

Variation in Nesting Success of the American Robin, *Turdus migratorius*

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Chiung-Fen Yen, Erwin E. Klass and Yeong-Choy Kam (1996) Variation in nesting success of the American Robin, *Turdus migratorius*. *Zoological Studies* 35(3): 220-226. We studied breeding ecology of the American Robin (*Turdus migratorius*) on the campus of Iowa State University. We estimated nest success, as measured by the Mayfield method, to be 53.6% for the 13-day incubation interval, 77.5% for the 12-day nestling interval, and 41.2% for the entire nesting cycle. Daily survival rates did not differ between small and large clutches, but nests on buildings experienced a much lower success rate (3.2%) than nests placed in trees and shrubs (44.0%). Early season nests placed in trees and shrubs were less successful (37.1%) than late season nests in trees and shrubs (66.7%) ($p < 0.05$). Daily survival rates during the nestling period were consistently higher than during the incubation period in all analyses. Predation was the major cause of mortality for eggs, whereas predation and starvation were the major causes of mortality for nestlings.

Key words: Bird, Ecology, Mayfield method.

Natural selection operates in part on variability in reproductive success. The observed reproductive pattern of a species must be considered an evolved complex of life-history traits that express the optimum fitness of individuals (Williams 1966, Lack 1968, Stearns 1976). The incubation and nestling stages of the life cycle often are the periods with birds suffering the greatest mortality (Ricklefs 1969 1973, Martin 1991 1992 1993), thus nesting success is a good index for studying population dynamics and reproductive potential in birds. Nesting success has been extensively documented in studies of avian breeding ecology (Nice 1957, Ricklefs 1969, Clark and Nudds 1991, Riley et al. 1992, Gregg et al. 1993, Martin 1993, Badyaev 1995, Robertson 1995).

The American Robin, *Turdus migratorius* is abundant throughout much of North America in a wide variety of habitats including urban lawns and parks. Its nest is large and conspicuous and is usually placed on a solid support in a tree or

shrub, or on a building. Robin nesting success has been studied previously (Howell 1942, Klimstra and Stieglitz 1957, Graber et al. 1971, Martin 1973, Willson 1978), but in all of these studies, nesting success was calculated using apparent success rates (the number of successful nests divided by the total nests observed). A number of investigators (Lack 1954 1966, Coulson 1956, Hammond and Forward 1956, Peakall 1960) have recognized that apparent nesting success rates are often biased. Hammond and Forward (1956) warned, "neglect of consideration for the length of time nests are under observation as compared to the total period they are exposed to predation would lead to a recorded success higher than that actually occurring." Mayfield (1961 1975) also recognized this problem and described a less biased method of calculating nesting success based only on observed time of exposure. The method assumes a constant survival rate over the time interval being studied. Klett and Johnson (1982) found the

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Mayfield method to be reliable and generally unbiased for estimating nesting success rates in upland nesting waterfowl. Johnson (1979) improved the method by providing robust statistical estimates for calculating variances and standard errors. Heisey and Fuller (1985) used these same estimators in constructing a computer program (MICROMORT) to estimate survival rates from telemetry data.

We quantified nesting success in an urban population of the American Robin using the Mayfield method, and analyzed the causes of egg and nestling mortality. Specifically, we asked the following questions. (1) Are nest survival rates of the American Robin affected by differences in brood size? (2) Do survival rates differ between the incubation and nestling periods? (3) Do survival rates differ between early and late season nests? (4) Do survival rates differ between nests placed in trees and those on buildings?

MATERIALS AND METHODS

The study was conducted in Ames, Iowa on the campus of Iowa State University in Ames, Iowa, an area of about 87 ha. This study area is almost identical to that described earlier by Weller (1971) and Willson (1978). The Iowa State University campus has been extensively landscaped with a large number of ornamentals which includes shrubs and trees that are not native to Iowa or are found only under cultivated conditions. Common tree include maple *Acer saccharinum*, *A. platanoides*, *A. ginnala*, oak *Quercus palustris*, *Q. alba*, *Q. bicolor*, hackberry *Celtis occidentalis*, downy hawthorn *Crateagus mollis*, *C. phaenopyrum*, honey locust *Gleditsia trianthos*, linden *Tilia cordata*, *T. americana*, Bradford pear *Pyrus calleryana*, white poplar *Populus* sp., crabapple *Malus* sp., pine *Pinus sylvestris*, *P. nigra*, *P. banksiana*, *P. resinosa*, spruce *Picea pungens*, fir *Pseudotsuga menziesii*, *Abies concolor*, cedar *Juniperus virginiana*, and hemlock *Tsuga canadensis*, whereas common shrub include honeysuckle *Lonicera tartarica*, lilac *Syringa reticulata*, viburnum *Viburnum prunifolium*, *V. dentatum*, and Japanese yew *Taxus cuspidata*. Observations began in early spring (mid-March 1987) with the arrival of robins and a search for nest began as soon as the birds started to defend their territories. Nests were located by searching the vegetation and by watching the behavior of breeding pairs. The nesting season extended from mid-March to mid-August 1987.

Once a nest was found, we marked its location on a map. We visited nests at least every 2 days to monitor clutch completion, progress of incubation, hatching, brood rearing, and eventual fate. We used a mirror on a pole or a ladder to observe nests placed too high to observe from the ground. We minimized the time spent at each nest to avoid attracting predators. Predation was assumed when one or more eggs disappeared from a nest between visits. Nestlings that were growing normally and disappeared between visits were assumed to have been taken by a predator. Nestlings that were not growing normally or were losing weight and later disappeared between visits were assumed to have starved. Of the 115 nests found, 95 nests with complete histories were considered for an evaluation of clutch size, and 87 of these had sufficient information for analyzing hatching and fledging success. An active nest was defined as a nest receiving at least two eggs, and a nest which fledged at least one young was considered successful. Nests with one, two, or three eggs or young were designated as small clutches or broods, whereas nests with four or five eggs or young were designated as large clutches or broods. The breeding season was divided temporally into "early" and "late" based on inspection of a bimodal frequency distribution of nest completion dates in which a definite break occurred on May 15.

We used the Mayfield method to calculate daily nest survival rates (Mayfield 1975, Johnson 1979). This method assumes a constant mortality rate within each stage of the nesting cycle. When calculating 'nest-days', losses were assumed to have occurred midway through the interval between visits of the observer. The computer program MICROMORT was used to calculate Mayfield survival rates and variances following Heisey and Fuller (1985), and Z-tests were used to test for differences in daily survival rates among compared groups (Bishop et al. 1975). A probability level of $p < 0.05$ was selected as an indication of statistical significance.

RESULTS

Clutch size of 95 nests averaged 3.5 with a frequency distribution as follows: 14 nests had 2 eggs, 33 had 3, 47 had 4, and 1 had 5. The incubation period, defined as the interval from the day before the last egg was laid to the hatching of the 1st young, was 13 days in 16 nests for which

exact information was available. The nestling period, defined as the interval from hatching of the 1st young to fledging of the 1st young, was 12 days in 24 nests for which exact information was available.

Nest success

Overall nest success for 87 robin nests was 41.2% (Table 1), but the estimated daily survival rate for the incubation period was significantly lower than that for the nestling period ($p < 0.05$). Thus, these two intervals were kept separate in subsequent comparisons.

The daily survival rates between the small (0.9706 ± 0.0087 , $n = 43$, number of exposure days = 375) and large broods (0.9919 ± 0.0057 , $n = 23$, number of exposure days = 248) are statistically the same ($p < 0.05$). During the incubation stage, the daily survival rate of nests on buildings was significantly lower ($p < 0.05$) than for nests in trees (Table 2). Once eggs were hatched, the survival rate was not significantly different between nests on buildings or in trees.

Among nests on buildings, survival rates during the incubation and nestling stages were not significantly different, whereas tree and shrub nests had a lower ($p < 0.05$) daily survival rate during the incubation stage. The small sample size of 4 nests and 33.5 exposure days of nests on buildings with nestlings reduced the power of the statistical tests, and these results should be interpreted with caution.

Table 1. Survival rates of American Robin nests

	Incubation (13 days)	Nestling (12 days)	Total (25 days)
Number of nests	87	66	87
Number of exposure days	710	623	1 333
Daily survival rate	0.9535 (0.0097)	0.9791 (0.0057)	0.9655 (0.0050)
Interval survival rate	0.5358 (0.0580)	0.7745 (0.0545)	0.4121 (0.0538)

Standard errors of the estimates are shown in parentheses.

The data were then grouped according to early and late season nests with nests on buildings excluded. Daily survival rates between incubation and nestling stages within each time period were statistically the same (Table 3). This allowed the data for incubation and nestling stages to be pooled to test for seasonal effects. The survival rate among early season nests (37.11%, $n = 33$) was significantly lower ($p < 0.05$) than that of late season nests (66.74%, $n = 36$).

Causes of nest failure

Predation was the greatest single cause of nest failure during the incubation period, followed by infertile eggs and dead embryos, and nest abandonment (Table 4). For nestlings, predation and starvation were the main causes of mortality (51.7% and 34.5%, respectively).

Table 2. Comparison of daily survival and success rates of American Robin nests placed on buildings, or in trees and shrubs

	Building ($n = 18$)		Trees and shrubs ($n = 69$)	
	Incubation (13 days)	Nestling (12 days)	Incubation (13 days)	Nestling (12 days)
Number of nests	18	4	69	62
No. of exposure days	114	33.5	596	589
Daily survival rate	0.8697 ^a (0.0329)	0.9221 ^{abc} (0.0432)	0.9536 ^b (0.0085)	0.9827 ^c (0.0054)
Interval success rate	0.1654 (0.0832)	0.2887 (0.2121)	0.5627 (0.0609)	0.7969 (0.0568)
Pooled interval rate	0.0316 (0.0332)		0.4398 (0.0585)	

Standard errors of the estimates are shown in parentheses; daily survival rate values sharing a common superscript are not significantly different ($p > 0.05$).

DISCUSSION

Nest success

Nest success varied according to where (buildings or trees and shrubs) and when (early or late season) robins built their nests. The two effects are probably not completely independent. Mortality was highest among nests placed on buildings (Table 2), and of the 18 nests placed on buildings, 16 were active in the early part of the season. All of the nests on buildings were under the eaves of roofs, and were usually supported by a ledge or small flat platform. Although these nests were somewhat protected from weather, they were highly visible and easily accessible to avian and mammalian predators. This agrees with earlier studies in that nest predation is the major cause of nesting mortality in many bird species (Ricklefs 1969, Martin 1993). On the contrary, nests in trees and shrubs were more concealed by foliage, especially as the season progressed, and seemed relatively

less accessible to predators. Robins probably were attracted to buildings during the early part of the season because they could not find suitable nest sites in trees where leaves were not fully grown. Few evergreens were available in the area where buildings were used as nest sites. Although birds were not marked, pairs continued to occupy territories after the nests on buildings had failed but most subsequent nests were in trees.

A seasonal effect on nest success was evident even if the nests on buildings were omitted from the analysis (Table 3). Daily survival rates were significantly lower among early nests probably for various reasons. Robins begin nesting early in the season before foliage on deciduous plants is fully developed, and so many of the available nest sites are suboptimal. As the season progresses, breeding robins are able to shift to larger deciduous trees which provide better concealment and protection for their nests. The high structural heterogeneity of nest habitats not only provides better concealment (Bowman and Harris 1980, Martin

Table 3. Comparison of daily survival and success rates between early and late season nests with nests on buildings excluded

	Early nest (<i>n</i> = 33)		Late nests (<i>n</i> = 36)	
	Incubation (13 days)	Nestling (12 days)	Incubation (13 days)	Nestling (12 days)
Number of nests	33	25	36	36
No. of exposure days	326	224	270	365
Daily survival rate	0.9573 (0.0112)	0.9688 (0.0116)	0.9815 (0.0082)	0.9863 (0.0061)
Interval success rate	0.5612 (0.0860)	0.6767 (0.0984)	0.7800 (0.0852)	0.8453 (0.0627)
Pooled interval rate	0.3711 (0.0802)		0.6674 (0.0844)	

Standard errors of the estimates are shown in parentheses.

Table 4. Causes of nest failure of American Robin eggs and nestlings

Cause	Eggs			Nestlings		
	<i>n</i>	% of egg mortality	% of eggs laid	<i>n</i>	% of nestling mortality	% of nestlings hatched
Predation	125	78.1	37.9	30	51.7	21.6
Starvation				20	34.5	14.4
Abandonment	12	7.5	3.6	2	3.4	1.4
Infertile or addled eggs	20	12.5	6.1			
Unknown	3	1.9	0.9	6	10.3	4.3
Total	160	100	48.5	58	100	41.7

and Roper 1988, Gregg et al. 1994) but also prevents common predators from developing search images (Storaas and Wegge 1987, Martin 1988), probably resulting in a low predation rate.

Brood size did not affect the daily survival rate, suggesting that parents could deliver enough food to all nestlings. Reduced food availability has been shown to have detrimental effects on the growth or survival rate in nestlings of blackbirds *Turdus merula* and yellow-eyed penguins *Megadyptes antipodes* (Klomp 1970, Margrath 1989, Van Heezik and Davis 1990). Nest survival rates were consistently lower for the incubation stage than for the nestling stage (Tables 1-3), but the difference was significant only among the large combined sample of nests placed in trees and shrubs. The difference is probably real and justifies obtaining separate estimates of survival rates for the two intervals. The difference may be the result of differential parental investment, i.e., the degree of intensity in which parents defended their nests. Robins seemed less likely to defend their eggs than their young from intruders and predators, an observation also reported by Howell (1942). Also, some early nest failures could achieve a higher nesting success in their second nest attempt.

Causes of nest failure

Estimates of the overall nest survival rates in this study (Table 1) are consistent with those of Knupp et al. (1977), but different from those in Ricklefs' study (1969). Predation was the most important cause of egg or young losses (Ricklefs 1969, Martin 1993). Nest contents usually disappeared without clues to the cause of disappearance. Occasionally, egg shells were found scattered under the nest. In these cases, the nest was usually undisturbed, but sometimes the nest lining was torn out.

The American crow, *Corvus brachyrhynchos*, and the common grackle, *Quiscalus quiscula*, were the most probable predators. The crow and grackle were both abundant in the study area, and one crow was seen standing on a robin nest which contained two broken eggs. Grackle nests were built in the vicinity of many of the robin nests. Grackles were observed within one meter of robin nests at least 10 times, and each time the robins chased them away.

Other possible predators were the raccoon, *Procyon lotor*; the fox squirrel, *Sciurus niger*; the eastern chipmunk, *Tamias straitus*; and the blue

Jay, *Cyanocitta cristata*. A raccoon was seen running away from a nest (nest height about 0.6 m) which had broken eggshells underneath.

Starvation in nestlings was usually noted when eggs hatched asynchronously. A nestling, which hatched one or two days later than its nestmates, had a smaller body mass compared to its siblings. Presumably, it was unable to compete as well for food from the parents. As a result, it grew slowly, whereas earlier hatched siblings had reached their maximum growth rate (C. F. Yen unpubl. data), and for several days were doubling their body mass every 24 h. As body size disparity increased for several days, the "starved" nestling had to compete with 3 or 4 older and larger siblings. We did not observe any nest in which all nestlings starved, and most of the starvation (70%) occurred late in the season. Weather conditions were much drier late in the season and reduced the availability of earthworms, *Lumbricus* spp., an important food source early in the season. Reduced food availability late in the season results in slower growth or lower survival rates (Margrath 1989, Van Heezik and Davis 1990). Starvation is a mechanism for birds to adjust brood size to food availability (Lack 1947 1954, Howe 1976 1978, O'Connor 1978). It has been cited as a significant source of mortality in a variety of species: e.g., common swift, *Apus apus* (Lack and Lack 1951), common blackbird, *Turdus merula* (Snow 1958), curve-billed thrasher, *Toxostoma curvirostre* (Ricklefs 1965), and common grackle (Howe 1976, Bancroft 1986).

Nest abandonment can be attributed to human disturbances or hatching failure of the entire clutch. Two early clutches which failed to hatch had dead embryos inside the eggs. The average monthly temperature for March, April, and May was 5.6 °C (range -0.4 to 11.5 °C), 12.3 °C (range 4.6 to 20 °C), and 19.2 °C (12.1 to 26.6 °C), respectively, and it is possible these embryos died because of a lack of attentiveness by the incubating parent. The rate of infertility (6.1%) of robin eggs in this study is nearly the same as that reported in earlier studies of the robin (Howell 1942, Knupp et al. 1977), and within the failure rate of 6%-10% reported for many passerines (Ricklefs 1969, Rothstein 1973, Koenig 1982, Bancroft 1986).

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美國知更鳥築巢成功率之研究

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本文報告在愛荷華州立大學校園美國知更鳥的生殖生態。利用 Mayfield 方法，我們估計知更鳥在胚胎期的存活率是 53.6%，在幼鳥期存活率是 77.5%，而在整個築巢期(胚胎加上幼鳥期)是 41.2%。幼鳥期的每日存活率在全部分析中皆高過胚胎期的存活率。大小鳥巢的每日存活率一樣，但建在屋簷下鳥巢的成功率(3.2%)明顯低於建在樹或灌叢的鳥巢(4.4%)。早期建在樹或灌叢的鳥巢的成功率(37.1%)明顯低於晚期的鳥巢(66.7%)。掠食是鳥蛋死亡的主要原因，而掠食及饑餓則是幼鳥死亡的主要原因。

關鍵詞：鳥，生態，Mayfield 方法。

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