VARIATION IN THE INCIDENCE OF HATCHING FAILURE IN THE CEDAR WAXWING AND OTHER SPECIES

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Hatching failure due to embryonic death or sterility is an important aspect of the breeding biology of songbirds, yet it has received little attention. Many nesting studies present the overall success rate of eggs but lump the failures due to predation and other factors with those due to sterility and embryonic death. Two recent exceptions are studies by Ricklefs (1969) and Jehl (1971). During 1968 and 1969, I conducted studies (Rothstein 1971a) which provided data relevant to egg hatchability in several species. The Cedar Waxwing (*Bombycilla cedrorum*) yielded especially significant data because eggs in nests near farms suffered a greater incidence of sterility or embryonic death than eggs in nests from other areas. Field work was conducted primarily in Cheboygan and Emmet Counties, Michigan, from mid-June until early August in both years. For comparative purposes, I have reported on some nests found in New Haven and Fairfield Counties, Connecticut, from early April until the first week in June in 1968 and 1969.

METHODS

I removed one or more eggs from most nests and examined the contents macroscopically. Many nests were watched until hatching occurred, or should have occurred. I thus had two means of determining hatchability, by examining the contents of collected eggs and by observing the fate of eggs left in nests that remained active through the time of hatching. However, the status, as regards hatchability, could not be determined for some eggs (e.g., eggs I removed so early in the incubation period that detectable embryonic development was not likely). Data were grouped by species, habitat, and, for the Cedar Waxwing, also by date of laying. The Exact Test for 2×2 Contingency Tables (Bailey 1959) was used to test for differences in hatching percentages between species, habitats, and dates of laying. Two-tailed tests were applied in all statistical treatments since no initial reason existed to suspect that certain species, habitats, or time intervals would differ in or affect hatchability.

Three ways of measuring hatchability are presented in table 1 for the seven species in which the fates of eight or more eggs are known. Columns A and B deal only with numbers of hatched and nonhatched eggs. It might, however, be more correct to analyze these data by the overall performance of each clutch, since egg failure might tend to affect some clutches heavily and others not at all. Consider the following hypothetical example and assume that, when it occurs, hatching failure affects more than one egg in a clutch: for two species two nests each are compared and all four nests have five eggs. In one species both nests have total hatching success. One nest in the second species has total failure and in the other nest three of five eggs fail. A comparison of success by eggs only (10–0 versus 2–8) yields a significant probability ($P < 0.001$) but is invalid because it is the clutches and not the eggs that are the independent events. Any type of analysis utilizing each nest as a datum would not even be nearly significant at the 5% level. Nests that had no hatching at all (100% failure) versus those with at least some hatching are tabulated in columns C and D. Nests in which all the eggs hatched (100% success) versus those in which one or more did not hatch are tabulated in columns E and F.

In assigning nests to columns D and F, I included only those nests in which hatchability was determined for more than half of the eggs in the entire clutch. Even though column pairs C–D and E–F are derived from the same pool of data, the figures for the total numbers of nests are not always equal because the status of all eggs could not be determined. For example, a nest with four eggs in which two hatched and the other two were removed by predators could be included in columns C and D but not in columns E and F.

RESULTS

HATCHABILITY WITHIN DIFFERENT CLUTCHES AND SPECIES

Three of the four species, with the largest samples in table 1, show a tendency for hatching failure to involve more than one egg in a clutch if it occurs at all. In the Chipping Sparrow (*Spizella passerina*), four of the five nests with at least some hatching failure had two or more eggs that did not hatch. Similarly, in two of three Eastern Kingbird (*Tyrannus tyrannus*) nests with any failure, the entire clutch of three eggs failed. Nineteen Cedar Waxwing nests showed some failure. Ten of these nests contained more than one egg that did not hatch. Nine nests had only one egg that definitely failed, but for three of these nests, the unsuccessful egg was the only one in the nest whose status was determined. These three nests should thus be excluded from this consideration. Only in the Robin (*Turdus migratorius*) is there a ten-

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TABLE 1. Egg hatchability of birds in Michigan.

Species	A Total no. of eggs	B % eggs not hatching	C[a] Total no. of nests	D % nests with total failure (no eggs hatching)	E[a] Total no. of nests	F % nests with total success (all eggs hatching)
Cedar Waxwing (*Bombycilla cedrorum*)	166	24.7	50	12.0	40	52.5
Chipping Sparrow (*Spizella passerina*)	114	9.7	37	5.4	36	86.1
Robin (*Turdus migratorius*)	48	10.4	20	5.0	13	69.2
Eastern Kingbird (*Tyrannus tyrannus*)	27	25.9	10	20.0	8	62.5
Black-billed Cuckoo (*Coccyzus erythropthalmus*)	12	8.3	6	0.0	4	75.0
Least Flycatcher (*Empidonax minimus*)	9	11.1	3	0.0	3	66.7
Barn Swallow (*Hirundo rustica*)	8	25.0	2	0.0	2	0.0

[a] The values in columns C and E are not always equal. See text for explanation and general description of criteria used in tabulating data.

dency for hatching failure to affect only a single egg in a clutch. Three of the four nests with any lack of success had only one failure. Because of the statistical difficulties caused by the tendency for hatching failure to affect more than one egg per clutch in at least some species, I will, throughout this paper, attempt to compare hatchability by clutches as well as by individual eggs.

Of the four species with large samples, the Cedar Waxwing and the Eastern Kingbird show relatively high rates of hatching failure (table 1). Considering eggs only (column B), hatching failure in the Cedar Waxwing is greater than in the Robin ($P < 0.05$) and the Chipping Sparrow ($P < 0.01$). Similar comparisons contrasting the Eastern Kingbird with the Robin and Chipping Sparrow do not yield statistical significance at the 5% level. It is, however, more proper to compare egg hatchability by nest. Comparing nests with total failure (column D), no species are significantly different, but in nests showing total success (column F), success occurred in a significantly ($P < 0.01$) lower proportion of waxwing clutches than Chipping Sparrow clutches.

HATCHABILITY IN OTHER STUDIES

Table 2 shows the hatchability of eggs of a selection of songbirds. I have tabulated data, generally from the literature, on the species I studied, their close relative, or other species of special interest. These data demonstrate a wide range of hatchability (even for the same species). The only sample that departs significantly from my own data on the same species is Putnam's (1949) for the Cedar Waxwing. Eggs in my study had a much higher incidence of hatching failure. A comparative analysis utilizing success by nest can be applied even though Putnam did not list failed eggs by nest. Eggs hatched in 48 of his nests;

TABLE 2. Egg hatchability in other studies.

Species	Total no. of eggs	% eggs not hatching	Source
Cedar Waxwing (*Bombycilla cedrorum*)	200	5.5	Putnam, 1949
	32	15.6	Young, 1949
Robin (*Turdus migratorius*)	165	10.9	Howell, 1942
	80	8.7	Young, 1949
	655	14.0	Kendeigh, 1942
	83	6.0	Rothstein, unpubl.
Eastern Phoebe (*Sayornis phoebe*)	157	18.0	Kendeigh, 1942
	223	2.7	Rothstein, unpubl.
	61	4.9	Rothstein, unpubl.
House Wren (*Troglodytes aedon*)	5816	7.0	Kendeigh, 1942
Catbird (*Dumetella carolinensis*)	46	4.3	Young, 1949
	195	8.0	Kendeigh, 1942
Eastern Bluebird (*Sialia sialis*)	332	16.0	Kendeigh, 1942
House Sparrow (*Passer domesticus*)	2930	12.3	Seel, 1968
European Tree Sparrow (*Passer montanus*)	1145	7.0	Seel, 1968
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)	139	7.2	Young, 1963
Red-winged Blackbird (*Agelaius phoeniceus*)	563	8.7	Young, 1963
	823	4.5	Smith, 1943
Common Grackle (*Quiscalus quiscula*)	87	3.4	Young, 1949
Dickcissel (*Spiza americana*)	19	26.3	Long, 1963
	44	22.7	Gross, 1921
American Goldfinch (*Spinus tristis*)	257	8.2	Holcomb, 1969
Song Sparrow (*Melospiza melodia*)	589	8.7	Nice, 1937
	184	6.0	Kendeigh, 1942

TABLE 3. Contents of unhatched eggs.

Species	No. examined	No. with dead embryo	No. with no development	% with no development
Cedar Waxwing	41	4	37	90.3
Chipping Sparrow	6	0	6	100.0
Robin—Michigan	4	0	4	100.0
Robin—Connecticut	4	2	2	50.0
Eastern Kingbird	5	2	3	60.0
Black-billed Cuckoo	1	0	1	—
Least Flycatcher	1	0	1	—
Barn Swallow	2	0	2	—
Eastern Phoebe—Connecticut	6	5	1	16.7
Eastern Phoebe—Michigan	3	2	1	33.3

11 eggs failed. The minimum frequency of nests that had total hatching success is then 37 of 48 or 77.1%. This is significantly more ($P < 0.03$) than the proportion (52.2%) of nests in my study having total success.

The manner of data presentation used by the various authors allows the detailed analysis of hatchability by separate clutches for only the two Dickcissel (*Spiza americana*) studies. Egg failure, while frequent in Dickcissels, usually did not affect more than one egg per nest. My unpublished Robin data from Connecticut also are like those for the Dickcissel and the Michigan Robins. Of the four nests with some hatching failure, only one had more than one failure. Seel's (1968) two species of *Passer* also show this tendency of only one unsuccessful egg per nest. This is unlike the situation in the waxwing, Chipping Sparrow, and kingbird nests that I studied.

CONTENTS OF UNSUCCESSFUL EGGS

I checked the contents of most of the unsuccessful eggs (table 3). Most had no development, but in one species, the Eastern Phoebe (*Sayornis phoebe*), embryonic death was more frequent than sterility. The phoebe is probably similar to other species in the incidence of embryonic death, but it deviates strongly from other species in the frequency of sterile eggs. Counting the seven eggs with dead embryos as fertile, only two of 284 eggs (0.7%) were sterile.

HATCHABILITY BY LOCALITY AND DATE OF LAYING

Table 4 presents the data in table 1 divided according to two habitat types: orchard (made up of apple trees) and nonorchard. All Barn Swallow (*Hirundo rustica*) and Least Flycatcher (*Empidonax minimus*) nests were in orchards and are excluded from table 4. All but one of the orchards were adjacent to occupied houses and active farms. Nonorchard habitats included both natural and strongly modified areas (pine plantations). Nests in these nonorchard habitats were generally much farther from roads, human habitation, and farms than nests in orchards. Waxwing nests were found in 12 orchard and 11 nonorchard localities.

The most striking feature of table 4 is the greater incidence of failure of waxwing eggs in orchards than in other habitats. The frequency of egg failures in nonorchard nests alone is remarkably close to that in Putnam's (1949) study, 5.6% and 5.5%, respectively. The frequencies of nests with total hatching failure and of nests with at least some failure were significantly higher in orchards than in nonorchards ($P < 0.02$ and $P < 0.01$, respectively, as determined from column pairs C–D and E–F in table 4). Furthermore, no nonorchard nest had more than one egg failure, whereas 10 of the 14 orchard nests with any failure had more than one unsuccessful egg. In three of the remaining four nests, the one unsuccessful egg was the only egg whose status was determined. No other species shows statistically significant differences in hatchability between the two habitats. The trends for the Robin and kingbird, however, are the same as for the waxwing.

Some orchards had extremely high rates of egg failure. In one orchard in 1968, only one of seven waxwing nests had any definite hatching. Of three eggs in this nest, only one hatched. All 19 eggs of known status in the other six nests failed to hatch. (Of the six nests, only three met my criteria for total failure.) Also in this orchard was the only Black-billed Cuckoo (*Coccyzus erythropthalmus*) nest with any degree of hatching failure. In 1969, this orchard had only one waxwing nest of known status; all three eggs hatched. Since, in 1968, this single orchard contributed so

TABLE 4. Egg hatchability and nest location of birds in Michigan.

Species	A Total no. of eggs	B % eggs not hatching	C[a] Total no. of nests	D % nests with total failure (no eggs hatching)	E[a] Total no. of nests	F % nests with total success (all eggs hatching)
Cedar Waxwing						
orchard	77	46.7	22	27.3	20	30.0
nonorchard	89	5.6	28	0.0	20	75.0
Chipping Sparrow						
orchard	63	4.8	20	0.0	20	90.0
nonorchard	51	15.7	17	11.8	16	81.3
Robin						
orchard	39	12.8	15	6.7	11	63.6
nonorchard	9	0.0	5	0.0	2	100.0
Eastern Kingbird						
orchard	20	35.0	7	28.6	6	50.0
nonorchard	7	0.0	3	0.0	2	100.0
Black-billed Cuckoo						
orchard	8	12.5	3	0.0	3	66.7
nonorchard	4	0.0	3	0.0	1	100.0

[a] The values in columns C and E are not always equal. See text for explanation and general description of criteria used in tabulating data.

much of the failure in the overall sums for orchard nests, it might be thought that excessive failure was restricted to this locality and not orchards in general. But one of the three nests in 1968 from other orchards also had total failure. Testing the data for 1969 alone shows hatching failure in orchard nests to be significantly higher than in nonorchard nests. Another orchard also had marked hatching failure in 1968. One nest each of a Loggerhead Shrike (*Lanius ludovicianus*), a Robin, and a kingbird located in this orchard had total egg failure. No waxwing nests were found in this orchard in 1968.

Cedar Waxwing egg and clutch size did not differ significantly between orchard and nonorchard habitats. Data for hatchability performance, clutch size, and egg size are available for 18 nests from each habitat. Clutch size in these orchard and nonorchard nests was 4.38 ± 0.14 and 4.22 ± 0.21, respectively. Mean egg dimensions (based on one egg from each clutch) were 21.55 ± 0.18 × 15.69 ± 0.12 mm for orchard and 22.04 ± 0.34 × 15.66 ± 0.12 mm for nonorchard eggs. No differences in clutch and egg size were found when all nests having complete hatching success were compared with those having one or more egg failures. (These analyses disregarded nest location.) An analysis of eggshell thickness, while demonstrating some important natural variation, has shown orchard and nonorchard eggs to have similar shell thicknesses (Rothstein 1972).

Kendeigh (1942) found that low hatchability in the House Wren (*Troglodytes aedon*) is correlated with high temperatures and thus indirectly with time of laying. While this may also be true for waxwings, an analysis of the data in this study (Rothstein, unpubl. data) does not indicate any relationship between date of laying and hatchability.

DISCUSSION

The high incidence of egg failure occurring among waxwings and possibly kingbirds and Robins (table 4) nesting near farms suggests the possibility of pesticide effects. No other cause seems likely, but even the argument for pesticide damage remains far from proved. One would not expect the Cedar Waxwing to be subjected to any sort of highly localized effect since it is well known to fly long distances in foraging (Allen 1930; Saunders 1911; and pers. observ.). The other four species nesting both in and away from orchards are more sedentary during the breeding season than the waxwing. Yet only one, the kingbird, showed a comparable incidence of egg failure in orchards. These arguments do not, however, preclude the possibility of pesticide effects since species of songbirds may accumulate pesticides at different rates (DeWitt and George 1960) and the tolerance of species to pesticides may differ (Bernard 1963).

Pesticide effects on songbirds generally take the form of increased adult or nestling mortality. No dead birds were found in the study areas, and little can be said as to nestling mortality because most nests were not checked after hatching. I know of no work demonstrating a relationship between a pesticide and hatching failure in songbirds. However, hatching failure in nonpasserines has been linked to pesticides (Genelly and Rudd 1956; Ames 1966; Hickey 1969; Wurster 1969; Ratcliffe 1970). But the abnormalities such as eggshell flaking, excessively thin-shelled eggs, and egg eating often accompanying the hatching failure in nonpasserines were not observed in this study.

The frequent occurrence of more than one failed egg per nest for most of the species studied in Michigan indicates that some common factor affected most or all of the clutch. There is no reason to believe that the pattern of incubation was abnormal in orchard nests. Some other factor affecting much or all of the clutch must be invoked. Pesticide effects, for which there is admittedly no direct evidence, would be such a factor.

Other factors that could influence hatchability can be rejected. Aggressive neglect, the situation in which birds attempting to breed in close proximity spend so much time in aggressive interactions that their reproductive efforts are impaired (Ripley 1961), could result in reduced hatchability; but the greatest concentration of waxwing nests was in a non-orchard habitat (Rothstein 1971b), and some orchards with only one to three nests had low hatching success. In addition, waxwings rarely engage in intraspecific conflicts and never seem to defend more than a small area around the nest (Putnam 1949; Lea 1942). Orchards, even though on occupied farms, were rarely visited by people. It is unlikely, then, that orchard birds spent an inadequate amount of time in incubation due to excessive disturbance by human activity. Lastly, one might expect young birds to be less efficient at breeding than older individuals, but there is no reason to suspect that young birds tend to breed in orchards.

It might be possible to explain more adequately the species and habitat differences in hatching success shown in this study if more were known about the factors involved in egg sterility and embryonic death in songbirds. A systematic study of hatching success would have important evolutionary implications since the failure of one or more eggs to hatch involves a loss of a high percentage of an individual's offspring. As table 2 shows, there are differences in the hatching success of various species and for the same species at different times and localities. Unfortunately, except for the deleterious influence of high temperature in the House Wren (Kendeigh 1942), almost nothing is known about the factors involved.

SUMMARY

Unusually high incidences of hatching failure due to egg sterility and embryonic death in three songbird species may be related to the proximity of the nests to farms. The Cedar Waxwing suffered the greatest hatching failure with 24.2% of all eggs and 46.7% of eggs in orchards near farms not hatching due to sterility or developmental failure. Hatching failure is examined both by the total number of eggs failing to hatch and by the number of nests with various degrees of failure. If it occurred at all in a nest, hatching failure in most species tended to affect more than one egg. Statistical tests treating each egg as an independent event may therefore be invalid.

Damage due to pesticides or other chemical agents may be the cause of the observed excessive hatching failure, but direct evidence is lacking. Other possible factors are mentioned and rejected. Hatching success in other studies is tabulated for comparative purposes. The paucity of work dealing with hatching failure in songbirds is stated and the need for such studies is noted.

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