.47	3.06
32	3	11	10	24				2.47	2.68	2.56		-0.21
33	3½	12	8	23½				2.95	4.70	3.54		-1.75
34	2	14	13	29				1.13	0.30	0.76		0.83
35	2	13	13	28			3.19	5.30	3.08	4.31	1.12	2.22
36	2½	12	10½	25	1.07	2.99	1.87	1.59	3.98	2.59	0.72	-2.39
37								2.24	1.84	2.08		0.40
38					2.01	3.16	2.49	2.53	4.72	3.44	0.95	-2.19
39							4.96	4.97	7.50	5.97	1.01	-2.53
40								1.81	4.36	2.85		-2.55
41							5.28	6.28	4.94	5.73	0.45	1.34
42	3½	13	13	29½			2.39	2.83	3.59	3.16	0.77	-0.76
43	3	11½	12	26½			2.27	2.21	3.63	2.86	0.59	-1.42
44					1.39	2.50	1.88	1.53	3.49	2.41	0.53	-1.96
45	3½	13½	12½	29½				2.50	2.38	2.45		0.12
46	2½	10	11	23½	3.33	0.57	2.04	3.03	1.02	2.09	0.05	2.01
47	2½	10	11	23½			4.11	5.38	3.27	4.38	0.27	2.11
48	3	12½	10	25½	2.34	3.86	2.93	3.33	5.12	4.03	1.10	-1.79
49	3½	13	15	31½				1.93	2.26	2.09		-0.33
50	2½	12	10	24½			2.09	3.50	2.53	3.14	1.05	0.97

[a] See Table 3a for species designation in relation to study number.

loss. The data for a few species permitted analysis of within-brood mortality separately for the egg and nestling periods (Table 4).

Daily mortality rates range from about 0.5 percent to more than 5 percent. It is evident that mortality rates may vary considerably from year to year (e.g. marsh wren and common goldfinch) and between localities (e.g. red-winged blackbirds), but no attempt has been made to analyze this aspect of nesting loss. One must always keep in mind that most studies are small and limited samples and thus are only crude estimates of nesting success for the entire population. For this reason, the data for any individual species will not be dwelled upon at length. The conclusions of this paper are derived largely from comparisons among species groups.

The studies are grouped according to nest location and habitat in Table 5. Hole-nesting and niche-nesting species suffer the least mortality during the nest period and marsh-nesting species are subject to the greatest losses. Species which nest on or near the ground have substantially lower nest survival than those which build nests in large bushes or trees above the reach of ground-dwelling animals. The orchard oriole builds a hanging nest in trees and enjoys higher nesting success than open-nesting species (Dennis, 1948). Another study which is difficult to place is that of the cactus wren (Anderson and Anderson, 1960), the only desert species represented in the sample. Its nest is an enclosed structure usually placed in treelike cholla cacti which

evidently provide excellent protection in view of the cactus wren's low mortality rate ($m = 1.00$).

Brewer blackbirds and common grackles feed in wet or marshy habitats, but usually nest in trees bordering their foraging habitats (species studies 42, 43). Overall mortality rates of both species are most similar to those of open-nesting birds above the ground, but the vertical components (-0.76, -1.42) and partial losses (0.77, 0.59) are closest to some marsh-nesting species (e.g. the red-winged blackbird). Grackles nesting in marshes have similar mortality rates to those nesting in bordering trees in one study (species study 44).

Most of the ground-nesting species in the sample inhabit open areas, but the ovenbird, which builds its nest on the forest floor, exhibits high nesting mortality ($m = 3.35$) as do field species, and suffers greater losses than forest and second-growth species nesting above the ground. Thus, the location of the nest rather than the habitat would appear to be the major factor influencing nesting success. Unfortunately, little is known of the nesting success of other ground-nesting warblers and finches in forests. When comparing mortality rates of marsh wrens and ovenbirds with hole-nesting species, it is evident that enclosed nests do not provide the protection against predators of hole nests which are built within such substantial materials as tree trunks, mud banks, and rock outcroppings. The value of an enclosed or covered nest may lie in concealment for the overbird, or protection from rain and cold for the marsh wren. The enclosed nest of the cactus

TABLE 4.—*Further analysis of vertical components and within-nest mortality in small Temperate Zone altricial land birds*

Species and study designation number	Vertical component (percent)		Partial loss (percent)		
	Nests $M_e\text{-}M_n$	Eggs $m_e\text{-}m_n$	Egg $m_e\text{-}M_e$	Nestling $m_n\text{-}M_n$	Total $m\text{-}M$
1. Costa hummingbird	0.39	0.49	0.66	0.56	0.60
9. Rough-winged swallow	0.25	0.20	−0.14	−0.09	−0.11
23. American robin	1.88	1.84	0.41	0.45	0.43
27. Eastern bluebird	0.57	0.21	0.17	0.53	0.30
28. Cedar waxwing	1.20	1.09	0.26	0.37	0.31
36. Red-winged blackbird	−1.92	−2.39	0.52	0.99	0.72
38. Red-winged blackbird	−1.15	−2.19	0.52	1.56	0.95
44. Common grackle	−1.11	−1.96	0.14	0.99	0.53
46. Chipping sparrow	2.76	2.01	−0.30	0.45	0.05
48. Song sparrow	−1.52	−1.79	0.99	1.26	1.10

TABLE 5.—*Nesting mortality parameters for small Temperate Zone altricial land bird species grouped according to nest location* [a]

Nesting mortality parameters (percent per day)	Open nests			Hole and niche nests
	In marshes	On ground	Above ground	
Overall individual mortality rate, m				
Number of species	3	5	9	7
Average	4. 52	3. 68	2. 12	1. 02
Range	3. 78, 5. 46	3. 14, 4. 38	0. 94, 2. 86	0. 68, 1. 53
Vertical component, $m_e - m_n$				
Number of species	3	5	8	3
Average	1. 90	−0. 79	0. 82	0. 29
Range	−1. 32, 4. 81	−3. 49, 2. 11	−0. 33, 2. 01	−0. 28, 1. 13
Partial loss, $m - M$				
Number of species	2	4	5	5
Average	0. 95	0. 90	0. 33	0. 26
Range	0. 78, 1. 12	0. 27, 1. 19	0. 05, 0. 60	−0. 12, 0. 60

[a] Excluding prothonotary warbler, cactus wren, orchard oriole, Brewer blackbird and common grackle (see text).

wren has been shown to aid temperature regulation of the young by providing a moderated environment (Ricklefs and Hainsworth, 1968).

The largest negative vertical components of mortality occur among ground-nesting species and some marsh birds. Within-nest losses are also very high. The starvation components of these species suggest that fields and marshes are characterized by more variable food supplies than forests and second-growth habitats.

Hole-nesting and niche-nesting birds exhibit small vectors. Species nesting above the ground in second-growth and forested areas generally have small within-nest components and positive vertical components, suggesting either that desertion is a major factor or that predation is heavier on eggs than nestlings because of substantial variability in the accessability of nests to predators (see above). The latter mechanism would be expected to be more prevalent in marshes, which are simple habitats, and where high breeding densities of some colonial species may limit the number of optimum nest sites. No matter how unlikely, predation cannot be ruled out as a factor causing positive vertical components in forest-nesting species.

Values for the rate of loss of individuals within nests during the egg period ranged from −0.30 to 0.99 percent per day with an average for the 10 studies of 0.32 (Table 4). Negative values indicate that the average

number of young hatched per successful nest was greater than the average number of eggs laid. This can be explained either by the loss of clutches before their completion or by greater losses of small clutches. For example, the within-nest component in the rough-winged swallow was −0.14 percent per day during the egg period. (Lunk, 1962). Clutches of six or fewer eggs had an observed survival of 79.3 percent, whereas larger clutches had an observed survival of 91.3 percent through the egg period.

The average value for within-nest loss during the incubation period is similar to that which would be expected owing to hatching failure alone. If 5.0 percent of all eggs fail to hatch (Table 1) and the egg period is 16 days (Table 3b) the apparent mortality rate would be 0.32 percent per day. The highest value, 0.99 percent for the song sparrow, would be expected to be due to cowbird parasitism, which was prevalent in that study (Nice, 1937).

Within-brood loss during the nestling period varied from −0.09 to 1.56 percent per day (average, 0.71). The single negative value—for the rough-winged swallow—can be attributed to the cause discussed above for this species. The within-brood components nestling mortality indicate that starvation is often a strong mortality factor. Three of the four highest values were observed for marsh-nesting blackbirds and grackles

which are often subject to heavy starvation (Young, 1963; Orians, 1966; Willson, 1966; Table 1). The song sparrow (Nice, 1937), whose environment was badly disturbed during four years of a seven-year study and which was the victim of heavy cowbird parasitism, also exhibited large within-brood loss. Nice, however, attributed, perhaps erroneously, the heavy loss of young to increased predation (Table 1) rather than to starvation.

The studies may be analyzed graphically by plotting the difference between mortality rates during the egg and nestling periods on one axis and the within-nest component of mortality on the other (Figure 1). Mor-

tality caused by adult death, predation, and weather produces negligible vectors on this coordinate system (Table 2). Other factors will produce vectors in the directions shown in Figure 1. The studies presented in Table 4 are shown graphically in Figures 2 and 3. In this sample, high mortality during the egg period relative to the nestling period (species studies 23, 28, 46) must be caused either by nest-site competition or desertion rather than hatching failure and cowbird parasitism because the later also would produce large within-clutch components. Because these species are open nesters, desertion, rather than nest-site competition,

FIGURE 2.—Partial loss during the egg period and vertical components of mortality rates of temperate passerine birds. Numbers correspond to species in Table 3a. Abcissa and ordinates are calibrated in percent per day. Vectors for the various mortality factors are as in Figure 1.
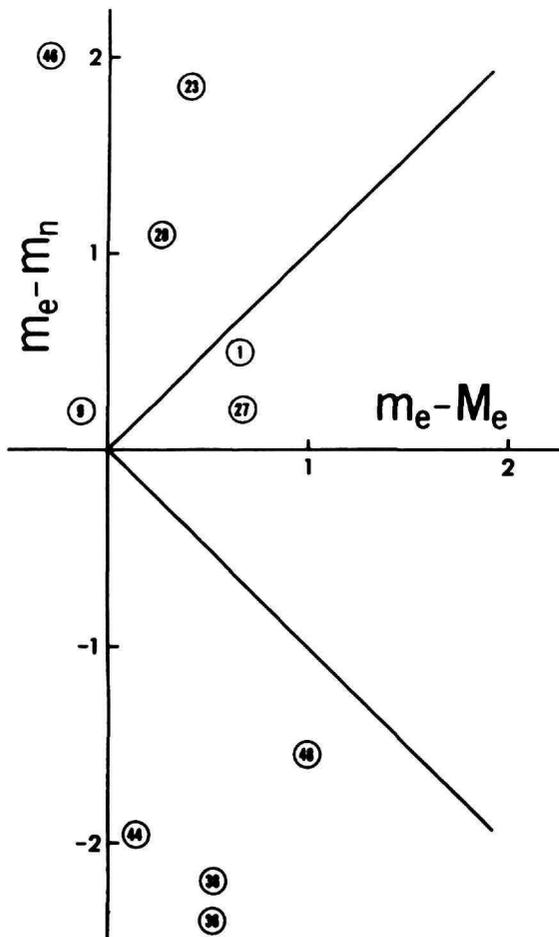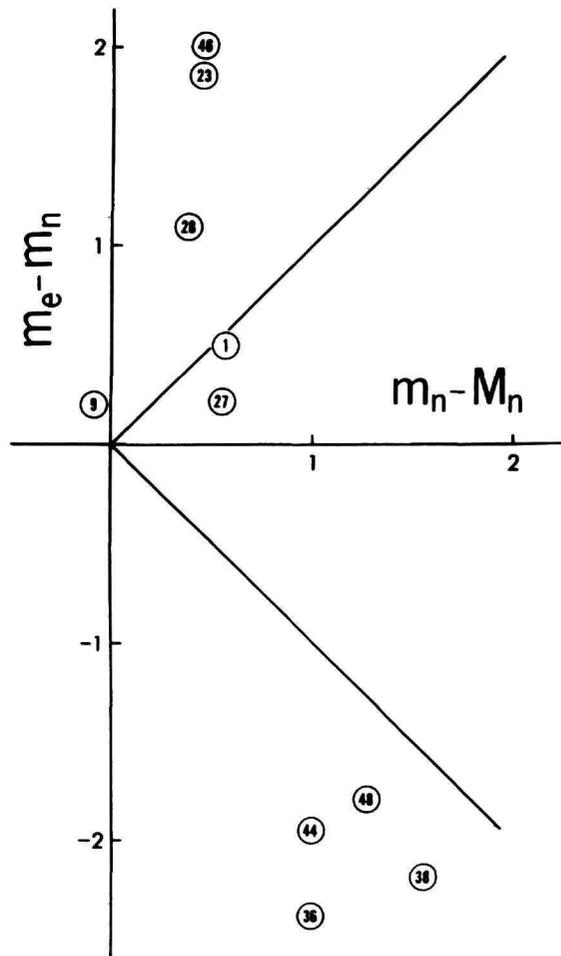
FIGURE 3.—Partial loss during the nestling period and vertical components of mortality rates of temperate passerine birds (from Table 3a). Scale and vectors are as in Figure 2.

must have been primarily responsible for the observed vectors. The position on the graph of two hole-nesting species, the rough-winged swallow (species study 9) and the eastern bluebird (species study 27) indicate that predation was probably the only significant mortality factor acting during the egg period. In the redwing blackbird (species studies 36, 38) and the common grackle (species study 44), hatching failure could account for the within-clutch component. Other factors acting strongly during the nestling period are responsible for the large negative vertical components in these species.

Interpretation is difficult when more than one factor (other than adult death, predation, and weather) act strongly. The high within-clutch component of the song sparrow (species study 48) may be attributed to cowbird parasitism, whose vector lies in the upper right quadrant of this graph (Figure 1). Apparently, another factor acting during the nestling period completely obscured the positive vertical vector which should result from cowbird parasitism. It is also possible that parasitism may bring about starvation of nestlings. Both Nice (1937) and Norris (1947) found that the presence of a cowbird nestling resulted in about one fewer host young being raised. This loss, however, usually is incurred during the egg-laying period rather than through the starvation of nestlings.

Factors which produce within-brood loss of nestlings also produce a negative vertical component of the same magnitude. Within-brood loss of species studies 1, 23, 27, 28, and 46 (Figure 3) are low (0.37–0.56) and their small negative vertical components are obscured by other factors acting more strongly during the egg period. It is interesting to note that large positive vertical components (desertion) are not present in the species whose within-brood losses are high owing to starvation.

The negative horizontal component of the rough-winged swallow (species study 9) has been discussed above. Within-brood losses of species studies 36, 38, 44, and 48 are large (0.99–1.50) and corresponding vertical components are large and negative, more so than would be predicted. Therefore, either predation and inclement weather produce a negative vertical vector, or starvation results in the loss of whole broods. Predation and weather accounted for the loss of 26.7 and 23.8 percent of the total eggs and young in Table 1. The average egg and nestling periods are 16.0 and 12.4 days, respectively, and thus the average daily

mortality rates are 1.93 and 2.13 percent. This difference would result in a vertical vector of -0.20 percent which would account for little of the difference between the observed and predicted vertical components (-0.56 to -1.40 percent). Thus, it seems necessary to reevaluate the effects of starvation by postulating considerable loss of whole broods to this agent, presumably by desertion of broods in which one or more of the young had died, or less likely by the starvation of entire broods. Infestation probably does not constitute a significant portion of the observed components. From Figure 3 one may estimate that about one third of nestling losses due to starvation involve the loss or desertion of whole broods.

We may also graph the difference between the rate of loss of individuals during the egg and nestling periods, $m_e - m_n$, against the difference between the rate of loss of nests during those periods, $M_e - M_n$ (Figure 4). Positive values of both components should be highly correlated because factors specifically producing high egg loss (desertion and, in some circumstances, predation) also result in high nest loss. In the chipping sparrow (species study 46), nest loss is higher than egg loss during the egg period which suggests selective destruction either of small clutches or of nests during the laying period. This is further implied by the negative within-clutch mortality component of this species. The low within-brood loss indicates that starvation was probably not a factor.

If starvation does not act on whole broods, the difference between rates of nest loss during the egg and nestling periods would remain near zero when the rate of nestling loss exceeds egg loss. In this sample, however, the nest loss component of two studies nearly equals the nestling loss component. This may be due partly to within-clutch losses from hatching failure and brood parasitism, especially in the song sparrow (species study 48), which tend to move the points up on the graph. In addition, Figure 4 indicates that in conjunction with starvation, whole brood losses occur at a proportionally higher rate among small broods; that is, it appears that more than one third of nestling losses in excess of egg losses were from entire broods. Here again, of course, any increased predation during the nestling period would have the same effect.

In Figure 5, the within-nest mortality component during the egg and nestling periods combined is graphed against the difference in mortality rates between incubation and nestling periods, as before. The
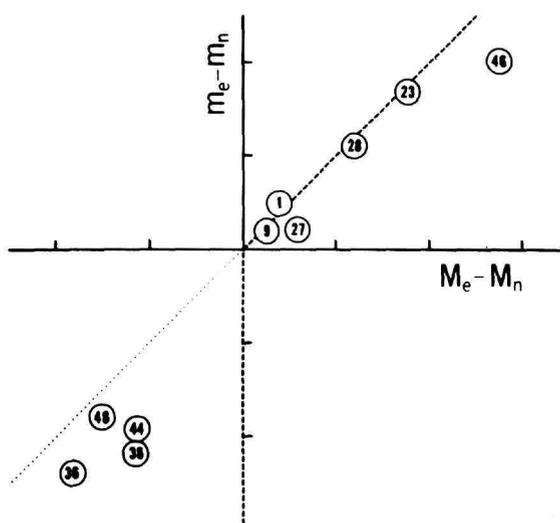
FIGURE 4.—Vertical components of individual mortality rates plotted against vertical components of whole nest mortality rates. Dashed line represents theoretical effects of desertion (or unbalanced predation) for positive values of $m_e - m_n$ and of starvation for negative values of $m_e - m_n$. Dotted line represents losses restricted to whole nests for negative values of $m_e - m_n$. Scale as in Figures 2 and 3. Data from Table 4.

FIGURE 5.—Vertical components of individual mortality rates versus partial loss during the nest period for Temperate Zone passerine birds (and one dove and one hummingbird). Dashed lines represent vectors for hatching failure and starvation (see text). Scale of daily mortality rates are in percent. Numbers correspond to species in Table 3a.

vectors which will be produced by within-nest loss during either the egg or nestling period are shifted toward the vertical axis a distance proportional to the amount which the nestling and egg periods, respectively, are of the total nest period. The predicted lines in Figure 5 are based on the average egg and nestling periods of the species shown. These data further indicate that starvation and desertion are not likely to be major factors in the same study. Apparently, the Mc-Cown longspur (species study 50) and perhaps the Costa hummingbird (species study 1) and Brewer blackbird (species study 42) are exceptions, yet studies such as that on the yellow-headed blackbird (species study 35) emphasize the difficulties in interpretation. This species has a very large within-nest mortality component with losses weighted heavily toward the egg period, and, in fact, lies on the vector for brood parasitism and hatching failure. Starvation caused a portion of the within-nest losses but the disappearance of eggs from within clutches was equally important (Table 1). The positive vertical component was caused primarily by high predation on eggs (27.7 percent compared with 12.0 percent of nestlings), perhaps resulting from the same circumstances discussed above for the marsh

wren. The fact that both of these are marsh-nesting species is interesting.

TROPICAL SPECIES.—Relatively few nesting-success data are available for tropical species and this account will rely strongly on Skutch (1966) for humid tropical

areas (Tables 6a and 6b) and Marchant (1960) for an arid tropical area (Tables 7a and 7b). In general, birds of humid tropical regions are less successful breeders than temperate species although some have comparable nesting success. Skutch (196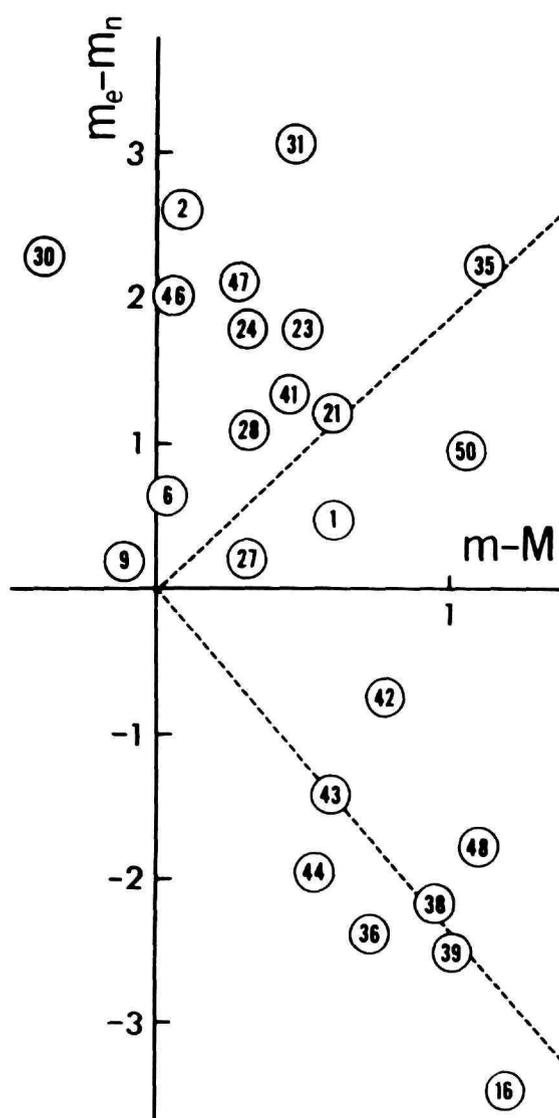6) found the survival of forest species to be lower than those of clearings and second growth (Table 8). Snow and Snow (1963) also demonstrated that nesting success

of robins is higher on plantations than in forested areas (Table 6a). Open habitats, however, are probably fairly recent in humid tropical areas because of their association with man, and thus predators may not have fully adjusted to these new conditions. Hole nests are more successful than open nests (Table 8), but less so than hole nests in temperate regions (Tables 3 and 5).

TABLE 6a.—*Nesting success of small altricial land birds in humid tropical regions*

Species and study designation number	Nests (number)	Eggs (number)	Nest success (percent) total period	Egg success (percent)			Source and locality
				Egg	Nestling	Total	
Ruddy ground-dove (*Columbigallina talpacoti*) 1	21	40	23. 8	50. 0	40. 0	20. 0	Skutch, 1956, Costa Rica
Black-and-white manakin (*Manacus manacus*) 2	227	454	ª 19. 4			16. 3	Snow, 1962, Trinidad
Gray-capped flycatcher (*Myiozetetes grenadensis*) 3	30	76	43. 3	61. 9	65. 9	40. 8	Skutch, 1966, Costa Rica
Yellow-bellied elaenia (*Elaenia flavogaster*) 4	20	36	20. 0	36. 1	46. 2	16. 7	Skutch, 1966, Costa Rica
Clay-colored robin (*Turdus grayi*) 5	24	62	25. 0	30. 7	52. 7	16. 1	Do.
Robins (*Turdus* spp.) 6 Forest ᵇ	57		21. 0				Snow and Snow, 1963, Trinidad
7 Plantation ᶜ	56		37. 5				Do.
Scarlet-rumped tanager (*Ramphocelus passerinii*) 8	80	156	43. 8	61. 6	68. 7	42. 3	Skutch, 1966, Costa Rica
Blue-gray tanager (*Thraupis episcopus*) 9	27	50	44. 4	68. 0	64. 7	44. 0	Do.
Yellow-faced grassquit (*Tiaris olivacea*) 10	44	105	29. 6	44. 8	57. 4	26. 7	Do.
Blue-black grassquit (*Volatinia jacarina*) 11	22	53		73. 7	76. 9	56. 6	Alderton, 1963, Canal Zone
House wren (*Troglodytes aedon*) ᵈ 12	25	90	72. 0	75. 6	82. 3	62. 2	Skutch, 1966, Costa Rica

ª Nest success during the egg period, 40.1 percent, during the nestling period, 48.4 percent.

ᵇ *T. fumigatus* and *T. albicollis*.

ᶜ *T. fumigatus* and *T. nudigenis*.

ᵈ Hole-nesting species.

TABLE 6b.—*Mortality rates of small altricial land birds in humid tropical regions*

Species study number	Length of nesting cycle (days)				Daily mortality rate of nests (percent)			Daily mortality rate of eggs (percent)			Partial loss, m–M (percent)	Vertical component, m_e–m_n (percent)
	Laying	Incubation	Nestling	Total	Egg M_e	Nestling M_n	Total M	Egg m_e	Nestling m_n	Total m		
1	1	12½	12½	26			5.53	5.14	7.33	6.20	0.67	−2.19
2	1	18	14	33	4.81	5.18	4.98			5.50	0.52	
3	2	16	20	38			2.20	2.67	2.09	2.36	0.16	0.58
4	1	15½	17½	34			4.73	6.18	4.42	5.27	0.54	1.76
5	2	12	15	29			4.78	8.45	4.27	6.31	1.53	4.18
6	2	12	15	29			5.38					
7	2	12	15	29			3.38					
8	1	12	12	25			3.30	3.73	3.13	3.44	0.14	0.60
9	1	13½	18	32½			2.50	2.66	2.42	2.53	0.03	0.24
10	1½	13	14	28½			4.28	5.54	3.97	4.63	0.35	1.57
11	2	10	9	21				2.54	2.93	2.71		−0.39
12	2½	16	18	36½			0.90	1.51	1.08	1.30	0.40	0.43

TABLE 7a.—*Nesting success of small altricial land birds in arid tropical regions—all data are from a four-year study by Marchant (1960) in Ecuador*

Species and study designation number	Nests (number)	Eggs (number)	Nest success (percent) total period	Egg success [a] (percent)		
				Egg	Nestling	Total
1. D'Orbigny ground-dove (*Eupelia cruziana*)	283	477	56.5	76.7	81.4	55.2
2. Groove-billed ani (*Crotophaga sulcirostris*)	27	111	51.8	69.2	82.9	55.8
3. Vermillion flycatcher (*Pyrocephalus rubinus*)	188	330	49.4	79.8	57.4	38.4
4. Short-tailed ground-tyrant (*Muscigralla brevicauda*)	36	103	38.9	57.3	69.5	37.3
5. Fulvous-headed pygmy-tyrant (*Euscarthmus molorhyphus*)	22	38	59.1	[b] 68.4	[b] 73.1	50.0
6. Long-tailed mockingbird (*Mimus longicaudatus*)	184	447	50.6	76.3	66.0	40.8
7. White-browed gnatcatcher (*Polioptila plumbea*)	35	84	62.8	[b] 72.7	[b] 60.7	44.1
8. Ecuadorian neorhynchus (*Neorhynchus peruvianus*)	264	472	50.0	80.2	74.3	51.0
9. Chestnut-throated seed-eater (*Sporophila telasco*)	254	419	37.4	65.7	67.7	36.8
10. Crimson finch (*Rhodospingus cruentus*)	96	241	64.5	76.4	84.3	59.1
11. Bonaparte warbling finch (*Poospiza hispaniolensis*)	68	147	47.1	83.0	54.2	37.7

[a] Includes only eggs and young whose fates are known.   [b] Fates of all eggs and young are known.

The tropical data, graphed on the coordinate system used in Figures 2, 3, and 5, appear strikingly different from the temperate region sample. The humid tropical species (Figure 6) almost completely lack the high within-brood losses and negative vertical components which characterize starvation. The large within-nest mortality component of the clay-colored robin (species study 5, m–M = 1.53 percent per day) is associated with high losses during the egg period which indicates hatching failure as the primary mor-

tality factor other than predation. Skutch (1966) makes no mention of brood parasitism, although there are numerous parasitic cuckoos and cowbirds in the tropics. Positive vertical components can be accounted for largely by within-clutch loss of eggs, thus eliminating desertion as a factor. It is also clear that predation does not act more strongly on either the egg or nestling periods. Skutch attributes the greatest portion of nesting mortality to predation and his paper should be consulted for a more detailed account of nesting success

TABLE 7b.—*Mortality rates of small altricial land birds in arid tropical regions*

Species study number [a]	Length of nesting cycle (days)				Daily mortality rate of nests (percent) total M	Daily mortality rate of eggs (percent)			Partial loss (percent) $m-M$	Vertical component (percent) m_e-m_n
	Laying	Incuba-tion	Nestling	Total		Egg m_e	Nestling m_n	Total m		
1	1	14	10	25	2. 28	1. 77	2. 06	2. 38	0. 10	−0. 29
2	4	14	9	27	2. 44	2. 05	2. 09	2. 16	−0. 28	−0. 04
3	1½	13½	13½	28½	2. 48	1. 51	4. 12	3. 36	0. 88	−2. 61
4	3	14	13	30	3. 15	3. 28	2. 80	3. 29	0. 14	0. 48
5	1	15	11	27	1. 95	2. 38	2. 85	2. 57	0. 62	−0. 47
6	3	12½	13½	29	2. 35	1. 75	3. 08	3. 09	0. 74	−1. 35
7	2	13	13	28	1. 66	2. 13	3. 85	2. 93	1. 27	−1. 72
8	1½	11½	10½	23½	2. 95	1. 70	2. 83	2. 87	−0. 08	−1. 13
9	1½	11	10	22½	4. 37	3. 37	3. 91	4. 47	0. 10	−0. 54
10	2	11	8	21	2. 09	2. 07	2. 14	2. 51	0. 42	−0. 07
11	2½	12	9	23½	3. 21	1. 29	6. 82	4. 15	0. 94	−5. 53

[a] See Table 3a for species designation in relation to study number.

TABLE 8.—*Comparison of nesting success of humid tropical species with respect to nest-type and habitat (from Skutch, 1966)*

Nest-type and habitat	Nests (number)	Eggs (number)	Nest success (percent) Total period	Egg success (percent)		
				Egg	Nestling	Total
Open or roofed nests in clearings or second growth (23 species)	434	883	34. 6	51. 1	59. 7	30. 4
Open or roofed nests in forests (30 species)	52	107	23. 1	45. 8	46. 9	21. 5
Hole nests (16 species, excluding the house wren *Troglodytes musculus*)	43	[a] 62	53. 5	67. 8	64. 3	43. 6

[a] Clutch size and egg success could be determined in few of the hole nests.

in tropical birds. Snow (1962) also states that 86 percent of nesting losses of the black-and-white manakin in Trinidad were due to predation.

Marchant's (1960) data indicate that starvation is an appreciable component of nesting loss in an arid region of Ecuador (Figure 7). The vertical components are negative in all but one case (average, −1.20 percent), and the average vector is similar to that predicted for starvation. Marchant attributes the extremely high rates of nestling loss of the Bonaparte warbling finch (species study 11) to starvation resulting, in one

season, from the rapid dessication of the environment after a rain suitable for breeding. The large negative vertical component which represents the loss of whole broods must have been brought about by desertion because, in nests which were not terminated prematurely, 17 young fledged from 23 eggs. Thus, in these nests, only about one fourth of the young starved. Starvation and desertion of eggs are both cited as significant factors in the mortality of the long-tailed mockingbird (species study 6). No comments are given to help explain the position of the Ecuadorian neorhynchus (spe-
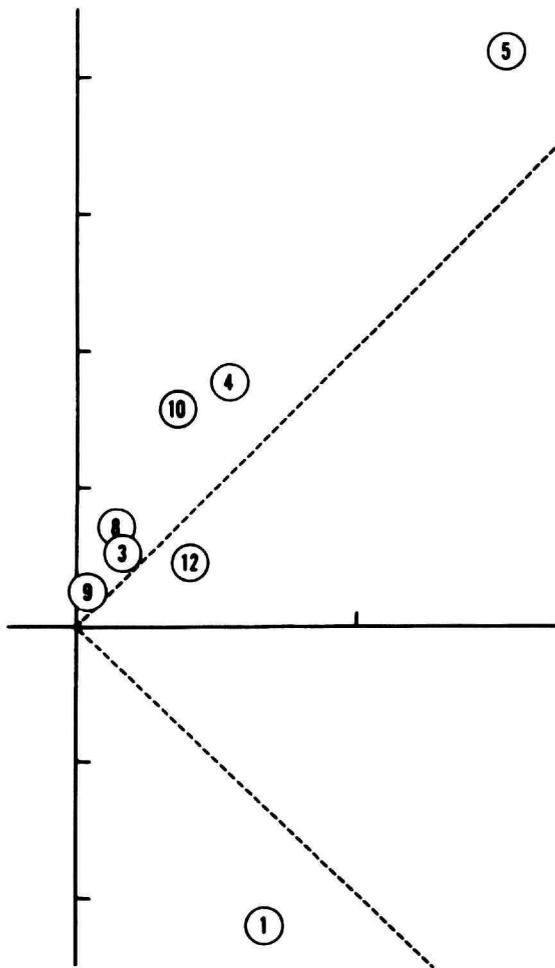
FIGURE 6.—Vertical components of individual mortality rates versus partial loss during the nest period for humid tropical passerines (and one dove). Numbers correspond to species in Table 6a. Scale and vectors as in Figure 5.
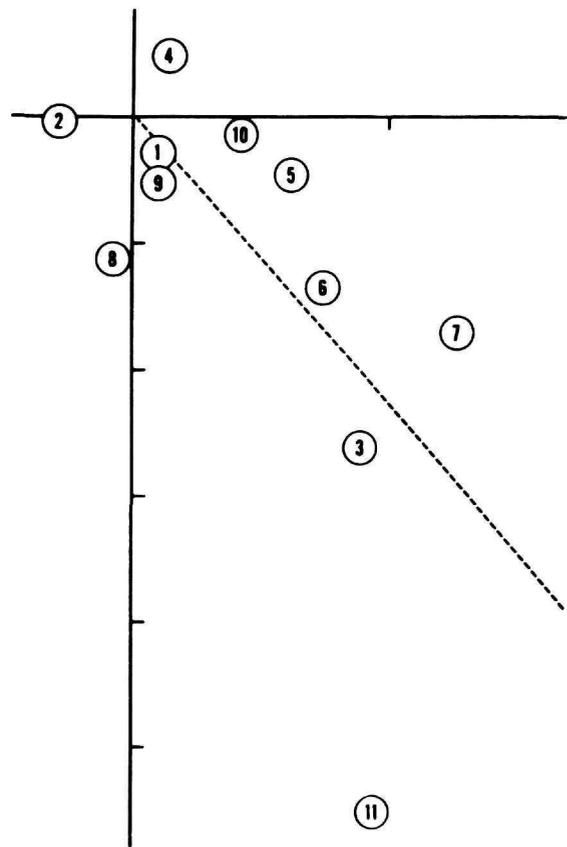
FIGURE 7.—Vertical components of individual mortality rates versus partial loss during the nest period for arid tropical passerines (and one dove and one cuckoo). Numbers correspond to species in Table 7a. Scale and vectors as in Figure 5.

cies study 8), but it must be assumed that desertion of nestlings, especially of small broods, was a significant factor.

Hatching failure is much lower in the Ecuadorian sample than for temperate North American species, averaging 4.3 percent (range, 2.7–5.9) of eggs surviving the egg period in six species.

ARCTIC SPECIES.—The few data available on arctic nesting success (Table 9a) are restricted primarily to finches (Fringillidae), all of which nest on, or near, the ground. Daily mortality rates calculated for these

species (Table 9b) indicate that mortality factors are weaker in the arctic compared with more southerly latitudes. Mortality rates of ground-nesting species in temperate areas are almost one half again as great. Oakeson (1954) found nesting success in a limited sample of the white-crowned sparrow to increase from California to the Arctic. Of 30 nests found near Berkeley, 12 (40 percent) were successful. At Friday Harbor, Washington, 19 of 32 nests (59 percent) fledged young, and at Mountain Village, Alaska, 6 of 8 nests were fully successful and 2 were partly successful.

TABLE 9a.—*Nesting success of small altricial land birds in arctic regions*

Species and study designation number	Length of study (years)	Nests (number)	Eggs (number)	Nest success (percent) total period	Egg success (percent)			Source and locality
					Egg	Nestling	Total	
Lapland longspur (*Calcarius lapponicus*)								
1	1	22	97	77. 7	77. 3	82. 8	63. 9	Sutton and Parmelee, 1955, Baffin Island
2			54				81. 5	Drury, 1961, Northwest Territories
3a	1	53	262	45. 2	80. 5	47. 8	38. 5	Williamson,Thompson, and
3b	1	38	175	44. 7	66. 9	54. 7	36. 6	Hines, 1966, Cape Thompson,
Combined	2	91	437	45. 1	75. 0	50. 3	37. 8	Alaska
Chestnut-collared longspur (*Calcarius ornatus*)								
4		10	44		79. 6	91. 5	72. 8	Harris, 1944, Manitoba
White-crowned sparrow (*Zonotrichia leucophrys*)								
5a	1	15	72	53. 3	68. 1	71. 4	48. 6	Williamson,Thompson, and
5b	1	13	60	69. 2	70. 0	83. 3	58. 3	Hines, 1966, Cape Thompson,
Combined	2	28	132	60. 7	69. 0	76. 9	53. 1	Alaska
Savannah sparrow (*Passerculus sandwichensis*)								
6a	1	8	47	75. 0	74. 4	80. 0	59. 5	Williamson,Thompson, and
6b	1	9	50	66. 6	94. 0	61. 7	58. 0	Hines, 1966, Cape Thompson,
Combined	2	17	97	70. 6	84. 5	69. 5	58. 8	Alaska
Common redpoll (*Acanthis flammea*)								
7		9	33	66. 7	72. 7	54. 2	39. 4	Grinnell, 1943, Manitoba
8a	1	46	177	19. 6	34. 5	44. 3	15. 3	Williamson,Thompson, and
8b	1	50	182	16. 0	39. 6	34. 7	13. 7	Hines, 1966, Cape Thompson,
Combined	2	96	359	17. 7	37. 1	39. 1	14. 5	Alaska
Snow bunting (*Plectrophenax nivalis*)								
9	1	16	80	93. 8	90. 0	83. 3	75. 0	Sutton and Parmelee, 1955, Baffin Island
10	2	5	24	100. 0	91. 7	95. 5	87. 5	Williamson,Thompson, and Hines, 1966, Cape Thompson, Alaska
Yellow wagtail (*Motacilla flava*)								
11	2	4	20	75. 0	95. 0	79. 0	75. 0	Williamson,Thompson, and Hines, 1966, Cape Thompson, Alaska

At Cape Thompson, Alaska, however, Williamson, Thompson, and Hines (1966) reported only 8 successes of 15 nests (53 percent) of the white-crowned sparrow. In fact, all of the species studied by these investigators exhibited low nesting success ($m = 3.89$) compared with other arctic studies ($m = 1.21$). Thus, arctic nesting success may be higher generally than the averages presented in Tables 9a and 9b. For example, Irving

and Krog (1956) reported that of 45 eggs (9 nests, 7 species), 84 percent left the nest spontaneously.

In six of seven arctic species mortality rates were greater during the nestling period than during the egg period and within-brood losses are high (Figure 8). Starvation is implicated but it is not unreasonable to assume that death from exposure also may be important. This factor would probably affect the young to a

TABLE 9b.—*Mortality rates* [a] *of small altricial land birds in arctic regions*

| Species study number [b] | Length of nesting cycle (days) | | | | Daily mortality rate of nests (percent) total M | Daily mortality rate of eggs (percent) | | | Partial loss (percent) $m-M$ | Vertical component (percent) m_e-m_n |
	Laying	Incubation	Nestling	Total		Egg m_e	Nestling m_n	Total m		
1	4	12	9	25		1.61	2.10	1.79		−0.49
2								0.82		
3					3.19	1.80	7.64	3.90	0.71	−5.84
4	4	12	10	26		1.43	0.89	1.22		0.46
5	4	11	9	24	2.08	2.47	2.93	2.64	0.56	−0.46
6	4	11	9	[c] 24	1.45	1.12	4.05	2.22	0.77	−2.93
8	4	10½	11½	26	6.08	6.20	8.17	6.79	0.71	−1.97
9	3½	12¼	12¼	28½	0.22	0.64	1.45	0.99	0.77	−0.81

[a] Mortality rates are calculated only for studies represented by more than 10 nests.

[b] See Table 3a for species designation in relation to study number.

[c] The length of the nesting cycle was estimated.

greater degree than eggs. Predation apparently causes negligible mortality in many arctic species. For example, from 22 nests of the Lapland longspur on Baffin Island (Sutton and Parmelee, 1955) more than one third of the eggs failed to produce fledglings, but only one of these nests was lost to a predator. None of 16 broods of the snow bunting, which nests in crevices, were destroyed by predators.

Geographical variation in the breeding success of open-nesting species is summarized in Table 10. Most of these inhabit open areas (fields, scrub, second-growth, and parklike or edge habitats associated with man) because nests are more readily found and observed in open areas than in deep woods (Skutch, 1966). The average length of the nest period is similar for all localities and, thus, differences in overall nesting success may be attributed almost entirely to differences in mortality rates.

The four areas are not strictly comparable because different types of habitats are sampled. The arctic species are typical of treeless tundra and riparian situations, the humid tropical species of wet second-growth and clearings, and the arid tropical species of desert-scrub. It is more realistic to compare humid tropical species ($m=4.09$) with temperate species building open nests above the ground ($m=2.12$, Table 5) rather than with the overall temperature zone average ($m=3.06$). The arid tropical species more properly would be compared with birds of the southwestern deserts of the United States than with eastern species.

TABLE 10.—*Geographical variation in nesting success of open-nesting passerines*

| Nesting parameter | Region | | | |
	Arctic	Temperate	Humid tropical	Arid tropical
Overall nest success (percent)	[a] 60.9 (6)	55.4 (12)	30.5 (9)	51.1 (9)
Overall egg success (percent)	60.0 (9)	46.6 (13)	32.4 (8)	43.9 (9)
Average nest period (days)	28.3 (6)	26.5 (14)	30.4 (10)	25.9 (9)
Mortality rate of nests (percent)	2.60 (5)	2.40 (12)	3.95 (9)	2.69 (9)
Mortality rate of eggs (percent)	2.55 (7)	3.06 (13)	4.09 (9)	3.25 (9)
Partial loss (percent)	0.70 (5)	0.69 (11)	0.47 (7)	0.56 (9)
Vertical component, (percent)	−1.72 (6)	0.10 (13)	1.22 (7)	−1.44 (9)

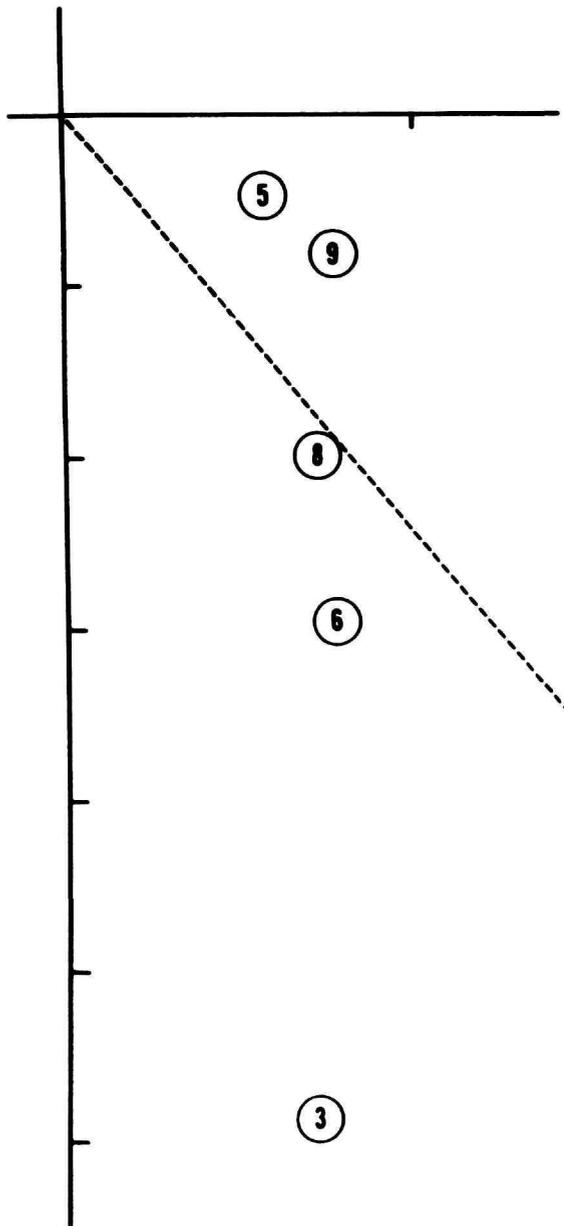[a] Number of species constituting each average is given in parentheses.

FIGURE 8.—Vertical components of individual mortality rates versus partial loss during the nest period for arctic passerines. Numbers correspond to species in Table 9a. Scale and vectors as in Figure 5.

The low mortality rate of the catcus wren ($M = 1.00$, Table 3b) and personal observation of other desert species in Arizona suggest that nesting success is generally higher in arid than in humid habitats. Thus, the mortality rates of dry tropical species may not be so nearly similar to those of temperate ecological counterparts as they would seem from Table 10.

Starvation is important to at least some species in all but humid tropical regions. The large starvation components of arid tropical birds probably are related to the sparce and unpredictable rainfall which controls the abundance of food resources. Marchant (1959) and Lloyd (1960) have shown that breeding is closely correlated with the occurrence of irregular rainfall. The absence of starvation components in the humid tropical data indicates either that food resources are highly predictable and clutch size is finely adjusted to this level, or that the availability of food does not limit clutch size in the tropics (Skutch, 1949, 1967). But it should be noted that the humid tropical sample includes only one field or marsh species, the blue-black grassquit which does exhibit a small negative vertical component. Temperate species which exhibit starvation vectors include three marsh-nesting icterids. The availability of food in marshes is known to fluctuate greatly (Orians, 1966). Several field-nesting species are characterized also by negative vertical components suggesting that food is relatively unpredictable in this habitat as well.

The large positive vertical compenents of three of the species studied by Skutch can be explained by within-nest loss. Desertion, therefore, appears to be of major importance only among temperate species. It should be kept in mind that desertion is not solely a feature of the environment, but rather it is the result of interactions between adult behavior and environmental factors. Thus, geographical differences with respect to desertion may be the result of variation in the intensity of parental care rather than the amount of disturbance to nests.

Clearly most of the variation in nest mortality rates between localities is related to predation which will be considered in the discussion. Nesting-success studies are further summarized by genera in Table 11 according to the length and direction of their vectors to emphasize geographical differences.

TABLE 11.—*Taxonomic summary of nesting success studies*

Region	Vertical component large and positive (>0.50)	Vertical component small	Vertical component large and negative (<−0.50)
Arctic		*Calcarius* (2) [a]	*Calcarius*
		Acanthus	*Passerculus*
			Zonotrichia
			Plectrophenax
Temperate	*Zenaidura* (2)	*Calypte*	*Eremophila*
	Telmatodytes	*Stelgidopteryx* [b]	*Seiurus*
	Troglodytes (3) [b]	*Iridoprocne* [b]	*Euphagus*
	Turdus (2)	*Sialia* [b]	*Agelaius* (4)
	Sialia (2) [b]	*Sturnus* [b]	*Quiscalus* (2)
	Bombycilla	*Dendroica*	*Melospiza*
	Protonotaria (2) [b]	*Agelaius*	
	Agelaius	*Spinus*	
	Icterus	*Carpodacus*	
	Xanthocephalus		
	Spizella (2)		
	Rhynchophanes		
Humid tropical	*Myiozetetes*	*Troglodytes* [b]	*Columbigallina*
	Elaenia	*Thraupis*	
	Turdus	*Volatinia*	
	Ramphocelus		
	Tiaris		
Arid tropical		*Eupelia*	*Pyrocephalus*
		Crotophaga	*Mimus*
		Muscigralla	*Polioptila*
		Euscarthmus	*Neorhynchus*
		Rhodospingus	*Sporophila*
			Poospiza

[a] Number of studies is given in parentheses if more than one.
[b] Hole-nesting species.

BREEDING DENSITY AND NESTING MORTALITY.—We may postulate that increasing nesting density causes greater mortality either through competition for food or more efficient predation. This appears to be the case at Cape Thompson, Alaska (Williamson et al., 1966; Table 12). The most abundant species in riparian situations, the common redpoll, exhibits extremely high nest mortality. Yellow wagtails and white-crowned sparrows, nesting in the same localities but in fewer numbers, had much higher nesting success. Mortality was high in the redpoll during the egg as well as during the nestling period and, thus, starvation through increased competition for food was not a major factor. Also, because the three species nest at the same time, unusually bad weather should have affected all species

to the same extent. We must conclude that predators specialized on the abundant redpoll nests, which is surprising because nests of wagtails and white-crowned sparrows are fairly similar. One would have expected that increased predator efficiency on the redpolls might have carried over to the less common species (Fretwell, 1968). That is, one would not expect predators to distinguish, on a species level, nests of similar construction, although this likely has occurred.

Corresponding situations could not be found for temperate and tropical localities. Nolan (1963) found that in a deciduous scrub habitat in Indiana ". . . the rates of nesting success of each of the 4 species whose nests were most numerous were not significantly different than the pooled results for the other 10 spe-

TABLE 12.—*Breeding density and nesting success at Cape Thompson, Alaska* [a]

Species	Average nesting density, pairs/100 acres [b, c]	Nests found (number)	Overall nest mortality rate (percent)
Yellow wagtail	9 (2)	4	[d] 1. 15
Savannah sparrow	13 (7)	17	1. 45
White-crowned sparrow	28 (2)	28	2. 08
Lapland longspur	35 (10)	91	3. 19
Common redpoll	80 (2)	96	6. 08

[a] Data from Williamson, Thompson, and Hines (1966).

[b] Only habitats where the species were present are included in the sample, i.e., riparian (willow, *Salix* sp.) for the yellow wagtail, white-crowned sparrow and common redpoll, and tundra for the savannah sparrow and Lapland longspur.

[c] Number of census plots with species present are given in parentheses.

[d] Calculated from estimated nesting cycle length of 25 days.

cies. . . " Fretwell (1968) found that in North Carolina, where field sparrows were common, their nesting success as well as that of other uncommon species was low and conversely where field sparrows did not nest in numbers the nesting success of all species was high. The field sparrow is generally the most abundant species in cleared areas and apparently its density controls the success of other less common species with similar nests. Thus, within an area nest mortality is independent of breeding density but between areas the overall density of similar species controls their success. It should be pointed out that Fretwell used Mayfield's (1961) method for calculating nesting mortality and thus avoided possible biases incurred when nests are found at different stages.

From Skutch's (1966) data on nesting success at his farm in Costa Rica we again can show that common species are at least as successful as rarer species, if not more so (Table 13).

On the Santa Elena Peninsula of Ecuador, the five commonest species in Marchant's (1961) study, each being represented by more than 180 nests, had an average daily nest mortality rate of 2.89 percent, whereas six species of which 20 to 100 nests were found had an average mortality rate of 2.42 percent.

Although the differences in both of the tropical studies between the mortality rates of common and uncommon species are not significant, they are suggestive

TABLE 13.—*Nest abundance and nesting success of some Costa Rican birds* [a]

Species	Nests found (number)	Nests successful (number)	Percent
Scarlet-rumped tanager	80	35	43. 8
Yellow-faced grassquit	44	13	29. 6
Gray-capped flycatcher	30	13	43. 3
Blue-gray tanager	27	12	44. 4
Clay-colored robin	24	6	25. 0
Combined	205	79	38. 5
18 less common species	229	71	31. 0

[a] Data from Skutch (1966) includes only nests found before the last egg was laid.

that in simpler habitats, or perhaps those with low productivity (i.e., arid and arctic), the uncommon species have relatively high success, whereas in the more humid tropical and temperate environments, nests of uncommon species are not distinguished from those of common species by predators. This phenomenon merits more detailed investigation.

RAPTORIAL SPECIES.—Nesting success of birds of prey is generally high, and because of their long nest periods calculated mortality rates are low (Table 14). Predation is apparently a negligible factor in raptorial species because of their ability to defend their nests. Fitch et al. (1946) reported, however, that jays destroyed eggs in 2 of 26 nests of the red-tailed hawk in California and blood-sucking flies were responsible for the deaths of 7 of 15 nestlings in one year. During the preceding year, none of 11 nestlings were lost.

Mortality rates of nests and eggs are generally less than 1.0 percent per day. In the African fish eagle young were lost almost eight times more rapidly than eggs, suggesting that starvation was a significant factor (Brown, 1960). Lack (1954) emphasized asynchronous hatching and selective starvation as a common feature of raptorial nesting behavior. Ratcliffe (1962) found that duck hawk nests contained averages of 3.4 eggs but only 1.9 young at all stages during the nest period. Nests of the raven, which held averages of 4.6 eggs and 4.2 young one to three days after hatching, contained an average of 2.55 young when found more than three days after hatching. Similarly, brood size of the marsh hawk declined from 4.1 at hatching to 3.2 at thirty-

five days (Hammond and Henry, 1949). Nest loss in this species was also quite high during the first half of the nest period (2.07 percent daily) compared with the egg period (0.83 percent daily). Conversely, mortality rates of golden and bald eagles were quite low during the nestling period (Table 14), which suggests that starvation was not a factor in these studies.

SEABIRDS [PROCELLARIIFORMES AND PELECANIFORMES].—Seabirds nest predominately on inaccessable islands, thus eliminating predation by most terrestrial animals. Most nest losses are "internal" (Pet-

tingill, 1939)—i.e., caused by hatching failure and crowded conditions resulting in direct intraspecific strife—although some avian predators such as gulls and frigate birds may take a heavy toll of unguarded eggs and chicks.

Some of the data available on nesting success in seabirds is presented in Table 15. Rates of egg loss in eight studies varied from 0.86 to 3.69 percent per day with an average of 2.17. Mortality rates of young are only about one third as great (0.13–1.19 percent in eight studies, average 0.66). Most losses of eggs in seabirds

TABLE 14.—*Nesting success and mortality rates of raptorial birds*

Species	Length of study (years)	Nests (number)	Eggs (number)	Egg period (days)	Nestling period (days)	Nest success [a] (percent)			Egg success [a] (percent)			Source and locality
						Egg	Nestling	Total	Egg	Nestling	Total	
African eagles (10 species)		77						70. 1				Brown, 1955, Kenya
Bald eagle (*Haliaetus leucocephalus*)	3	32	57	34	80				64. 9 (1. 27)	59. 5 (0. 65)	38. 6 (0. 84)	Hensel and Troyer, 1964, Alaska
African fish eagle (*Haliaetus vocifer*)	3	12	25	44	70				92. 0 (0. 12)	52. 2 (0. 93)	48. 0 (0. 64)	Brown, 1960, Kenya
Golden eagle (*Aquila chrysaetos*)	2	51	[b] 102	40	70				79. 4 (0. 58)	86. 4 (0. 21)	68. 7 (0. 34)	McGahan, 1968, Montana
Red-tailed hawk (*Buteo jamaicensis*)	3	87		30	45			73. 6 (0. 41)				Orians and Kuhlman, 1956, Wisconsin
	2	[c] 22				86. 3 (0. 40)	73. 7 (0. 68)	63. 7 (0. 60)				Fitch, Swenson, and Tillotson, 1946, California
White-tailed kite (*Elanus leucurus*)		23	94	35	[d] 40						78. 7 (0. 32)	Dixon, Dixon and Dixon, 1957, California
Marsh hawk (*Circus hudsonius*)	3	60		36		71. 7 (0. 93)	[e] 68. 6 (2. 07)					Hammond and Henry, 1949, North Dakota
Great-horned owl (*Bubo virginianus*)	3	41		34	66			80. 5 (0. 22)				Orians and Kuhlman, 1956, Wisconsin

[a] Mortality rates are given in parentheses.

[b] Estimated from average clutch size of two.

[c] Not including four nests which were deserted because of the investigators' disturbance.

[d] Estimated nestling period.

[e] Based on the survival of 51 nests through the first 16–20 days of the nestling period.

TABLE 15.—*Nesting success and mortality rates of seabirds* [*Procellariiformes and Pelecaniformes*]

Species	Length of study (years)	Nests number	Eggs number	Egg period (days)	Nestling period (days)	Nest success [a] (percent) total period	Egg success [a] (percent)			Source and locality
							Egg	Nestling	Total	
Madeiran storm petrel (*Oceanodroma castro*)		67	67	42	64				43.3 (0.79)	Allan, 1962, Ascension Island
Red-billed tropic bird (*Phaethon aethereus*)		328	328	43	100		69.2 (0.86)	74.4 (0.30)	51.5 (0.46)	Stonehouse, 1962, Ascension Island
White-tailed tropic bird (*Phaethon lepturus*)		821	821	41	80		48.1 (1.77)	63.0 (0.58)	30.3 (0.99)	Stonehouse, 1962, Ascension Island
Brown booby (*Sula leucogaster*)		185	370	47	120	9.7 (1.39)	19.2 (3.46)	25.4 (1.14)	4.9 (1.80)	Dorward, 1962, Ascension Island [b]
		150	300	47	120	26.0 (0.81)			13.0 (1.22)	
Blue-faced booby (*Sula dactylatra*)		631	1262	45	120	8.9 (1.47)	18.5 (3.69)	23.9 (1.19)	4.4 (1.87)	Dorward, 1962, Ascension Island[b]
		68	136	45	120	17.7 (1.05)	27.9 (2.80)	31.6 (0.94)	8.8 (1.47)	
Pelagic cormorant (*Phalacrocorax pelagicus*)	1	37	141	35	45		49.6 (2.00)			Drent, et al. 1964, Mandarte Island, British Columbia
	2	39	°101	35	45			76.2 (0.60)		
Double-crested cormorant (*Phalacrocorax auritus*)	2	66	273	33	39		60.4 (1.54)	95.2 (0.13)	57.4 (0.77)	Drent, et al, 1964, Mandarte Island, British Columbia
Shag (*Phalacrocorax aristotelis*)	4	294	893	28	53		70.8 (1.23)	87.1 (0.26)	61.7 (0.60)	Snow, 1960, Lundy Island, English Channel

[a] Daily mortality rate is given in parentheses.
[b] Data from two colonies are presented separately.
[c] Young hatched.

are due to their rolling out of nests—particularly in boobies (Dorward, 1962)—becoming overheated in the sun, and being destroyed by avian predators. Drent et al. (1964) found that 32 percent of eggs of the pelagic cormorant were preyed upon and 18 percent

were addled. Nine and 28 percent of eggs of the double-crested cormorant were lost to predators in two years, and 24 and 18 percent were found addled.

Starvation appears not to be a significant factor in mortality of the young of species which lay only one

egg. It will be shown below that mortality rates of tropic birds decrease as the chicks grow, whereas these rates increase when starvation is a major factor, as in blackbirds and grackles (Peterson and Young, 1950; Young 1955, 1963). The primary source of chick mortality is crowded conditions in colonies and the resulting death of unattended young caused by other adults (Stonehouse, 1962; Nelson, 1966). The tropical boobies lay two eggs but only one chick is raised, the other starving if two eggs survive the incubation period (Dorward, 1962). Thus, nest success is always approximately twice egg success and the former value is of greater interest from the standpoint of selective forces because the loss of the second egg is probably a part of the reproductive strategy.

Starvation may play a role in the mortality of cormorants which raise broods of two to four young. Snow (1960) found that the survival of young varied between 90.2 and 95.5 percent during three years of a four-year study on the shag, but that only 66.9 percent of chicks survived during the fourth year. Clutch size was also somewhat reduced (2.8 compared to 3.0–3.2 eggs) which often is observed in birds in response to poor feeding conditions (Lack, 1954). Egg survival (68.7–73.6 percent) varied little during the study period.

SEABIRDS [CHARADRIIFORMES].—The gulls and terns (Table 16) have different mortality patterns than other seabirds in that nestling mortality rates generally exceed egg rates. Egg losses are somewhat lower (average 1.18 percent per day, range 0.13–1.91 for eleven studies, not including Hagar, 1937, where introduced rats caused high mortality, and Ashmole, 1962, which does not include data for the nestling period) and, as in other seabirds, "internal" factors are primarily responsible. Nestling mortality rates averaged 2.34 percent for fourteen studies (range, 0.35–5.74), about twice that of the egg period. In the Alcidae, the reverse situation occurs. Egg losse are rather high (1.97 percent, range 1.29–2.81) as in the Procellariiformes and Pelecaniformes and chick losses are substantially reduced (average 1.06 percent, range 0.63–1.78).

Pettingill (1939) estimated that less than one fourth of all losses in the arctic tern were caused by external factors. In the pigeon guillemot, 18 percent of eggs were found adled, 3.5 percent rolled out of nests, and 13 percent were taken by crows, nearly all within the first five days after being layed (Drent et al. 1964). High tides destroyed 30 percent of eggs of the black guillemot and 18 percent were infertile (Winn, 1950).

Most of the mortality noted by Tuck (1960) in the thick-billed murre was "internal." Of egg losses, 19 percent were caused by rock falls, 8 percent rolled into crevices, but only 1 percent were taken by gulls. The remainder were suspected to have fallen off ledges. Similarly chicks suffered heavily from falling off ledges (41 percent of losses), exposure (38 percent), and falling into cracks (12 percent). Thoreson (1964) also cites several internal factors in the cavity-nesting Cassin's Auklet such as the cave-in of burrows due to wind erosion. One third of all eggs in that study were deserted because of human disturbance—a factor not often mentioned in nest-success studies. Where predators have been introduced onto offshore islands, nesting losses may be quite high. Rats took 67 percent of eggs and 50 percent of young of the least terns studied by Hagar (1937). An additional 19 percent of eggs were destroyed by storm tides. High tides killed 41 percent of black guillemot young studied by Winn (1950) and several also fell victims to gulls and crows.

Coulson and White (1958) have demonstrated that nesting success of the black-legged kittywake increases with age. Birds in their first and second breeding years had overall fledging successes of 35.8 and 55.8 percent, respectively, while those which had bred at least twice previously had 69.7 percent fledging success.

The Arctic tern is the only species in which starvation is cited as a significant factor (Hawksley, 1957). Of the 90 chicks hatched, 37 percent starved, mostly in nests with two young. The fledging success from broods of one and two was 71 and 35 percent, respectively. In six of eleven studies on Laridae presented in Table 16, nestling mortality rates exceeded egg mortality rates by more than 0.50 percent per day. This does not necessarily indicate starvation, however, as would be the case in altricial nidicolous birds, because individual young occasionally wander off on their own and are killed by predators or other adults. The only gulls and terns in which mortality rates are much lower during the nestling period than during the egg period are the black-legged kittywake (Cullen, 1957) and the least tern (Hagar, 1937) The former nests .on ledges on vertical cliffs. Egg mortality in this species is about average for gulls and terns, but chick loss is extremely low. Needless to say, kittywake chicks do not wander far from their narrow nest ledges. In the last tern study, rats were the major mortality factor, and it is reasonable to assume that they would prey more heavily on eggs than on chicks.

TABLE 16.—*Nesting success and mortality rates of seabirds [Charadriiformes: Laridae and Alcidae]*

Species	Length of study (years)	Nests (number)	Eggs (number)	Egg Period (days)	Nestling period (days)	Egg success a(percent)			Source and locality
						Egg	Nestling	Total	
LARIDAE:									
Black noddy									
(*Anous tenuirostris*)			178	35		23. 6			Ashmole, 1962, Ascension
						(4. 13)			Island
Arctic tern									
(*Sterna paradisea*)	1	100	144	24	27	63. 2	25. 3		Pettingill, 1939, Bay of Fundy,
						(1. 91)	(5. 10)		New Brunswick
			308			64. 0	54. 3		Hawksley, 1957, Bay of Fundy,
						(1. 86)	(2. 26)		New Brunswick
Least tern									
(*Sterna albifrons*)		428	820	23	27	25. 9	35. 4		Hagar, 1937, New England
						(5. 90)	(3. 85)		
Black-legged kittywake									
(*Rissa tridactyla*)			348	27	38	68. 9	87. 5		Cullen, 1957, Great Britain
						(1. 38)	(0. 35)		
Ring-billed gull									
(*Larus delawarensis*)		100	300	29	b 40	72. 3	30. 9		Emlen, 1956, Michigan
						(1. 12)	(2. 94)		
Glaucous-winged gull									
(*Larus glaucescens*)	4	1136	2967	30	40	59. 8	56. 9		Drent et al, 1964, British
						(1. 71)	(1. 41)		Columbia
Lesser black-backed gull									
(*Larus fuscus*)	2		293	b 30	b 40	96. 2	54. 7		Darling, 1938, Great Britain
						(0. 13)	(1. 51)		
	2		716			60. 9	10. 1		Paludan, 1951, Denmark
						(1. 71)	(5. 74)		
California gull									
(*Larus californicus*)		100	293	27	40	86. 7	69. 7		Behle and Goates, 1957,
						(0. 53)	(0. 90)		Utah
Herring gull									
(*Larus argentatus*)	2		324	29	42	91. 8	41. 4		Darling, 1938, Great Britain
	2		641			(0. 29)	(2. 10)		Paludan, 1951, Denmark
						70. 3	38. 3		
			247			(1. 22)	(2. 28)		Paynter, 1949, Bay of Fundy,
						71. 3	61. 9		New Brunswick
						(1. 17)	(1. 14)		
ALCIDAE:									
Thick-billed murre									
(*Uria lomvia*)	1	400	632	34	19	38. 5	88. 7		Tuck, 1960, Cape Hay,
						(2. 81)	(0. 63)		Canada

See footnotes at end of table.

TABLE 16.—*Nesting success and mortality rates of seabirds [Charadriiformes: Laridae and Alcidae]*—Continued

Species	Length of study (years)	Nests (number) [.]	Eggs (number)	Egg Period (days)	Nest-ling period (days)	Egg success (percent)			Source and locality
						Egg	Nestling	Total	
Black guillemot (*Cepphus grylle*)		46	84	29	39	52. 4 (2. 23)	50. 0 (1. 78)		Winn, 1950, Bay of Fundy, New Brunswick
Pigeon guillemot (*Cepphus columba*)	4	109	200	31	35	62. 0 (1. 54)			Drent et al, 1964, British Columbia
	3		91				90. 1 (0. 30)	74. 1 (0. 86)	
	1		44				40. 9 (2. 56)		
Cassin's auklet (*Ptychoramphus aleutica*)	1	75		37	45	41. 4 (2. 38)	64. 5 (0. 98)		Thoreson, 1964, Oregon
		[c] 50				62. 0 (1. 29)			

[a] Mortality rates are given in parentheses.

[b] Estimated.

[c] Excluding nests deserted because of human disturbance.

Nest-site dependence may more generally determine the relationship between egg and nestling loss in seabirds, as summarized in Table 17. The Procellariiformes and Pelecaniformes, which exhibit altricial or semialtricial development (Nice, 1962) and hence are not physically capable of leaving the nest until well grown, and the Alcidae, which are semiprecocial, that is, capable of walking, but restricted to the nest because of its location until flight capabilities are attained, suffer relatively little nestling loss. Most of the Laridae, except for cliff-nesting species such as the kittywakes, often wander away from the nest site and thus from parental protection. Of the many dangers to which

unattended chicks are exposed, other adults of the same species are perhaps the most significant. This explanation for the discrepancy in nestling mortality rates does not account for the reverse difference in egg mortality. Cliff nesting, which affords the young some protection from other adults, results in high egg losses due to their rolling out of place. But many of the Pelecaniformes (i.e., cormorants) build substantial nests which should prevent most egg loss caused by rolling. In fact, cormorants do have lower egg mortality (2.00, 1.54, 1.23 percent per day) than brown and bluefaced boobies which do not build nests (3.46, 3.69, 2.80 percent per day). Interesting comparisons

TABLE 17.—*Egg and nestling mortality rates in seabirds*

Order or family	Number of species	Egg mortality rate (percent)		Nestling mortality rate (percent)	
		Average	Range	Average	Range
Procellariiformes and Pelecaniformes	7	2. 17	0. 86–3. 69	0. 66	0. 13–1. 19
Laridae	11	1. 18	0. 13–1. 91	2. 34	0. 35–5. 74
Alcidae	4	1. 97	1. 29–2. 81	1. 06	0. 63–1. 78

could be made with species of boobies which build nests in trees.

SHOREBIRDS.—Precocial chicks characteristicly leave the nest shortly after hatching. Most of the data available for shorebirds, therefore, encompasses only the egg period. Eleven studies from widely different localities and habitats are summarized in Table 18. Mortality rates average 1.44 percent per day during the egg period (range, 0.27–3.53 percent) which is similar to

that for gulls and terns. Soikkeli (1967) found the mortality rate of dunlin chicks during the first two weeks after hatching to be 1.76 percent per day, or about two thirds again as great as during the egg period. Most of the losses occured during the first three days out of the egg. No difference seems to exist between temperate and arctic species but it is clear that the rate of egg loss of precocial shorebirds is lower than that of ground-nesting altricial passerines, espe-

TABLE 18.—*Nesting success and mortality rates of shorebirds* [*Charadriiformes: Haematopodidae, Charadriidae, Scolopacidae*]

Species	Nests (number)	Eggs (number)	Egg period (days)	Egg success [a] (percent) total period	Source and locality
HAEMATOPODIDAE:					
Black oystercatcher					
(*Haematopus bachmani*)					
	16	38	29	71. 1 (1. 18)	Drent et al, 1964, British Columbia
CHARADRIIDAE:					
Golden plover					
(*Pluvialis dominica*)					
	35	139	29	70. 5 (1. 25)	Williamson, Thompson, and Hines, 1966, Cape Thompson, Alaska
Semipalmated plover					
(*Charadrius semipalmatus*)					
	3	12		100. 0	Williamson, Thompson, and Hines, 1966, Cape Thompson, Alaska
Piping plover					
(*Charadrius melodus*)					
	174	668	32	91. 7 (0. 27)	Wilcox, 1959, New York
Ringed plover					
(*Charadrius hiaticula*)					
			[b] 29	36. 0 (3. 53)	Laven, 1940, Germany
SCOLOPACIDAE:					
Upland plover					
(*Bartramia longicauda*)					
	47		25	66. 0 (1. 67)	Buss and Hawkins, 1939, Wisconsin
Ruddy turnstone					
(*Arenaria intrepes*)					
			25½	72. 0 (1. 29)	Bergman, 1946, Finland
Dunlin					
(*Calidris alpina*)					
	42		25	80. 9 (0. 85)	Holmes, 1966, Alaska
	123	479	25	78. 1 (0. 99)	Soikkeli, 1967, Finland
Semipalmated sandpiper					
(*Ereunetes pusillus*)					
	7	28		96. 4	Williamson, Thompson, and Hines, 1966, Cape Thompson, Alaska
Western sandpiper					
(*Ereunetes mauri*)					
	7	28		96. 4	Williamson, Thompson, and Hines, 1966, Cape Thompson, Alaska

[a] Mortality rates are given in parentheses.　　　　[b] Estimated.

cially in temperate regions. But shorebirds also nest in slightly different habitats than passerines, prefering either wetter or more barren situations.

WATER BIRDS.—A sample of nesting success in several different groups of water birds (Anseriformes, Ciconiiformes, and Gruiformes) is presented in Table 19. Except for the Ciconiiformes (herons and ibises) water birds have precocial young, and reliable data on posthatching survival were not found. Nest mortality rates during the egg period in eight studies average 1.03 percent per day (range, 0.17 to 1.98). Lack (1954, Table 15) has summarized hatching success in ten

species of ducks which averaged 66.5 percent (range, 45 to 90) of eggs laid. Williams and Marshall (1938) found that hatching success of seven species of ducks in the United States varied between 26 and 85 percent. In the ruddy duck the difference between nest and individual egg mortality rates was 0.16 percent per day, whereas in two rails differences were negative (-0.23 and -0.31) suggesting the selective loss of nests before the completion of laying or of small clutches. Rails generally have large clutches (average 9–11 eggs in the species in Table 19) and the laying period occupies at least a third of the total egg period.

TABLE 19.—*Nesting success and mortality rates of water birds*

Species	Nests (number)	Eggs (number)	Egg period (days)			Nest success [a] (percent) total period	Egg success [a] (percent) total period	Partial loss	Source and locality
			Laying	Incubation	Total				
COLYMBIDAE: Pied-billed grebe (*Podilymbus podiceps*)	138		6	23	29	70. 3 (1. 22)			Glover, 1953, Iowa
ARDEIDAE: Least bittern (*Ixobrychus exilis*)	38		4½	18	22½	84. 2 (0. 77)			Weller, 1961, Iowa
Little blue heron (*Florida caerulea*)	30	124	4	22	26	93. 3 (0. 17)	74. 2 (0. 75)	0. 58	Meanley, 1955, Arkansas
ANATIDAE: Ruddy duck (*Oxyura jamaicensis*)	71	546	8	25	33	73. 2 (0. 94)	69. 4 (1. 10)	0. 16	Low, 1941, Iowa
Canada goose (*Branta canadensis*)	1094		5	24	29	56. 1 (1. 98)			Klopman, 1958, various
RALLIDAE: Coot (*Fulica americana*)	16	119	7½	24	31½		47. 9 (2. 32)		Gullion, 1954, California
Sora rail (*Porzana carolina*)	36	266	9	17	26	61. 1 (1. 88)	66. 5 (1. 57)	−0. 31	Walkinshaw, 1940, Michigan
Clapper rail (*Rallus longirostris*)	56		10	20	30	89. 3 (0. 38)			Kozicky and Schmidt, 1949, New Jersey
King rail (*Rallus elegans*)	16	147	11	22	33	75. 0 (0. 87)	81. 0 (0. 64)	−0. 23	Meanley, 1953, Arkansas

[a] Mortality rates are given in parentheses.

Predation, adverse weather, and high tides are probably the most important mortality factors in the marsh habitat.

Survival of water birds nests in marshes is much higher than for passerines in similar habitats. Apparently, adaptation to aquatic life permits the use of safer nesting sites in these species. Passerines breeding in marshes typically build their nests as far off the water as possible, rendering them quite' conspicuous. Greater nesting densities and smaller size also may contribute to increased nest mortality of passerines in the marsh habitat.

Little is known of the survival of water birds after they hatch and leave the nest. Meanley (1955) found that 81 percent of 32 little blue herons survived through the first two weeks after hatching, before leaving the nest. The calculated mortality rate (1.48 percent) is much higher than for nests during the egg period (0.75 percent).

Teal (1965) has compiled data on the nesting success of tree-nesting species of herons, egrets, and an ibis in the salt marshes of coastal Georgia (Table 20).

Overall nest mortality is comparable to water birds nesting among marsh grasses (average, 1.46 percent per day, range 0.0 to 3.13 during the egg period). Predation accounted for most losses (0 to 50 percent of eggs and 0 to 30 percent of young). Hatching failure was 2–3 percent in the egrets and 8–11 percent for the other species. Starvation accounted for the loss of 0–10 percent of the young in the five species. Teal attributed the high success of the black-crowned night heron to its large size and aggressive disposition. None of the eight nests of this species were lost to predators. Chick mortality rates were lowest among the larger species (Table 21) owing to their ability to defend nests against predators and the larger size of the chicks. Conversely, the nests often are left unguarded during the egg period, leaving the nest vulnerable, and the two smaller species which have less conspicuous nests exhibited higher egg success than two of the larger species.

GAME BIRDS.—Hickey (1955) has reviewed nesting success in game birds (Phasianidae and Tetraonidae). Calculated nest mortality rates for this sample (Table 22) average 2.96 percent per day for 15 studies (range,

TABLE 20.—*Nesting success and mortality rates of five species of Ciconiiformes in a Georgia salt marsh* [a]

Species	Nests (number)	Eggs (number)	Nest period (days) Egg	Nest period (days) Nestling	Nest success [b] (percent) Egg	Nest success [b] (percent) Nestling	Egg success [b] (percent) Egg	Egg success [b] (percent) Nestling	Partial loss (percent) Eggs	Partial loss (percent) Nestling	Vertical component (percent) Nests	Vertical component (percent) Eggs
Common egret (*Casmerodius albus*)	35	99	28	18	54.3(2.18)	89.5(0.62)	52.6(2.30)	84.6(0.93)	0.12	0.31	1.56	1.37
Snowy egret (*Leucophoyx thula*)	30	96	[c] 27	28	73.3(1.15)	50.0(2.48)	64.6(1.62)	38.7(3.39)	0.47	0.91	−1.33	−1.77
Louisiana heron (*Hydranassa tricolor*)	15	47	27	25	86.7(0.53)	53.9(2.47)	72.3(1.20)	44.2(3.27)	0.67	0.80	−1.94	−2.07
Black-crowned night-heron (*Nycticorax nycticorax*)	8	24	29	21	100.0(0.00)	87.5(0.64)	91.7(0.30)	77.3(1.23)	0.30	0.59	−0.64	−0.93
White ibis (*Eudocimus albus*)	14	36	[c] 29	18	42.9(2.92)	83.3(1.02)	38.9(3.26)	71.4(1.87)	0.34	0.85	1.90	1.39

[a] Data from Teal (1965).
[b] Mortality rates given in parentheses.
[c] Estimated.

TABLE 21.—*Adult body weight and nest mortality rates of Ciconiiform birds in a Georgia salt marsh* [a]

Species	Adult weight (grams)	Nest mortality rate (percent) M_e	M_n
Snowy egret	350	1.15	2.48
Louisiana heron	450	0.53	2.47
Black-crowned night heron	800	0.00	0.64
White ibis	800	2.92	1.02
Common egret	900	2.18	0.62

[a] Nesting success data from Teal (1965). Source of weight data: Gross (1923), Hartman (1946, 1955), Hartman and Brownell (1961), Norris and Johnston (1958), Palmer (1962), Poole (1938).

1.55 to 4.66 percent) during the egg period. This is about 0.5 percent less than individual egg mortality rates for ground-nesting passerines in similar habitats. Taking into account the discrepancy between egg and nest survival, the mortality rates must be nearly the same for the two groups.

Survival of the precocial young of game birds has been recorded in several studies. In four cases, 54 to 88 percent of the chicks survived from hatching to the age of eight or nine weeks. Calculated mortality rates average 0.64 percent (range, 0.23 to 0.98) for this period, which is much lower than during the egg period. Of course, mortality rates are not constant during the period out of the nest. Survival is lowest just after hatching and increases as the young grow (see Figure 9). Mortality rate of the greater prairie chicken during the first four weeks after hatching was 2.45 percent per day in one study (Lehman, 1941), which is greater than nest mortality during the egg period.

Predation is probably the greatest mortality factor on the eggs of game birds. Foxes took 37 percent of ruffed grouse losses in New York and other predators accounted for an additional 52 percent of losses (Bump et al., 1947). Coyotes were responsible for the destruction of 42 percent of bobwhite quail cluches in Texas (Lehman, 1946). Other factors, including predators, caused 12 percent additional mortality. Predation, especially by raptorial birds, is also a significant factor in the loss of chicks (Bump et al., 1947).

DEVELOPMENT AND SURVIVAL.—During the course of development, physical capabilities of young birds increase with a resulting decrease in mortality rates. Daily mortality rates of five species are graphed as a function of age in Figure 9. Initially, the glaucous-winged gull and the California quail suffer high losses, but mortality rates decrease rapidly. Although the curves for the two species are similar, the glaucous-winged gull grows nearly twice as fast as the California quail (Ricklefs, 1968b) and thus, relative to growth, the survival capabilities of the latter increase more rapidly. This phenomenon will be discussed in more detail in a subsequent paper.

Initial mortality rates of the two tropic birds are much lower than for the above species. Tropic birds raise only one young per brood and the relative intensity of parental care must be quite high. Because of their remote nesting localities, tropic birds must also have few predators.

When starvation plays a prominent role in nestling survival, mortality rates may increase as the young grow in size and require energy at a more rapid rate. Peterson and Young (1950) and Young (1963) have demonstrated this phenomenon in three species of marsh-nesting blackbirds and grackles. Mortality rates of young marsh hawks (Hammond and Henry, 1949) do not decrease with age (Table 23), probably because of increasing effects of starvation which balance increasing physical capabilities.

Virtually nothing is known of the survival of altricial birds after they leave the nest. Data for the cactus wren and ovenbird indicate that fledgling mortality rates are lower than those of nestlings (Ricklefs, 1968a; Table 24), but there may be a brief period of marked increase in losses while the young gain experience immediately after leaving the nest. Mortality rates for fledgling English blackbirds (Snow, 1958) were 4.18 percent per day for the first five days out of the nest and 1.64 percent during the next ten to fifteen days. Calculated nest mortality rates were 6.68 percent in Wytham Wood and 2.35 percent in the Botanic Garden at Oxford. Smith (1967) found that 83 of 95 fledgling black-capped chickadees survived to the time of family breakup (3–4 weeks). These data indicate a fledgling mortality rate averaging between 0.5 and 0.6 percent during this period, which is probably lower than during the nestling period. Eleven of the young died during a severe storm less than a week after the birds fledged and thus subsequently only one of 84 young perished.

TABLE 22.—*Nesting success and mortality rates of game birds*

Species	Nests (number)	Egg period (days)			Nest success [a] (percent) egg period	Chick age (days)	Chick success [a] (percent)	Source and locality [b]
		Laying	Incu-bation	Total				
PHASIANIDAE:								
California quail								
(*Lophortyx californicus*)	96	14	22	36	18 (4. 66)			Glading, 1938, California
Bobwhite								
(*Colinus virginianus*)	602	13	24	37	36 (2. 73)			Stoddard, 1931, Georgia-Florida
	189				46 (2. 08)			Lehmann, 1946, Texas
						56	71 (0. 61)	Klimstra, 1950, Iowa
European partridge								
(*Perdix perdix*)	143	14	24	38	32 (2. 96)			Yeatter, 1934, Michigan
	435				32 (2. 96)			McCabe and Hawkins, 1946, Wisconsin
Ring-necked pheasant								
(*Phasianus colchicus*)	445	11	24	35	23 (4. 12)			Hamerstrom, 1936, Iowa
	310				20 (4. 50)	56	88 (0. 23)	Randall, 1940, Pennsylvania
	563				58 (1. 55)	56	<70 (0. 64)	Leedy and Hicks, 1945, Ohio
	149				36 (2. 88)			Rasmussen and McKean, 1945, Utah.
	527				26 (3. 78)			Baskett, 1947, Iowa
TETRAONIDAE:								
Prairie chicken								
(*Tympanuchus cupido*)	100	11	23	34	50 (2. 02)			Hamerstrom, 1939, Wisconsin
						28	50 (2. 45)	Lehmann, 1941
Sage grouse								
(*Centrocercus urophasianus*)	161	10	22	32	60 (1. 58)			Rasmussen and Griner, 1938, Utah
	238				35 (3. 23)	63	54 (0. 98)	Keller, Shepard, and Randall, 1941, Colorado
	134				34 (3. 32)			Patterson, 1949, Wyoming
Ruffed grouse								
(*Bonasa umbellus*)		11	23	[c] 34	59 (1. 55)			Bump et al, 1947, New York

[a] Mortality rates are given in parentheses.

[b] As compiled in Hickey (1955), except for the ruffed grouse.

[c] Estimated.

Interpretation and Discussion

Developing organisms must sacrifice mature charac-teristics—and thus survival capabilities—for the sake of growth and for the attainment of future stages of de-velopment. Similarly, adults must accept a reduction in survival rate for the sake of breeding. Clearly, re-production involves a compromise between survival and fecundity which must be adjusted to optimum levels through adaptation. In species with precocial chicks a greater part of adaptation to reduce mortality rates falls upon the young than in species whose de-velopment is progressively more altricial. In such birds, parental care is increased and the adults take a larger share of the burden of this adaptation. The accom-plishment of a given decrease in the mortality rates of the young must involve risks and also results in bene-fits, both of which will vary with environmental mor-tality factors. The evolved level of adaptation is that beyond which added risks more than balance new benefits, and the resulting mortality rate reflects the relationship of costs and benefits to the level of adapta-tion. We may ask, "Are observed variations in mor-tality rates the result of differing levels of adaptation of
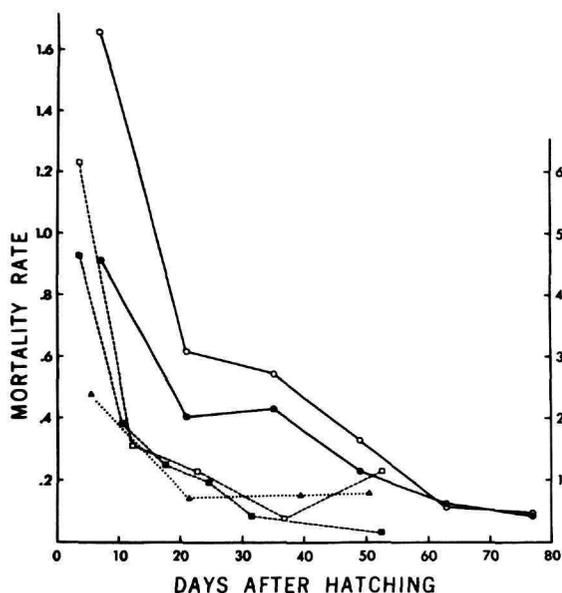
FIGURE 9.—Relationship between age and mortality rates in the young of five species of precocial and semialtricial birds: left-hand scale, white-tailed tropic bird (solid line, open circles) and red-billed tropic bird (solid line, solid circles) from Stonehouse (1962); right-hand scale, California quail (dashed line, open squares), Williams (1959), glaucous-winged gull (dashed line, solid squares), Drent et al. (1964), ring-necked pheasant (dotted line, open triangles), Errington and Hammerstrom (1937). Mortality rates are expressed in percent per day.

the species, or does the environment primarily determine mortality rates and all species have achieved similar levels of adaptation?" The question is, of course, somewhat circular because the purpose of adaptation is to modify the environment to one's advantage. How should we classify the mortality rates of raptorial species which are low partly because of their large size and defense capabilities? Do we say that their environment differs from that of smaller birds because of reduced predator pressure and facilitated homeostasis, or, that their large size is an adaptation to reduce nesting mortality? Obviously, the body size of raptorial birds is well suited for the organisms they prey upon and thus is not strictly an adaptation of the reproductive strategy. Similarly, the hole nests of woodpeckers clearly alter the nestling environment and reduce mortality rates but the ability to excavate hole nests depends on adaptations of adult morphology for gathering food under bark. Is this adaptation to be included as a part of the reproductive strategy? Any answer to these questions will necessarily be arbitrary. A more satisfactory approach, comparing a uniform group, such as passerines, in different environments, will be employed below.

Some components of mortality rates almost certainly are determined environmentally. For example, where feeding conditions fluctuate unpredictably owing to weather, two extreme strategies are possible. A pair

TABLE 23.—Survival of marsh hawk nestlings in successful nests [a]

Age interval (days)	Number of nests	Number of young	Average number of young per nest	Survival within nest (percent)	Mortality rate within nest (percent)
0–5	43	175	4. 07		
				98. 28	0. 35
6–10	43	172	4. 00		
				94. 75	1. 08
11–15	39	148	3. 79		
				96. 57	0. 70
16–20	35	128	3. 66		
				90. 71	1. 95
21–25	25	83	3. 32		
				100. 30	−0. 06
26–30	15	50	3. 33		
				95. 50	0. 92
31–35	11	35	3. 18		

[a] Data from Hammond and Henry (1949).

TABLE 24.—*Survival of some passerine young during the fledgling period*

Species	Mortality rate during nest period (percent)			Number of fledglings	Period out of nest (days)	Mortality rate (percent)	Source and locality
	m_s	m_n	m				
Black-capped chickadee	1. 52	0. 33	0. 90	61 (1964)	0 to 7	a 2. 82	Smith, 1967, British Columbia
				50 (1964)	7 to 21–28	0. 00	
				34 (1965)	0 to 21–28	0. 11–0. 14	
Cactus wren			b 0. 65	39	0 to 21 c	0. 60–0. 67	Ricklefs, 1968a, Arizona
	1. 25	0. 81	b 1. 00				Anderson and Anderson, 1960
Ovenbird	2. 95	4. 70	3. 54	70	0 to 30–35	1. 66–1. 93	Hann, 1937, Michigan
English blackbird			b, d 6. 68	140	0 to 5	4. 18	Snow, 1958, England
			b, e 2. 35	113	5 to 15–20	1. 36–2. 05	
	2. 79	1. 75	2. 29				Lack, 1954, England

a All deaths resulted from a particularly severe storm less than one week after fledgling.

b Nest mortality rates (M) rather than m.

c Average (range, 3–40 days).

d Wytham Wood, near Oxford.

e The Botanic Garden in Oxford.

can attempt either to raise only as many young as can be fed in the worst year and not exhibit starvation in any year, or adjust brood size to the best feeding conditions and have young starve in most years. Clearly an optimum strategy between these extremes is defined, depending on the cost of raising young which eventually starve, by the environmental conditions and cannot be further improved upon by specific adaptations. Thus, the level of starvation is determined largely by the magnitude and unpredictability of fluctuations in food supply. We have seen that in arid regions starvation is an important mortality factor. It can be shown that rainfall, to which breeding in desert species is closely related (Lloyd, 1960; Marshall, 1961) is most variable and unpredictable where it is sparsest (Figure 10). In some cases, yearly fluctuations in food supply may be predicted by environmental conditions prior to the breeding season and birds adjust their clutch sizes accordingly (Lack, 1954; Cody, 1966). This greater sophistication of clutch-size determination must represent a higher level of adaptation and certainly reduces mortality levels, but it is also achieved with little risk. More important, the increased level of adaptation is permitted by the predictability of fluctuations and thus is largely environmentally determined.

Increased adaptation to reduce mortality caused by direct environmental factors, such as inclement weather, is limited by the risks to adults and reduction of fecundity imposed by strategies such as increased sturdiness and insulation of nests and intensified parental care such as brooding. In this system, adaptation

is restricted in a different manner than with starvation. The environment is permissive, allowing the possibility of reducing mortality rates of individual young essentially to zero. With starvation the nature of the environment precludes the reduction of mortality rates below a given level depending on energetic aspects of reproduction.

Predation is the most important mortality factor for most species. The outcome of predator-prey interactions reflects the relative effectiveness of predator and
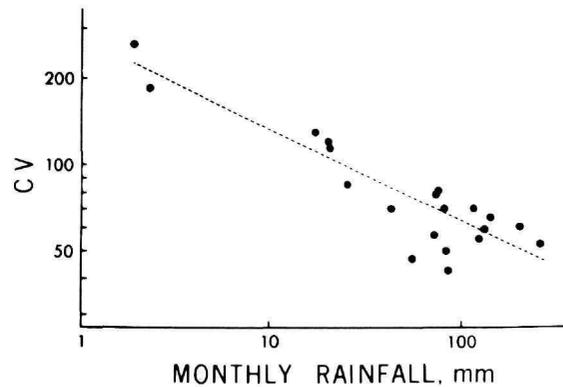

FIGURE 10.—Coefficient of variation versus average rainfall for each of four months (February, May, August, November) at five Temperate Zone localities: Cape Spartel, Tangiers; Miyako, Japan; Phoenix, Arizona; Philadelphia, Pennsylvania; and Portland, Oregon. Variability based on 25-year periods (data from Clayton, 1944).

prey adaptations. The observed variation in mortality rates due to predation is large, from less than one half percent per day in many raptorial and oceanic species to perhaps more than 5 percent in some small land birds and precocial species.

A large part of this variation is correlated with body size of the adults. Teal (1965) has demonstrated a good negative correlation between body weight and nestling mortality of herons nesting in the same colony (Table 20). The relationship between mortality and body weight is shown graphically in Figure 11 for temperate passerine and raptorial species. Nesting mortality decreases as approximately the -0.5 power of adult body weight, with considerable variation due to nesting ecology, and, of course, sampling error. Part of the overall relationship may be due to the sharp claws and aggressive dispositions of birds of prey rather than to their large size. But it also seems that small prey species may be taken by a wider variety of predators than large species simply because they are smaller than a greater number of predator species. Additionally, the nests of many large birds are preyed upon by relatively small predators which are capable of climbing to their nest sites and, thus, the physical capa-
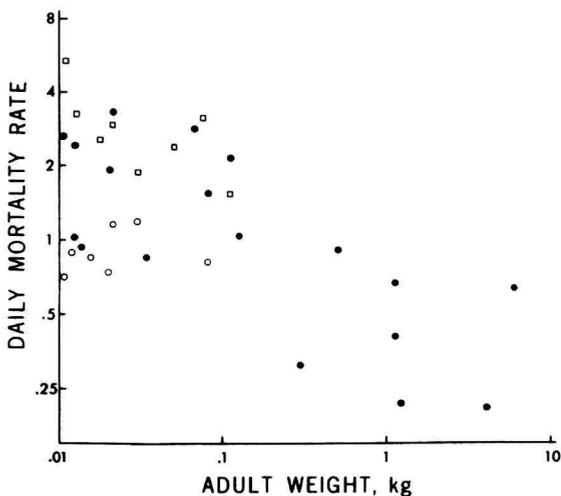

FIGURE 11.—Mortality rates of nestlings as a function of body weight in Temperate Zone altricial land birds. Solid circles: above-ground, open-nesting passerines and raptorial species; open circles: hole-nesting species; open squares: ground-nesting and marsh-nesting species. Adult body weight data from Baldwin and Kendeigh (1938), Hartman (1946, 1955), Hartman and Brownell (1961), Imler (1937), Norris and Johnston (1958), and Wetherbee (1934).

bilities of the young become important in reducing mortality. Jays and opposums may occasionally steal hawk eggs when the nests are left unguarded but they are no match for well-grown young.

Differences in mortality rates among passerines related to habitat and nest construction are striking. We have seen that species nesting in marshes and fields have higher mortality rates than those nesting in trees, and additionally that hole and niche nests are more secure than open nests. These habitats must present differences either in predation pressure or the ability of species to evolve antipredator adaptation. The structural simplicity of field and marsh habitats would seem to favor predators by reducing the complexity of their hunting tasks. Furthermore, the structural restrictions of the habitat must prevent adaptations against specific groups of predators and limit adaptations to generalized defenses such as crypsis. The forest habitat provides nest sites, such as at the tips of small branches, which completely eliminate a whole size class of predators.

No striking differences exist between most field and forest species in their levels of adaptation. Nest construction, development rates, brood size, and dependency periods seem to be roughly similar. If it is true that desertion is more prevalent in forest habitats than in field habitats, it would seem that adults of field-nesting species are willing to accept greater risks in the care of their offspring.

Major environmental differences of widely separated geographical localities result in a large variation in nesting mortality owing to predation. At one extreme we find isolated oceanic islands practically devoid of life except for the seabirds which use them for nesting, and at the other extreme, the tropical forests which exhibit the greatest diversity or terrestrial life. Mortality rates seem to follow the trend in species diversity.

Terrestrial predators are few on offshore islands because these are difficult to colonize and many are devoid of alternative food resources during the months that seabirds do not nest. As we would expect, adaptations against terrestrial predators are poorly developed in insular forms. When rats and domesticated animals are introduced onto offshore islands they increase mortality rates many fold (e.g., Hagar, 1937). Other predatory seabirds are potentially strong sources of mortality, but effective antipredator adaptations such as parental guarding (e.g., Nelson, 1966) appear to be evolved with little risk to the adults.

Differences in nest mortality rates of passerine birds

due to predation from arctic to tropical regions reflect the outcome of opposing adaptations of predators and prey. Either individual predator species are more efficient in tropical areas, or prey species are beset by a wider variety of predator species and thus are forced to adapt to a wider variety of predation strategies. There is no reason to suppose that individual predator species are capable of finding prey at a higher rate or maintaining larger populations in the tropics than in temperate and arctic regions. The outcome of a limited two-species predator-prey system would not seem to vary with changes in latitude: physical structure of the habitat differs little for birds, overall densities of breeding birds are comparable or perhaps somewhat higher in tropical than in temperate or arctic areas, but individual species are probably not so abundant on the average (see Davis and Davis, 1962; Davis and Guion, 1961; Skutch, 1966), and considering the low nesting success and wider spacing of broods in the tropics (Ricklefs, 1966), nest densities are probably lower in the tropics. The occurrence of breeding in the tropics is nearly as seasonal in some areas as in temperate regions, although on the average nesting seasons are longer, especially compared to arctic localities (Ricklefs, 1966). Additionally, tropical predators have comparable or lower reproductive rates (litter and clutch sizes) than temperate and arctic species (See Lord, 1960, for mammals; Brown, 1952–53, 1955, for tropical eagles; Lack, 1954, and Cody, 1966, for birds in general). Thus, if individual predators are no more efficient, and if predator species are no more abundant, we can explain the higher predation rates in the tropics by postulating a wider variety of predator species for each prey species. This is precisely the "food web" pattern of energy flow suggested by many ecologists for tropical regions. That prey are beset by an increased number of predator species with different hunting strategies is born out by observers such as Skutch (1949, 1954, 1960, 1967) who indicate that there indeed is a greater diversity of predator types in the tropics responsible for nesting losses in birds. Numerous arboreal mammals (including primates), nest-robbing birds (especially toucans) and snakes, not to mention ants and parasitic insects, are conspicuous in tropical forests but virtually absent in similar temperate habitats.

If tropical predators are opportunistic and employ generalized rather than narrowly directed hunting techniques, they may be less efficient than their temperate counterparts. We may also ask how prey adap-

tations differ in the tropics. Do prey species adopt a generalized antipredator strategy in their nesting cycles? This would tend to increase predator efficiency (as it does in field and marsh habitats). Or do prey species direct their adaptations primarily at one group of predators? An analysis of nest construction of oscine birds from a temperate and a tropical region show that the tropical sample builds a greater diversity of nest-types (Table 25). Apparently, predation pressure largely precludes ground-nesting in the tropics, whereas many temperate forest species nest on or near the ground (Taylor, 1965; Preston and Norris, 1947). In the tropics, numerous species construct domed or pensile nests, choose special localities, as over water, and have evolved nesting relationships with termites and wasps. Thus, nest construction and placement of some species is more specialized than in temperate regions. The same may be true of adult behavior.

TABLE 25.—*Nest construction and placement of temperate and tropical passerines* [a]

Type of nest construction and placement	New York [b] Number of species	New York [b] Per- centage	Canal Zone [c] Number of species	Canal Zone [c] Per- centage
Nest construction:				
Open	63	71	45	47
Domed or enclosed	5	6	24	25
Pensile	3	3	15	16
Niche or natural cavity	18	20	12	12
Total number of species	89		96	
Height:				
Ground	24	27	6	6
Understory or shrubs and bushes	20	22	38	40
Trees	45	51	52	54
Total number of species	89		96	
Special placements:				
Over water	2		8	
Near wasps or bees	0		9	

[a] Neal G. Smith greatly aided in putting this table together.
[b] Species list from Bull (1964).
[c] Species list from Eisenmann and Loftin (1967). Only species whose nests are well known are included.

Skutch (1949) cites a reduction in the number of feeding trips to the nest and more secretive behavior of some species to avoid predator detection, although this has not been properly analyzed. Oropendulas do not incubate at night during the early stages of the egg period, presumably to avoid being trapped by predators in their pensile nests (Schaeffer, 1957; N. G. Smith, personal communication).

In conclusion, we may recognize four types of factors which act to restrict the ability of birds to reduce the mortality rates of their young. First, and perhaps most important is that adaptations often have multiple effects, some good and some bad, and therefore adapted strategies are at best only compromises. In general, any trend toward enhancing the survival of offspring will involve added risks to the parents. Secondly, unpredictability of environmental resources leads to increased mortality of the young through starvation. In spite of these losses, adaptations to reduce mortality from starvation could not be improved upon—except by sacrificing fecundity, which is essentially avoiding the problem rather than adapting to it. Unpredictability of food imposes which might be called "statistical restrictions" on survival levels which cannot be exceeded by biological systems. Thirdly, adult adaptations for nonreproductive activities impose restraints on the range of adaptations which may be exploited in breeding activities. Body size, morphological adaptations for foraging, habitat selection and others fall into this category. Finally, the survival of every species is challenged by other adapting systems bent on their own survival and these are the greatest cause of mortality in most species. The equilibrium between predator and prey adaptations remains one of the most fascinating and elusive of biological problems.

Appendix I

The Strength of Selection on Development Rates

The selective strengths of environmental factors in producing specific adaptations to reduce mortality rates are directly related to their contribution to nesting losses. Unfortunately, it would be very difficult to ascertain differences in fitness resulting from changes in most aspects of reproductive behavior. It is only possible to guess that equivalent adaptation in different species will most benefit those with the highest mortality rates—i.e., selection for equivalent changes is proportional to the mortality rate. On the other hand, changes in fitness brought about by altering the duration of exposure to mortality factors may be treated mathematically quite easily, as will be shown in subsequent papers. Adjustments in the length of various phases of the nesting cycle are general adaptive responses to most mortality factors, largely excepting brood parasitism, hatching failure and starvation. For many species, the strength of those factors which influence developmental rates is nearly as great as the overall mortality rate. In others, factors which do not exert selection on the length of the nesting cycle may contribute substantially to total mortality. It will be useful to distinguish these quantitatively for subsequent analyses of the relationship between mortality and development. As we have seen, it is possible to recognize these factors and make suitable corrections from patterns of nesting losses.

The strength of selection on the length of the nesting cycle is summarized in Table 26 for different groups of passerine birds using four rules to adjust mortality rates:

1. If nest loss is known and its rate during the egg period exceeds that during the nestling period, no correction is needed. It has been demonstrated that loss of nests due to starvation is probably negligible under these conditions.

2. If nest loss during the nestling period exceeds that of the egg period, it has been shown that desertion is probably a minor factor and that the excess mortality during the nestling period is primarily due to starvation. This can be corrected by setting the mortality rate during the nestling period equal to that of the egg period, thus eliminating the starvation component.

3. When individual losses are known and mortality rates during the egg period exceed those of the nestling period, most of the within-nest loss is due to hatching failure and brood parasitism and this can be subtracted from the overall rate of nest loss. If the within-nest loss is not known, the subtraction of 0.4 percent per day (Table 5) should improve the estimate of selective forces in most cases.

4. If individual loss is known and the rate of mortality is greater during the nestling period than during the egg period, it is sufficient to correct the egg period rate for hatching failure by subtracting about 0.3 percent per day (Table 1) and to set the nestling period rate equal to the corrected rate for the egg period.

TABLE 26.—*Relative strength of selection on development rates in passerine birds*

Region and nest-type	Number of species	Average relevant mortality rate (percent)		Residual nonrelevant mortality rate (percent per day)
		Per day	Range	
Temperate				
Marsh-nesting	3	3. 70	2. 84–5. 06	0. 82
Ground-nesting	5	2. 55	1. 53–4. 11	1. 13
Tree- and shrub-nesting	9	1. 82	0. 87–2. 43	0. 30
Hole- and niche-nesting	7	0. 83	0. 21–1. 63	0. 19
Tropical				
Humid areas	11	3. 86	2. 20–5. 38	0. 23
Arid areas	11	1. 82	0. 99–3. 15	1. 43
Arctic	8	1. 66	0. 34–5. 90	0. 89

Since nestling losses of precocial birds are caused by factors similar to those acting on small land birds, the same corrections may be applied to estimate the strength of selection acting on development rates. Average values calculated for six species of shorebirds are 1.54 percent per day, for nine species of waterbirds, 1.08 percent, and for six species of game birds, 3.02 percent.

The relative strength of factors acting on raptorial birds and seabirds are more difficult to ascertain. In large raptorial birds, mortality which is relevant to development rates must certainly average less than 0.5 percent per day, based on mortality rates presented in Table 14, and probably is closer to 0.2–0.3 percent for most species. Seabirds present additional problems. In the Procellariiformes and Pelecaniformes, most chick mortality (average, 0.66 percent per day) would be reduced by increasing the rate of nestling development but it is difficult to estimate how much of the egg mortality (average, 2.17 percent) is relevant until more detailed studies of losses have been made. This is also true of the Charadriiformes (average mortality rates, 1.49 percent and 2.02 per day during the egg and nestling periods, respectively). Losses of eggs in seabirds due to hatching failure and rolling out of nests is quite high, perhaps one half of total egg mortality in most species. Thus, egg mortality rates pertinent to the evolution of development rates should be about one-half total mortality rates, or about 1.08 and 0.75 percent per day for the two groups of seabirds. These values are not much lower than for some groups of land and waterbirds and are not nearly as low as in raptorial species.

Except for the possibility of starvation in some gulls and terns, most of the mortality of young seabirds bears on the evolution of development rates. A conversion factor of three fourths would probably give a reasonable and conservative correction for losses and thus we may estimate that selective forces are approximately 0.5 and 1.5 percent per day during the nestling period in the two groups of seabirds. Additionally, it must be kept in mind that mortality rates of seabirds decrease markedly with age.

Appendix 2

Alphabetical List of Bird Names

African fish eagle, *Haliaetus vocifer*
American robin, *Turdus migratorius*
Arctic tern, *Sterna paradisea*
Bald eagle, *Haliaetus leucocephalus*
Black-and-white manakin, *Manacus manacus*
Black-capped chickadee, *Parus atricapillus*
Black-crowned night heron, *Nycticorax nycticorax*
Black guillemot, *Cepphus grylle*
Black-legged kittywake, *Rissa tridactyla*
Blue-black grassquit, *Volatinia jacarina*
Blue-faced booby, *Sula dactylatra*
Blue-gray tanager, *Thraupis episcopus*
Bobwhite quail, *Colinus virginianus*
Bonaparte warbling-finch, *Poospiza hispaniolensis*
booby, *Sula* spp.
Brewer blackbird, *Euphagus cyanocephalus*
Brown booby, *Sula leucogaster*
Brown-headed cowbird, *Molothrus ater*
Cactus wren, *Campylorhynchus brunneicapillus*
California quail, *Lophortyx californicus*
Cardinal, *Richmondena cardinalis*
Cassin auklet, *Ptycoramphus aleutica*
Cedar waxwing, *Bombycilla cedrorum*
Chestnut-collard longspur, *Calcarius ornatus*
Chestnut-throated seed-eater, *Sporophila telasco*
Chipping sparrow, *Spizella passerina*
Clay-colored robin, *Turdus grayi*
Common goldfinch, *Spinus tristis*
Common grackle, *Quiscalus quiscula*
Common redpoll, *Acanthis flammea*
Common swift, *Apus apus*
Costa hummingbird, *Calypte costa*
Crimson finch, *Rhodospingus cruentus*
Curve-billed thrasher, *Toxostoma curvirostre*
D'Orbigny ground-dove, *Eupelia cruziana*

Double-crested cormorant, *Phalacrocorax auritus*
Duck hawk, *Falco peregrinus*
Dunlin, *Calidris alpina*
Eastern bluebird, *Sialia sialis*
Eastern phoebe, *Sayornis phoebe*
Ecuadorian neorhynchus, *Neorhynchus peruvianus*
English blackbird, *Turdus merula*
Field sparrow, *Spizella pusilla*
finches, (Fringillidae)
Fulvous-headed pygmy-tyrant, *Euscarthmus molorhyphus*
Glaucous-winged gull, *Larus glaucescens*
Gray-capped flycatcher, *Myiozetetes grenadensis*
Greater prairie chicken, *Tympanuchus cupido*
Great-horned owl, *Bubo virginianus*
Golden eagle, *Aquila chrysaetos*
Horned lark, *Eremophila alpestris*
House finch, *Carpodacus mexicanus*
House wren, *Troglodytes aedon*
jays, *Cyanocitta, Aphelocoma,* etc (Corvidae)
Lapland lonspur, *Calcarius lapponicus*
Least tern, *Sterna albifrons*
Little blue heron, *Florida caerulea*
Long-billed marsh wren, *Telmatodytes palustris*
Long-tailed mockingbird, *Mimus longicaudatus*
Madeiran storm petrel, *Oceanodroma castro*
Marsh hawk, *Circus hudsonius*
Marsh wren, *Telmatodytes palustris*
McCown longspur, *Rhynchophanes mccowni*
Mourning dove, *Zenaidura macroura*
Orchard oriole, *Icterus spurius*
oropendulas, *Zarhynchus wagleri* and others (Icteridae)
Ovenbird, *Seiurus aurocapillus*
Pelagic cormorant, *Phalacrocorax pelagicus*
Pigeon guillemot, *Cepphus columba*
Prothonotary warbler, *Protonotaria citrea*
Purple grackle, *Quiscalus quiscula*
Raven, *Corvus corax*
Red-billed tropic bird, *Phaethon aethereus*
Red-tailed hawk, *Buteo jamaicensis*
Red-winged blackbird, *Agelaius phoeniceus*
robins, *Turdus* spp.
Rough-winged swallow, *Stelgidopteryx ruficollis*
Ruddy duck, *Oxyura jamaicensis*
Ruddy ground-dove, *Columbigallina talpacoti*
Ruffed grouse, *Bonasa umbellus*
Savannah sparrow, *Passerculus sandwichensis*
Say phoebe, *Sayornis sayus*
Scarlet-rumped tanager, *Ramphocelus passerinii*
Shag, *Phalacrocorax aristotelis*
Short-tailed ground-tyrant, *Muscigralla brevicauda*
Snow bunting, *Plectrophenax nivalis*
Song sparrow, *Melospiza melodia*
Starling, *Sturnus vulgaris*
Thick-billed murre, *Uria lomvia*
toucan (Ramphastidae)
Traill flycatcher, *Empidonax traillii*
Tree swallow, *Iridoprocne bicolor*
Vermillion flycatcher, *Pyrocephalus rubinus*
White-browed gnatcatcher, *Polioptila plumbea*
White-crowned sparrow, *Zonotrichia leucophrys*

White-tailed kite, *Elanus leucurus*
White-tailed tropic bird, *Phaethon lepturus*
Yellow-bellied elaenia, *Elaenia flavogaster*
Yellow-faced grassquit, *Tiaris olivacea*
Yellow-headed blackbird, *Xanthocephalus xanthocephalus*
Yellow wagtail, *Motacilla flava*
Yellow warbler, *Dendroica aestiva*

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