Aspects of the breeding ecology of the American Robin (*Turdus migratorius*) on campus of Iowa State University

by

Chiung-Fen Yen

A Thesis Submitted to the
Graduate Faculty in Partial Fulfillment of the
Requirements for the Degree of
MASTER OF SCIENCE

Major: Animal Ecology

Iowa State University
Ames, Iowa

1988

TABLE OF CONTENTS

GENERAL INTRODUCTION

The American Robin (<u>Turdus</u> <u>migratorius</u>) ranges over most of the North American continent in coniferous forest, deciduous forest, and savanna. The species is a common breeding bird in cities and towns throughout its range (Howell 1942; Nickell 1944). The greatest concentrations of nesting pairs are often found in cemeteries, orchards, parks, and college campuses, where ornamental trees and shrubbery provide excellent nesting cover (Nickell 1944). The Iowa State University campus has been extensively landscaped with ornamentals including representatives of at least 40 families and 199 species of woody plants (Brady 1962). The American Robin is common on campus and was first studied in the 1940s by Klimstra and Stieglitz (1957) who reported basic information on clutch size and hatching success. Robins again received some attention when mortality and population declines occurred during the 1960s following several years of DDT applications for Dutch elm disease control (Weller 1971). Willson (1978) was the last to study the campus robin population in 1977 and reported a complete recovery following the elm disease control program.

Robins are conspicuous and so accustomed to being near human activity that they can be easily approached and studied from a variety of perspectives. Nests are easily found and nesting pairs are relatively tolerant of human disturbance at the nest site. Robins arrive in Iowa about mid-March. Males progress into breeding readiness soon after arrival and females begin to lay before April (Kemper and Taylor 1981). The clutch size ranges from 2 to 5, and pairs often raise 2-3 broods per season. The earliest fledging is in early May and the last fledging occurs in mid-July (Willson 1978).

Section I of this thesis is a study of nesting success in the campus robin population using modern unbiased methods of estimating survival rates (Mayfield 1961, 1975). Sources of egg and nestling mortality were documented to better understand the types of selective pressures on this species. Specifically, I asked the following questions: (1) Is the nest survival rate of the robin affected by differences in clutch size? (2) Do survival rates differ between early and late season nests? (3) Do survival rates differ between nests placed in trees and shrubs, and those on buildings?

Section II of this thesis is a quantitative study of site characteristics of robin nests placed in vegetation. My purpose was to determine if seasonal variation occurred in site selection, and if nest success is related to nest site characteristics.

Section III describes the growth of robin nestlings by fitting body weight and tarsus length data into three equations (Richard, Vonberttalanfy, and Logistic) (Ricklefs 1967, 1968) and evaluates the effects of season, egg size, and brood size on their growth.

The American Robin is a common and conspicuous species on the campus of Iowa State University and is easily studied. The species could be used advantageously for long-term investigations that could answer many basic questions regarding avian ecology. I hope that this study will provide information that can be used as a beginning for future work.

EXPLANATION OF THESIS FORMANT

This thesis follows the guidelines set up for the alternative thesis format. It consists of three papers, each intended for publication in an ornithological journal. Chiung-Fen Yen has helped to plan the study, carried out the field study, and was responsible for the aquisition and analysis of data and writing the paper with guidance and editorial assistance from Dr. Erwin Klaas.

SECTION I:

VARIATION IN NESTING SUCCESS OF THE AMERICAN ROBIN (*TURDUS MIGRATORIUS*)

ABSTRACT

Breeding ecology of the American Robin (*Turdus migratorius*) was studied in 1987 on the campus of Iowa State University. Nest success, as measured by the Mayfield method, was estimated 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 rate during the nestling period was 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.

INTRODUCTION

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 trait that expresses the optimum fitness of individuals (Williams 1966; Lack 1968; Stearns 1976). The incubation and nestling stages of the life cycle often are the periods suffering the greatest mortality (Ricklefs 1969, 1973), 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 (for review see Nice 1957; Ricklefs 1969).

The American Robin (<u>Turdus</u> <u>migratorius</u>) 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; Knupp et al. 1977; 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 nest 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 (later called the Mayfield 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 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.

This study was undertaken to quantify nesting success in an urban population of the American Robin using the Mayfield method, and to analyze the causes of egg and nestling mortality. Specifically, I asked the following questions: (1) Are nest survival rates of the American Robin affected by differences in clutch 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?

STUDY AREA AND METHODS

The study was conducted 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 by Weller (1971) and Willson (1978). Observations began in early spring (mid-March) with the arrival of robins. Nest searching 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 field season extended from mid-March to mid-August 1987.

Once a nest was found, its location was marked on a map. Nests were visited at least every 2 days to monitor clutch completion, progress of incubation, hatching, brood rearing, and eventual fate. A mirror on a pole or a ladder was used to observe nests placed too high to observe from the ground. The time spent at each nest was minimized 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 that disappeared between visits were assumed to have starved. Of the 115 nests found, only 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. Clutch sizes were not adjusted to account for possible removal of Robin eggs by Brown-headed Cowbirds (Molothrus ater). 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.

Daily nest survival rates were calculated using the Mayfield method (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 $P \leq 0.05$ 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 was laid to the hatching of the first young, was 13 days in 16 nests for which exact information was available. The nestling period, defined as the interval from hatching of the first young to fledging of the first young, was 12 days in 24 nests for which exact information were 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.

Survival rates did not vary among nests grouped according to clutch or brood size. 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 building and tree nests.

Among building nests, 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 building nests with nestlings reduced the power of the statistical tests, and these results should be interpreted with caution.

The data were then grouped according to early and late season nests with building nests 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 a 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 Mortality

Predation was the greatest single cause of mortality 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 1. Survival rates of American Robin nests on the Iowa State University campus, 1987. Standard error of the estimates are shown in parentheses

	Incubation (13 days)	Nestling (12 days)	Total (25 days)
Number of nests	87	66	87
Number of exposure days	710	623	1333
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)

Table 2. Comparison of daily survival and success rates of American robin nests placed on buildings versus trees and shrubs on the Iowa State University campus, 1987. Standard errors of the estimates are shown in parentheses; daily survival rate values sharing a common superscript are not significantly different

	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	112	33.5	596	589
Daily survival rate	0.8679^{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)	

Table 3. Comparison of Daily survival and success rates of early versus late season nests of American Robin trees and shrubs on the Iowa State University campus, 1987. Standard errors of the estimates are shown in parentheses

	Early nests (N = 33)		Late nests (N = 36)	
	Incubation (13 days)	Nestling (12 days)	Incubation (13 days)	Nestling (12 days)
Number of nests	33	25	36	37
No. of exposure days	328	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)	

Table 4. Causes of mortality of American Robin eggs and nestlings on the Iowa State University campus in 1987

	Eggs			Nestlings		
Causes	n	% of egg mortality	% of eggs laid	n	% 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

DISCUSSION

Nest success

Nest success varied with where (buildings vs trees and shrubs) and when (early vs late season) robins built their nests, and the two effects are probably not completely independent. Mortality was very high 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 building nests 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. 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 building nests had failed but most subsequent nests were in trees.

A seasonal effect on nest success was evident even if building nests were omitted from the analysis (Table 3).

Daily survival rates were significantly lower among early nests probably for various reasons. Early nests built in vegetation had less concealment because foliage on deciduous trees and shrubs had not fully developed. It can be assumed that many of the individuals in the breeding population were 1-year old. Thus, early season nests represented their first breeding attempt. Crawford (1977) reported that less experienced female Red-winged and Yellow-headed Blackbirds (Agelaius phoeniceus and Xanthocephalus xanthocephalus) have a lower nesting success than experienced individuals. Thus, experience gained in early nesting attempts may help some robins to be more successful in late season attempts. Also, mean height of early season nests were lower than those of late season nests (Section II), and lower nests may be more exposed to predators, especially ground-foraging small mammals. Howell (1942) and Young (1955) also reported a lower success rate among early robin nests.

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 from intruders and predators than their young, an observation also reported by Howell (1942). Also, some nests may be more susceptible to predators and after these nests are destroyed, the ones surviving to hatching are at less risk.

Causes of mortality

Estimates of the overall nest survival rates in this study (Table 1) are consistent with those of Knupp et al. (1977), but different from Ricklefs' study (1969). Predation was the most important cause of egg or young losses. 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 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 maximum growth rate (Section III) and for several days were doubling their body mass every 24 hours. As body size disparity increased for several days, the "starved" nestling had to compete with 3 or 4 older and larger siblings. 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. 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 ambient temperature was quite cool during the early season, 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 was nearly the same as that reported in earlier studies of same species (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).

LITERATURE CITED

Bancroft, G. T. 1986. Nesting success and mortality of the Boat-tailed Grackle. Auk 103:86-99.

Bishop, Y. M. M., S. E. Fienberg, and P. W. Holland. 1975. Discrete multivaritae analysis. Massachusetts Institute of Technology Press, Cambridge, Massachusetts.

Coulson, J. C. 1956. Mortality and egg production of the Meadow Pipit with special references to altitude. Bird Study 3:119-132.

Crawford, R. D. 1977. Breeding biology of year-old and older female Red-winged and Yellow-headed Blackbirds. Wilson Bull. 89:73-80.

Graber, R. R., J. W. Graber, and E. L. Kirk. 1971. Illinois birds: Turdidae. Illinois Nat. His. Surv. Biol. Notes 75.

Hammond, M. C., and W. R. Forward. 1956. Experiments on causes of duck nest predation. J. Wildl. Manage. 20:243-247.

Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. J. Wildl. Manage. 49:668-674.

Howard, D. V. 1967. Variation in the breeding season and clutch size of the robin in Northeastern United States and the Maritime Provinces of Canada. Wilson Bull. 79:432-440.

Howe, H. F. 1976. Egg size, hatching asynchrony, sex and brood reduction in Common Grackle. Ecology 57:1195-1107.

Howe, H. F. 1978. Initial investment, clutch size, and brood reduction in the Common Grackle (Quiscalus quiscula L.). Ecology 59:1109-1122.

Howell, J. C. 1942. Notes on the nesting habits of the American Robin (Turdus migratorius). Am. Midl. Nat. 28:243-247.

Johnson, D. H. 1979. Estimating nest success: The Mayfield method and an alternative. Auk 96:651-661.

Klett, A. T., and D. H. Johnson. 1982. Variability in nest survival rates and implications to nesting studies. Auk 99:77-87.

Klimstra, W. D., and W. O. Stieglitz. 1957. Notes on reproductive activities of robins in Iowa and Illinois. Wilson Bull. 69:333-337.

Knupp, D. M., R. B. Owen, Jr., and J. B. Dimond. 1977. Reproductive biology of American Robins in northern Maine. Auk 94:80-85.

Koenig, W. D. 1982. Ecological and social factors affecting hatchability of eggs. Auk 99:526-536.

Lack, D. 1947. The significance of clutch size. Ibis

89:302-352.

Lack, D. 1954. The natural regulation of animal numbers. Oxford University Press, London. 341 pp.

Lack, D. 1966. Population studies of birds. Clarendon Press, Oxford. 409 pp.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen Press, London.

Lack, D., and E. Lack. 1951. The breeding biology of the Swift (Apus apus). Ibis 93:501-546.

Martin, K. 1973. Breeding density and reproductive success of robins in relation to habitat structure on logged area of Vancouver Island, British Columbia. Unpublished thesis, Edmonton, University of Alberta, Canada.

Mayfield, H. 1961. Nesting success calculated from exposure. Wilson Bull. 73:255-261.

Mayfield, H. 1975. Suggestion for calculating nesting success. Wilson Bull. 87:456-466.

Nice, M. M. 1957. Nesting success in altricial birds. Auk 74:305-321.

O'Connor, R. J. 1978. Brood reduction in birds selection for fracticide, infanticide, and suicide? Anim. Behav. 26:79-96.

Peakall, D. B. 1960. Nest records of the Yellow hammer. Bird Study 7:94-102.

Ricklefs, R. E. 1965. Brood reduction in the Curve-billed

Thrasher. Condor 67:505-510.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contrib. Zool. 9:1-48.

Ricklefs, R. E. 1973. Fecundity, mortality, and avian demography. Page 336-435 in D. S. Farner, ed. Breeding biology of birds. Natl. Acad. Sci., Washington, D. C.

Rothstein, S. I. 1973. Variation in the incidence of hatching failure in the Cedar Waxwing and others species. Condor 75:164-169.

Snow, D. W. 1958. The breeding of Blackbird (*Turdus merula*) at Oxford. Ibis 100:1-30.

Stearns, S. C. 1976. Life-history tactics: A review of the ideas. Q. Rev. Biol. 51:3-47.

Weller, M. W. 1971. Robin mortality in relation to Dutch elm disease control programs on the Iowa State University campus. Ia. St. J. Sci. 45:471-475.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am. Nat. 100:687-692.

Willson, G. D. 1978. Reproductive biology of American Robins following a Dutch elm disease control program. Proc. Ia. Acad. Sci. 85(3):91-96.

Young, H. 1955. Breeding behavior and nesting of Eastern Robin. Amer. Midl. Nat. 53:329-352.

SECTION II:

NEST SITE CHARACTERISTICS OF AN URBAN POPULATION OF THE AMERICAN ROBIN (*TURDUS MIGRATORIUS*)

ABSTRACT

Univariate and multivariate analyses were used to characterize nest sites of American Robins (Turdus migratorius) nesting on the campus of Iowa State University, and to determine the relationship between nest site characteristics, seasonal changes, and nest success. Robins nested on buildings and in a wide variety of trees and shrubs. Site selection varied with the season; buildings and evergreens were used more frequently in the early half of the season whereas deciduous trees were chiefly used in the late half of the season. Principal component analysis indicated that tree size and foliage cover immediately surrounding the nest were variables that consistently characterized robin nest sites. Discriminant function analysis identified the volume of foliage below the nest (PFB) and distance of the nest to the center of the supporting plant (DC) as variables that primarily discriminated nest sites between seasons. In a univariate analysis, 5 variables related to tree size were significant by different between seasons. Discriminant function analysis detected a significant difference between characteristics of successful and failed nests, whereas none of the variables measured were significant in a univariate analysis. Although shade was not measured as a distinct

variable, observations indicate that shade may be very important in seasonal variation in nest site selection.

INTRODUCTION

The American Robin (Turdus migratorius) has shown a remarkable ability to adapt to a wide variety of habitats (Stauffer and Best 1986). Robins range over most of the North American continent in coniferous forest, deciduous forest, and savanna. They also occur commonly in cities and towns (Howell 1942; Nickell 1944), and even farmstead shelter belts (Yahner 1983). During the breeding season, the greatest concentration of nesting pairs often is found in cemeteries, orchards, parks, campuses, lake settlements, and towns (Howell 1942). Robins build nests composed of mud and dry grass in trees, shrubs, and on buildings or other artificial structures where adequate cover and supporting ledges are available.

Nest site characteristics of the American Robin have been previously described, but most available information is qualitative and limited to a few descriptive variables (Howell 1942; Nickell 1944; Klimstra and Stiegltz 1957; Graber and Graber 1963; Willson 1978; Stauffer and Best 1980, 1986). This study was undertaken to quantitatively describe site characteristics of robin nests placed in vegetation, to determine seasonal variation in site selection, and to determine if nest success was related to nest site characteristics.

STUDY AREA AND METHODS

The study was conducted in Ames, Iowa on the Iowa State University campus, an area of about 87 ha that is similar to that described by Weller (1971) and Willson (1978). Observations began in early spring with the arrival of robins, and nest searching began as soon as robins started to defend their territories. Nests were located by searching the vegetation and watching the behavior of breeding pairs. The field season extended from mid-March to mid-August during 1987.

Once a nest was found, its location was marked on a map. The nest was visited at least every 2 days to monitor the progress of incubation, brood rearing, and eventual fate. Nests which fledged at least one young were considered successful. The breeding season was divided temporally into "early" and "late" based on the inspection of a bimodal frequency distribution of nest completion dates in which a definite break occurred on May 15.

Nest site variables of 115 nest locations in trees or shrubs were measured. Nest sites for which season or nest fate could not be determined with certainty were excluded from statistical analysis. Species names for 14 cultivars could not be determined and were excluded from analyses comparing evergreen and deciduous species.

Most nest site characteristics were measured soon after the nest became inactive. These characteristics logically fall into two groups: "macro" variables generally describe the location of the nest in the territory and the relative size of the tree or shrub in which the nest was located. "micro" variables describe the features of the vegetation in an area about one meter in radius surrounding the nest. Macro variables measured included the linear distance between a nest and the nearest building and sidewalk (measurements were restricted to distances less than 10 m), the height of nests and supporting structures as measured with a clinometer, the canopy diameter of the supporting plant, and, for nests in trees, the diameter of the trunk at breast height. Micro variables included plant volume within a hemisphere having an aproximation radius of 1 m above and below the nest estimated to the nearest 25%; the distance to the center and the periphery of the canopy; and the number, diameter, and angles (to the nearest 10°) of branches supporting the nest. In addition to these variables, nest orientation relative to the trunk of the supporting plant (e.g., north/south) was recorded, and the building configuration or nature of nest supports were matched with a series of graphic models (Figs 1, 2) developed by Steven Phelps (former student at Iowa State University).

Nest site characteristics of avian species have been often analyzed using univariate methods (chi-square, and analysis of variance) and in recent years multivariate techniques (principal component and discriminant function analyses) have become increasingly popular as a means of characterizing nesting habitat (Hespenheide 1971; Noon 1981; Collins 1983; Stauffer and Best 1980, 1986). Both approaches are useful and usually are used in combination to answer different questions and to provide alternative perspectives. In this study, principal component analysis (SAS Institute Inc. 1985) was used to identify the major axes of variation in the nest site variables, i.e., to derive a small number of linear combinations (principal components) from the original set of variables while still retaining as much of the information from the original variables as possible. In this manner, principal component analysis provided a method for grouping correlated one-dimensional variables and simplifying the description of nest site characteristics. Discriminant function analysis (SAS Institute Inc. 1985) provided a mathematically objective method for comparing groups of nests on the basis of related variables. The relative importance of each variable to the comparison was determined by examining the standardized discriminant function coefficient for each variable. Nest site variables from successful and failed nests, and early and late season nests were compared using discriminant function analysis. This provided a test of whether physical characteristics of successful nests differed from those of failed nests, and if characteristics of early season nests differed from those of late season nests. Three variables (supporting height, supporting canopy diameter, and distance to the center of the support) did not meet the assumption of normality and were transformed to natural logarithms for multivariate analysis. Only variables which had complete data sets were used. Chi-square analysis was used to test for differences among discrete variables (building configuration, orientation of the nest, and nature of the nest support). Means of all variables are reported plus or minus one standard deviation; statistical significance was set at $P \leq 0.05$.

RESULTS AND DISCUSSION

Robins built their nests in a wide variety of places including trees, shrubs, buildings, old carriages, wood piles, and under a small house trailer. Earlier studies have reported similar variability (Howell 1942; Young 1955; Klimstra and Stiegltz 1957; Willson 1978; Knupp et al. 1977). Among the 115 nests built in vegetation, 65% were in trees whereas 22% were in shrubs (Table 1). Nests were never placed in dead vegetation.

A total of 38 tree species were used as nest sites, with no particular species being preferred, whereas honeysuckle was used most of 8 shrub species for nest sites (Table 1). Willson (1978) reported that robins seem to prefer maple, oak, and pine trees.

During the early part of the season, 22 of 40 nests (55%) were built in evergreen species, whereas late in the season, 47 of 49 nests (96%) were built in deciduous plants. The difference is highly significant ($X^2 = 2381$, df = 1, $P < 0.001$). Robins presumably avoided deciduous trees in the early season because leaves had not started to emerge at the time nest building started. Moreover, 18 of 20 nests (90%) placed on buildings were early season nests (Section I), and all building nests were shaded by an eave or other overhanging structure. Howell (1942) reported that 58% and 25% of his early nests were in evergreen and deciduous trees, respectively, whereas in the late season it was 38% and 48%. Knupp et al. (1977) and Willson (1978) also found similar seasonal variation in plant utilization. These observations suggest that shade from solar radiation or protective concealment from above is an important nest site characteristic for the American Robin.

Nest sites in trees and shrubs were further characterized by a series of variables estimated for most of the active nests in the study area (Table 2). Average nest height among 115 nests was 2.5 m which is the same as that reported by Willson (1978) in the same study area but higher than that reported in other areas (Young 1955; Klimstra and Stieglitz 1957; Graber and Graber (1963). This variation in nest height is probably due to the availability of vegetation at the various locales. Foliage volume and branches above nests tended to receive higher percentage estimates than foliage volume below nests (Table 2).

Principal component analysis was performed using 13 nest site variables from 115 robin nests. This analysis produced four eigenvectors with values greater than 1.0 which accounted for 65.8% of the total variation. This low cumulative value suggests that other variables not considered in this study may also be important in characterizing robin nest sites. The first principal component accounted for 33.3% of the total variation (Table 3), and was positively related to height of the supporting plant, supporting canopy diameter, nest height, distance from the nest to the periphery, and diameter of branches supporting the nest. Thus, principal component 1 corresponds to the general size of the tree or shrub. Principal component 2 accounted for 13.5% of the total variation (Table 3) and was positively related to foliage above and below the nest, branches above and below the nest, and distance to the center of the supporting plant. Thus, principal component 2 corresponds to the area immediately surrounding the nest. Variables positively corresponding to the third principal component were branches above the nest whereas distance to the nearest sidewalk, plant volume below the nest, and distance to the center of the supporting plant were negatively related. Component 4 was positively associated with foliage below the nest, distance to periphery and number of branches supporting the nest, whereas distance to the nearest sidewalk and diameter of the branch supporting the nest was negatively related.

In summary, principal component analysis indicates that variables related to tree size and foliage cover immediately surrounding the nest were consistently associated with robin nest sites.

Seasonal differences in nest site characteristics

Analysis of variance was used to compare individual nest site variables between early and late season nests (Table 4). Late season nests tended to be built higher (NH) in larger trees (SH) with a greater canopy diameter (SCD). Also, late nests tended to be farther from the center (DC) and periphery (DP) of the supporting plant than that of early season nests (Table 4).

All 13 variables were further investigated using discriminate function analysis, and a significant difference was detected between early season and late season nest-site characteristics ($F_{13,62} = 2.00$; $P = 0.035$; Fig. 3). The volume of foliage below the nest and distance from the nest to the center of the supporting plant were the two most effective discriminators between early and late season groups. The least effective discriminators were the number of branches supporting the nest, plant volume of branches above the nest, and distance to the nearest sidewalk. The standardized discriminant function is as follows: discriminant score = 0.904 [foliage below nest] + 0.7630 [distance to the center of support] - 0.390 [plant volume of branches below nest] + 0.344 [distance to periphery] - 0.315 [foliage above nest] + 0.205 [angles of branches] + 0.205 [supporting height] - 0.173 [supporting canopy diameter] +

0.123 [diameter of branches supporting nest] + 0.079 [nest height] - 0.028 [number of branches supporting nest] - 0.020 [plant volume of branches above nest] - 0.014 [distance to sidewalk]. The distance of the nest to the center of the supporting plant (a measure of plant size) was the only variable that was identified as important in both the univariate and discriminate function analyses.

In summary, these results are consistent with the observation that robins shifted their nest sites from mostly evergreen plants and buildings in the early part of the season to predominantly deciduous trees in the late part of the season. Deciduous trees in this study area tend to be large compared to evergreens.

Effect of site characteristics on nest success

An analysis of variance was used to compare successful and unsuccessful nest sites with the 13 variables used above. None of the means for individual variables were significantly different (Table 5). However a discriminant function analysis resulted in significant differentiation between nest sites classified according to nest fate ($F_{13,62} = 2.0$; $P = 0.034$; Fig. 4). Supporting canopy diameter, diameter of branch supporting the nest, and distance to the periphery of the canopy were the three most effective discriminators. All of these are measures of relative size of the supporting plant. Distance to sidewalk and foliage above nest were the two least effective discriminators. Nest height also contributed little to the discrimination of nests according to fate, which is consistent with the findings of Martin (1973). However, Yahner (1983) reported that the height of the supporting plant and the distance of the nest from the main stem were associated with success of robin nests in Minnesota shelterbelts. The standardized discriminant function is as follows: discriminant score = -1.189 [supporting canopy diameter] + 0.886 [diameter of branches supporting nest] + 0.760 [distance to periphery] - 0.715 [angles of branch supporting nest] + 0.714 [distance to the center support] + 0.653 [foliage below nest] - 0.605 [supporting height] - 0.484 [branches below nest] + 0.273 [number of branches supporting nest] - 0.156 [branches above nest] - 0.151 [nest height] - 0.042 [foliage above nest] + 0.023 [distance to sidewalk].

It has been shown previously that nests on buildings, most of which were early season nests, had a low survival rate (see Section I). Also, early nests placed in vegetation had a lower success rate than late nests. Because robins begin nesting early in the season before foliage on deciduous plants is fully developed, 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.

Other nest site characteristics

Nest success was unrelated to building configuration (Fig. 1), shape of the nest support (Fig. 2), and nest orientation (Fig. 5) (X^2=3.1, df=4; X^2=6.6, df=4; X^2=10.5, df=7, respectively). Building configuration categories 3, 5, and 6 were excluded from the analysis because of low sample sizes (Fig. 1).

Solar radiation, which some authors have suggested may affect nest temperature and the amount of incubation/brooding required (Kendeigh 1963; Martin and Roper 1987), may be important to robins, but robins did not position their nests in any specific direction relative to the center of the supporting plant (Fig. 5). Regardless of orientation, all nests were placed in positions that seemed to avoid direct sunlight. Even nests on buildings were placed under eaves or some other overhanging structure that provided optimal shade. The effect of solar radiation on the nest and the influence that shade might have on nest site selection are topics that deserves more extensive study.

Table 1. Plants used by the American Robin as nest sites on the Iowa State University campus in 1987

Species	No. of nests
Trees	
Deciduous species N=27	
Maple (*Acer saccharimum*, *A*. *platanoides*, *A*. *ginnala*)	9
Oak (*Quercus palustris*, *Q*. *alba*, *Q*. *bicolor*)	3
Hackberry (*Celtis occidentalis*)	5
Buckthorn (*Rhamnus cathartica*)	2
Downy hawthorn (*Crataegus mollis*, *C*. *phaenopyrum*, *C*. spp.)	7
Honey locust (*Gledistsia trianthos*)	2
Linden (*Tilia cordata*, *T*. *americana*	6
Bradford pear (*Pyrus calleryana*)	3
White popular (*Populas* sp.)	1
Crabapple (*Malus* sp.)	5
Chokecherry (*Prunus virginiana*, *P*. *calleryana*)	2
Sycamore (*Platanus occidentalis*)	3
Ash (*Fraxinus americana*, *F*. *pennsylvanica*)	2
Elm (*Ulmus pumila*, *U*. *americana*)	2
Creeper (*Parthenocissus quinquefolia*, *P*. *trucuspidata*)	2
Dogwood (*Cornus* sp.)	2

Table 1 (cont.)

Evergreen species N=11	
Pine (*Pinus sylvestris*, *P*. *nigra*, *P*. *banksiana* *P*. *resinosa*)	7
Spruce (*Picea pungens*)	2
Douglas fir (*Pseudatsuga menziesii*)	1
White fir (*Abies concolor*)	2
Red cedar (*Juniperus virginiana*)	3
Eastern hemlock (*Tsuga canadensis*)	1
Saucer magnolia (*Magnolia soulangeang*)	1
Winged wahoo (*Euonynous alata*)	2
Shrubs	
Deciduous species N=5	
Honeysuckle (*Lonicera tartarica*, *L*. spp.)	14
Lilac (*Syringa reticulata*)	2
Viburnum (*Viburnum prunifolium*, *V*. *dentatum*)	1
Evergreen species N=1	
Japaneses yew (*Taxus cuspidata*)	5
Unknown cultivars N=5	14
Total	115

Table 2. Nest site characteristics of the American Robin on the Iowa State University campus, 1987

Variables	N	Range	Mean±SD
Macro Variables			
Distance to the nearest building (m)	63	0.9-9.9	4.9±3.4
Distance to the nearest sidewalk (m)	99	0.0-8.0	2.7±1.9
Supporting height (m)	115	1.0-20.5	7.0±4.4
Supporting canopy diameter (m)	115	1.2-16.5	5.7±3.4
Supporting DBH (cm)	55	8.5-104.0	34.3±19.6
Nest height (m)	115	0.7-6.0	2.5±1.0
Micro Variables			
Plant volume within 1 m of nest (estimated to nearest 25%)			
Foliage above (%)	113	0.0-75.0	31.2±18.5
Branch above (%)	113	0.0-75.0	25.7±16.5
Foliage below (%)	113	0.0-50.0	13.3±16.7
Branch below (%)	113	0.0-50.0	12.4±15.7
Distance to the center of support (m)	114	0.0-6.6	1.4±1.4
Distance to periphery (m)	114	0.0-6.9	1.9±1.2
Number of branches supporting nest	113	1.0-5.0	2.2±1.0
Diameter of branches supporting nest (cm)	113	0.7-15.5	3.4±2.9
Angles of branches supporting nest (nearest 10°)	113	0.0-80.0	38.1±27.4

Table 3. Correlation of habitat variables and the first four principal components of American Robin nest sites. Coefficient that are highly correlated are underlined

Variables	PC1	PC2	PC3	PC4
Distance to the sidewalk (DS)	0.00	0.04	-0.51	-0.43
Support height (SH)	0.41	0.11	-0.01	0.17
Support canopy diameter (SCD)	0.39	0.20	0.13	0.09
Nest height (NH)	0.36	0.09	0.01	0.17
Plant volume within 1 m of nest				
Foliage above (PFA)	-0.15	0.57	0.17	-0.17
Branch above (PBA)	-0.22	0.31	0.32	-0.27
Foliage below (PFB)	-0.14	0.50	-0.31	0.40
Branch below (PBB)	-0.29	0.30	-0.34	0.21
Distance to center (DC)	0.16	0.31	0.49	-0.15
Distance to periphery (DP)	0.34	0.01	-0.20	0.36
Number of branches supporting nest (NBSN)	-0.25	-0.19	0.28	0.41
Diameter of branches supporting nest (DBS)	0.34	-0.01	-0.12	-0.35
Angles of branch supporting nest (ABS)	-0.25	-0.21	0.20	0.03
Variation explained (%)	33.3	13.5	9.7	9.1

Table 4. Comparison of site characteristics among early and late season American Robin nests. F-values were obtained from a one-way analysis of variance; significant variables are underlined. See Table 3 for variable definitions

	Early Season		Late Season		
Variables	Mean±SD (N)	Range	Mean±SD (N)	Range	PR>F
DS	2.9±1.8 (34)	0.0-1.8	2.7±2.2 (43)	0.0-7.6	0.7429
SH	5.3±3.8 (41)	1.0-17.5	6.9±4.0 (49)	2.3-19.5	0.0123
SCD	4.3±2.2 (40)	1.4-13.0	6.0±3.4 (49)	1.2-14.7	0.0056
NH	2.0±1.0 (41)	0.7-5.7	2.6±1.0 (49)	1.1±6.0	0.0169
DFA	31.3±19.4 (40)	0.0-75.0	30.2±17.1 (48)	0.0-75.0	0.9008
PBA	29.4±17.8 (40)	0.0-75.0	22.9±14.4 (48)	0.0-50.0	0.2753
PFB	12.5±17.0 (40)	0.0-50.0	15.6±17.6 (48)	0.0-50.0	0.0705
PBB	17.5±16.2 (40)	0.0-50.0	10.4±14.4 (48)	0.0-50.0	0.2514
DC	1.1±1.5 (40)	0.0-6.0	1.5±1.3 (49)	0.1-5.4	0.0025
DP	1.4±0.7 (40)	0.2-3.0	2.0±1.2 (49)	0.0-5.7	0.0079
NBSN	2.3±1.0 (40)	0.0-5.0	2.2±1.0 (48)	1.0-5.0	0.3429
DBS	2.8±2.4 (40)	0.8-12.5	3.5±2.5 (48)	0.8-13.0	0.1765
ABS	42.0±28.3 (40)	0.0-80.0	39.4±27.5 (48)	0.0-80.0	0.4762

Table 5. Comparison of site characteristics between successful and failed American Robin nests. F-values obtained from one-way analysis of variance. See Table 3 for variable symbol definitions

	Successful		Failed		
Variables	Mean±SD (N)	Range	Mean±SD (N)	Range	PR>F
DS	2.8±2.3 (42)	0.0-8.0	2.8±1.6 (35)	0.0-7.0	0.8485
SH	5.8±3.7 (50)	1.6-15.5	6.7±4.4 (40)	1.0-19.5	0.7278
SCD	5.1±3.3 (50)	1.2-14.7	5.5±2.7 (39)	1.9-13.0	0.9175
NH	2.4±1.1 (50)	0.9-6.0	2.4±0.8 (40)	0.7-4.2	0.7603
DFA	31.6±16.8 (49)	0.0-75.0	29.5±19.8 (39)	0.0-75.0	0.9570
PBA	26.0±17.6 (49)	0.0-75.0	25.6±14.6 (39)	0.0-50.0	0.7063
PFB	16.8±17.9 (49)	0.0-50.0	10.9±16.0 (39)	0.0-50.0	0.3342
PBB	13.3±17.0 (49)	0.0-50.0	14.1±13.8 (39)	0.0-50.0	0.3410
DC	1.3±1.5 (50)	0.0-6.0	1.3±1.3 (39)	0.0-5.8	0.3275
DP	1.8±1.2 (50)	0.0-5.7	1.7±0.8 (39)	0.2-4.2	0.1848
NBSN	2.2±1.1 (49)	1.0-5.0	2.3±0.9 (39)	0.0-4.0	0.5146
DBS	3.6±3.1 (49)	0.8-13.0	2.7±1.1 (39)	0.8-5.3	0.0866
ABS	37.9±27.5 (49)	0.0-80.0	43.8±28.1 (39)	0.0-80.0	0.1301

Figure 1. Possible American Robin nest location relation to various building configuration on the Iowa State University campus

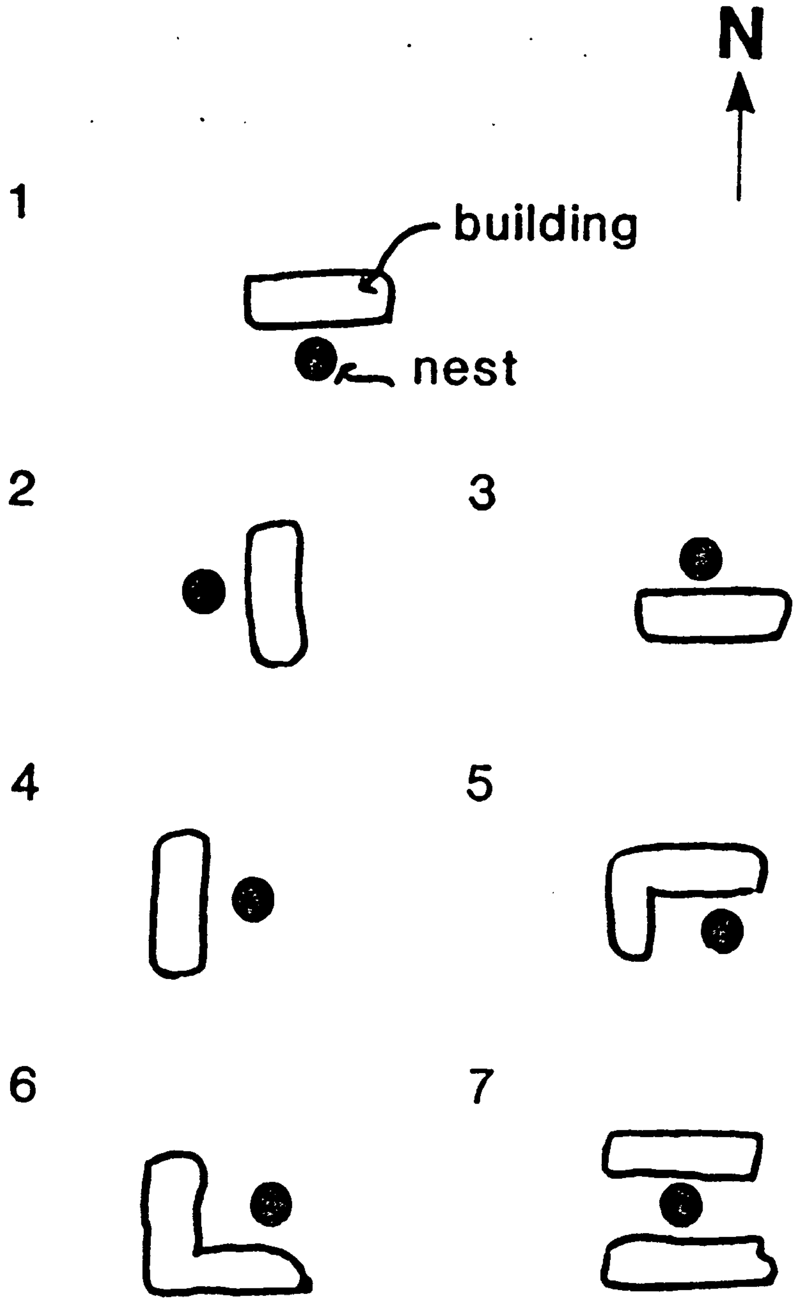

N
1
building
nest
2
3
4
5
6
7

Figure 2. Possible American Robin nest location on variously shaped branches of trees and shrubs

1: Single branch

2: Trunk fork

3: Branch fork

4: Trunk-branch axil

5: Branch-small branch axil

6: Multiple branch

Figure 3. Distribution of standardized discriminant scores for 34 early robin nest site (solid bars) and 42 late nest sites (cross-hatched bars)

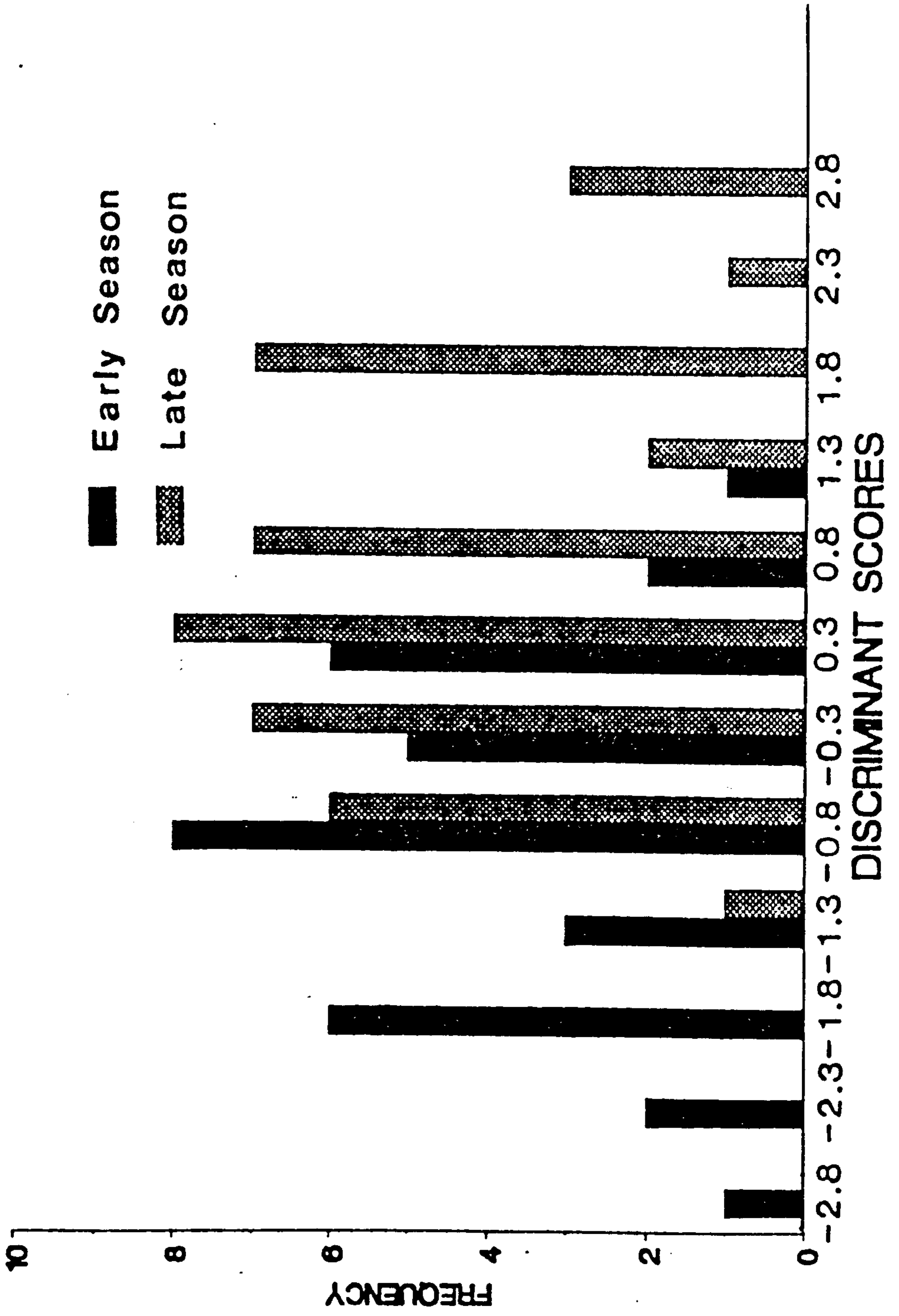

Early Season
Late Season
FREQUENCY
0
2
4
6
8
10
DISCRIMINANT SCORES
-2.8
-2.3
-1.8
-1.3
-0.8
-0.3
0.3
0.8
1.3
1.8
2.3
2.8

Figure 4. Distribution of Standardized discriminant scores for 41 successful American Robin nest sites (solid bars) and 35 failed nest sites (cross-hatched bars)

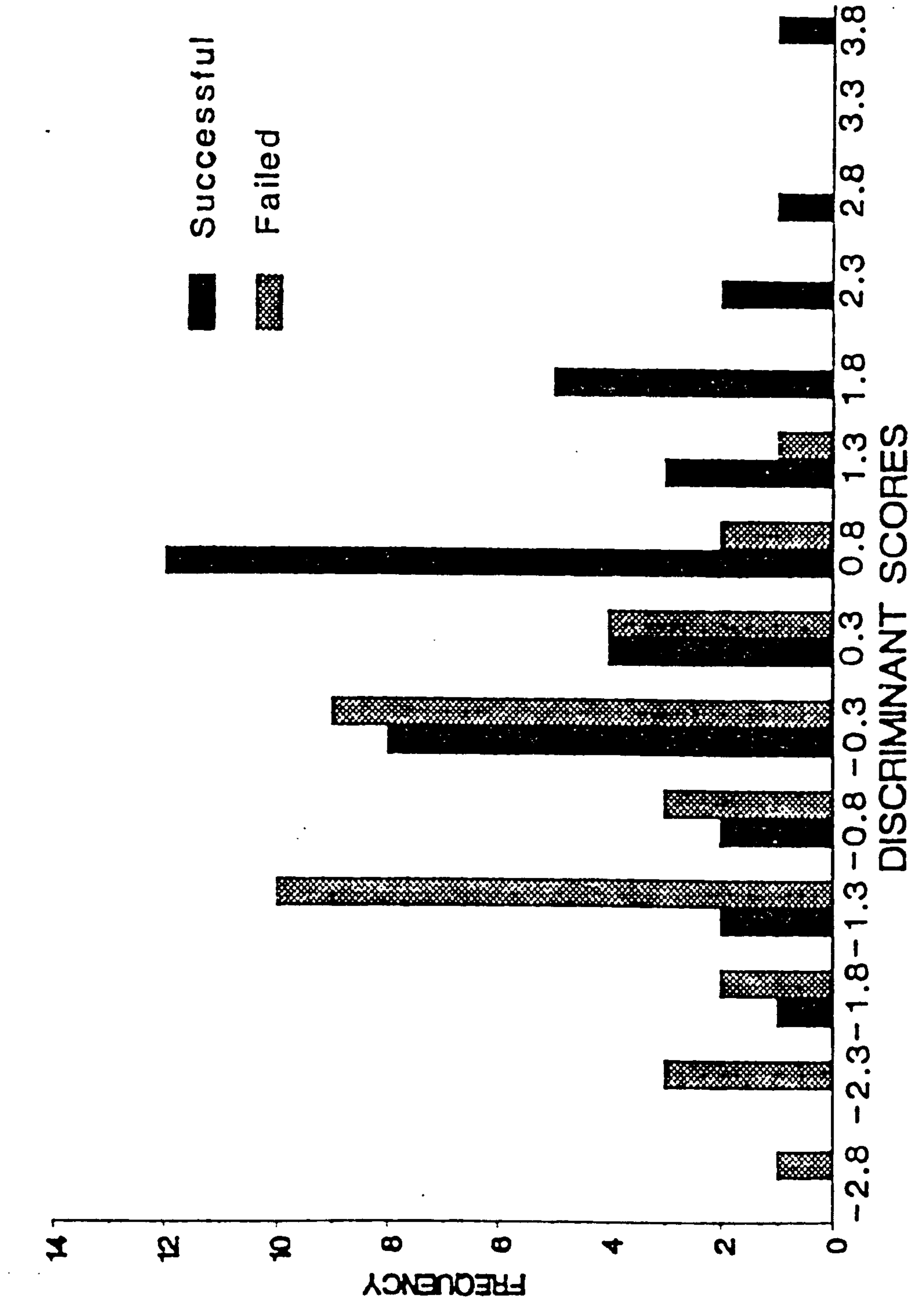
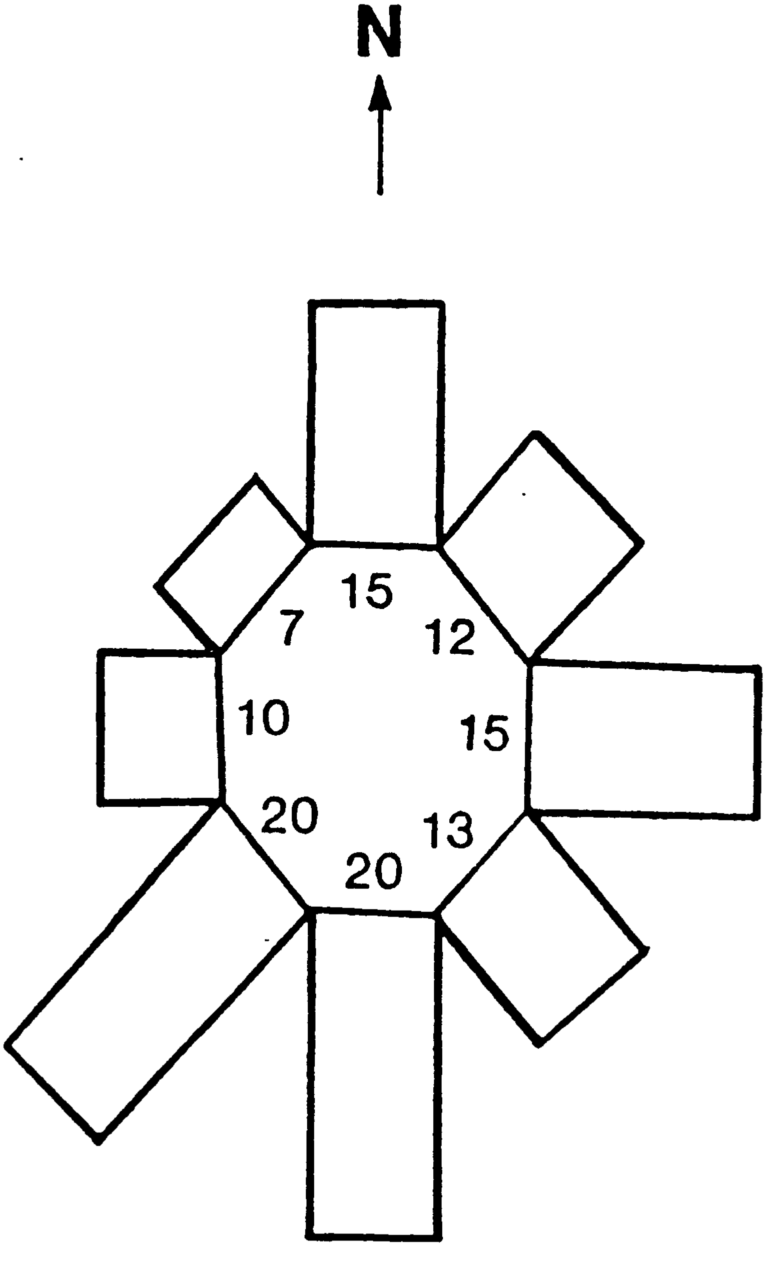

■ Successful
▨ Failed
FREQUENCY
0
2
4
6
8
10
12
14
DISCRIMINANT SCORES
-2.8
-2.3
-1.8
-1.3
-0.8
-0.3
0.3
0.8
1.3
1.8
2.3
2.8
3.3
3.8

Figure 5. Directional orientation of American Robin nests relative to the center of the supporting plant. Numbers represent the frequency of nests in each of the 8 directions


N
15
7
12
10
15
20
13
20

LITERATURE CITED

Collins, S. 1983. Geographic variation in habitat structure for the wood warblers in Maine and Minnesota. Oecologia 59:246-252.

Graber, R. R., and J. W. Graber. 1963. A comparative study of bird populations in Illinois, 1906-1909 and 1956-1958. Illinois Nat. Hist. Surv. Bull. 28:383-528.

Hespenheide, H. A. 1971. Flycatcher habitat selection in the eastern deciduous forest. Auk 88:61-74.

Howell, J. C. 1942. Notes on the nesting habits of the American Robin (<u>Turdus migratorius</u>). Amer. Midl. Nat. 28:243-247.

Kendeigh, S. C. 1963. Regulation of nesting time and distribution in the House Wren. Wilson Bull. 75:418-427.

Klimstra, W. D., and W. O. Stieglitz. 1957. Notes on reproductive activities of robins in Iowa and Illinois. Wilson Bull. 69:333-337.

Knupp, D. M., R. B. Owen, Jr., and J. B. Dimond. 1977. Reproductive biology of American Robins in northern Maine. Auk 94:80-85.

Martin, K. 1973. Breeding density and reproductive success of robins in relation to habitat structure on logged area of Vancouver Island, British Columbia. Unpublished M. S. thesis, Edmonton, University of Alberta.

Martin, T. E., and J. J. Roper. 1987. Nest predation and nest-site selection of a Western population of the Hermit Thrush. Condor 90:51-57.

Nickell, W. P. 1944. Studies of habitats, location and structural material of nests of the Robin. The Jack-Pine Warbler 22(2):48-64.

Noon, B. R. 1981. The distribution of an avian guild along a temperate elevational gradient: The importance and expression of competition. Ecol. Monogr. 51:105-124.

Rao, C. R. 1964. The use and interpretation of principal component analysis in applied research. Sankhya A, 26: 329-358.

SAS Institute Inc. 1985. SAS user's guide: Statistics, Version 5 edition. SAS Institute Inc., Cary, NC.

Stauffer, D. F., and L. B. Best. 1980. Habitat selection by birds of riparian communities: evaluating effects of habitat alteration. J. Wildl. Manage. 44:1-15.

Stauffer D. F., and L. B. Best. 1986. Nest-site characteristics of open-nesting birds in riparian habitats in Iowa. Willson Bull. 98(2):231-242.

Weller, M. W. 1971. Robin mortality in relation to Dutch elm disease control programs on the Iowa State University campus. Ia. St. J. Sci. 45:471-475.

Willson, G. D. 1978. Reproductive biology of American Robins following a Dutch elm disease control program. Proc. Ia. Acad. Sci. 85(3):91-96.

Young, H. 1955. Breeding behavior and nesting of the Eastern Robin. Amer. Midl. Nat. 53:329-352.

Yahner, R. H. 1983. Site-related nesting success of Mourning Doves and American Robins in shelterbelts. Wilson Bull. 95(4):573-580.

SECTION III:

SOME SOURCES OF VARIATION IN GROWTH OF AMERICAN ROBIN (*TURDUS MIGRATORIUS*)

ABSTRACT

Prefledging growth of nestling American Robins (Turdus migratorius) was studied in 1987 on the campus of Iowa State University. Body weight and tarsus length were measured every day after hatching, and the data were fitted to three theoretical equations (Richard, Van Berttalanfy, and Logistic) using a least squares method. The data were best explained by the logistic equation. Growth statistics (asymptote, growth rate, and inflection point) did not vary among nestlings from different clutch sizes or different brood sizes. The asymptote of body weight, but not of tarsus length, was significantly ($P < 0.05$) higher among early season broods than late season broods. Reduced food availability was believed to be the main factor accounting for the observed seasonal difference. The seasonal affect observed on body weight but not on tarsus length suggests that skeletal size is controlled more by genetic than by environmental factors.

INTRODUCTION

Studies on the growth and development of young birds provide insight into ecological and social factors such as food supply, parental care, and mortality that are important to a species during its reproductive cycle (Lack 1968; Ricklefs 1969, 1973, 1979; Case 1978). Previous studies have shown that growth and survival of nestlings can be influenced by egg size (Parsons 1970; Schifferli 1973; Ankeney 1980), brood size (Best 1977, Petersen et al. 1986; Bryant 1978; Cronmiller and Thompson 1980; Hahu 1981; Murphy 1983), and season (Best 1977, Petersen et al. 1986; Ross 1980).

Although the American Robin (*Turdus migratorius*) is abundant throughout much of North America in a wide variety of habitats including urban lawns and parks, little attention has been given to measuring its growth rate. Howell (1942) conducted a detailed descriptive study of the growth of robin nestlings, but he did not compare seasonal or brood size variation. Robins breed from Mid-March to July and have two to three broods in one breeding season (Howell 1942; Willson 1978). Clutch size ranges from one to five eggs. Given that food availability varies seasonally, and is perhaps limited, it would be interesting to know whether the growth of nestlings is influenced by season or brood size.

The objectives of this study were to describe the growth of robin nestlings, and evaluate the effect of season, egg size, and brood size on their growth.

STUDY AREA AND METHODS

The study was conducted on the campus of Iowa State University in Ames, Iowa, an area of about 87 ha similar to that described by Weller (1971) and Wilson (1977). Observations began in early spring with the arrival of robins. Nest searching began as soon as robins started to defend their territories. Nests were located by searching the vegetation and watching the behavior of breeding pairs. The field season extended from mid-March to mid-August during 1987.

The length and width of eggs were measured to the nearest 0.1 mm with a dial caliper, and the egg weight was measured with a 10-g Pesola balance graduated to the nearest 0.1 g. Nestlings were marked on the skin between dosal feather tracts with a felt-tip pen and measured every 24 hours. Body weight was measured with a 100-g Pesola balance to the nearest 0.1 g, and the length of the right tarsus was measured with a dial caliper to the nearest 0.1 mm. The progress of incubation and brood rearing were monitored to determine the eventual fate of the nests. Nests which fledged at least one young were considered successful. The breeding season was divided temporally into "early" and "late" based on the inspection of a bimodal frequency distribution of nest completion dates in which a definite break occurred on May 15.

Each bird's weight and tarsus length was fitted to three different equations (Richard, Von Berttalanfy, and Logistic) (Ricklefs 1967, 1969) using least square methods and the SAS program (SAS Institute 1985). For all statistical tests, brood means rather than individual nestlings were used as sample units because measurements of nestlings within a brood were not independent. Only birds which were measured on 4 or more dates were considered, and means were weighted by the number of birds in the nest. The first day of post-hatching life was designated as day one; thus, young aged one day were between 0 and 24 hours old.

Two-way analysis of variance was used to examine variation in growth rate and the magnitude of growth among seasons (early vs late), clutch size (2 or 3 eggs vs 4 or 5 eggs), and brood size (1, 2, or 3 young vs 4 or 5 young). Two-way analysis of variance was also used to examine variation in egg weight among seasons (early vs late) and clutch sizes (2 or 3 eggs vs 4 or 5 eggs). Egg weight was used as a covariate to correct for egg size in analyzing parameters of the model. T-tests were used to compare growth differences between clutch sizes. A probability level of $P \leq 0.05$ was preselected as an indication of statistical significance. Statistical analysis followed procedures in

Sokal and Rohlf (1980) and were carried out using SAS programs (SAS Institute Inc. 1985)

RESULTS AND DISCUSSION

The logistic growth curve was used to estimate the growth of robin nestlings because it most closely fit the data. The logistic equation is:

$$W_{(t)} = \frac{A}{1 + e^{-K(t-I)}}$$

where $W_{(t)}$ is the body weight or tarsus length at age t hours, A is the asymptotic weight achieved by the average nestling, e is the natural logarithm, K is a constant proportional to the specific rate of growth, and I is the age in hours at the point of inflection on the growth curve, or the point of maximum growth rate which occurs at one half the asymptotic weight on a logistic curve.

Egg weight was used as a covariate to correct for egg size in estimating parameters of the logistic model, but it did not result in a better fit of the data. Thus, all the analyses in growth pattern comparisons were performed excluding the egg weight as a covariate.

At hatching, robins were typically altricial hatchlings. As nestlings aged, changes in mass (Figs 1, 2) and tarsus length followed the sigmoid pattern found for robins (Howell

1942) and many others passerines (Ricklefs 1969).

The growth patterns of nestling body weight and tarsus length were not significantly different between clutch sizes and seasons (Table 1). A significant interaction occurred between clutch size and season; large clutches had a lower asymptote than small clutches in the early part of the season but a larger asymptote in late season. The interaction is believed to be spurious.

In an analysis comparing brood size and seasonal effects, the asymptote of body weight, but not of tarsus length, for early season nestlings was significantly higher ($P < 0.05$) than that of late season nestlings (Fig. 1). However, the growth rates of both measures were the same ($P > 0.05$) between early and late season nestlings (Tables 2, 3 and Fig. 2).

Earlier workers reported that egg weight has a significant effect on growth (Schifferli 1973; Skoglund et al. 1952). In this study, no differences were detected in egg size between early and late seasons, and between large and small clutch sizes ($F_{1,22} = 0.07$, $P = 0.79$; $F_{1,22} = 0.04$, $P = 0.84$ respectively). Therefore, egg size was not a factor responsible for the observed variation in body weight.

Seasonal variation in food abundance was probably the most important factor accounting for the seasonal difference in the asymptote of body weight. The late season of 1987 was much drier than the early season, and the lack of rainfall undoubtedly affected the availability of earthworms (*Lumbricus* sp) which are an important food source during the breeding season (Wheelwright 1986; Satchell 1983). Robins were observed feeding their young with substitutes such as various fruits which are low in protein. In other words, limited food or food low in protein may affect nestling growth and eventually have an effect on the observed asymptote (Ricklefs 1976). Van Balen (1973) and Bryant (1975) have documented a significant relationship between nestling asymptote weight and food abundance for several passerine species. Also, when weather conditions affect the abundance or availability of a food supply, marked effects can be found on parental feeding success (Dunn 1973) and growth of young (Dunn 1975).

It is also possible that higher temperatures in the late season may inhibit nestling growth (Petersen et al. 1986; Murphy 1985). The maximum daily temperature in this study gradually increased throughout the breeding season (April: 20° C, May: 27° C, June: 30° C, and July: 30° C).

That growth in body weight and tarsus length were stastitically the same in both large and small broods (Tables 1, 2) is consistent with Cronmiller and Thompson's (1980) study of Red-winged Blackbirds but different from several other studies in which increasing brood size inversely affected growth parameters (Van Balen 1973; Best 1977; Howe 1976, 1978; Bryant 1978; Ross 1980). In most of these studies, the effect of brood size on growth was attributed to differences in the nestlings' nutrition or thermal environment. Brood size in this study did not influence robin's growth (Tables 1, 2) but the data are biased. Nestlings which starved and later disappeared from nests were excluded from the analysis because they lacked the required minimum of four measurements. Starvation in most of these cases was probably influenced by brood size because larger siblings survived. Robin nests are more insulated than those of other passerines because of a thick mud layer around the nest (Skowron and Kern 1980). Therefore, the development of the tarsus in nestling robin was not affected by the differential surface/volume ratio between brood sizes.

Tarsus length did not vary with season, clutch size or brood size (Tables 1, 3), which suggests that skeletal size is controlled more by genetic than by environmental factors. However, Brookes and May (1972) found that growth of the tarsus varied with temperature differences in precocial domestic chickens.

Table 1. Comparison of growth rate (K) and asymptote (A) of body weight and tarsus length of nestling robins in relation to season and clutch sizes using two-way analysis. Significant ($P \leq 0.05$) F-value is underlined

		Body weight		Tarsus length	
Source	df	K	A	K	A
Season (S)	1	0.24	2.43	0.54	0.70
Clutch size (CL)	1	0.06	0.70	0.26	0.18
S X CL	1	2.71	4.92	0.06	0.03
Residual	23				

Table 2. Comparison of growth rate (K) and asymptote (A) of body weight and tarsus length of nestling robins in relation to season and brood sizes using two-way analysis. Significant ($P \leq 0.05$) F-value is underlined

		Body weight		Tarsus length	
Source	df	K	A	K	A
Season (S)	1	2.00	<u>5.68</u>	1.35	1.22
Brood size (BR)	1	1.00	1.25	0.06	0.00
S X BR	1	0.30	<u>0.55</u>	1.23	0.02
Residual	23				

Table 3. Comparison of growth rate (K) and asymptote (A) of body weight and tarsus length of nestling robins for large (4, 5 young) and small brood (1, 2, 3 young) and early and late seasons. Only the dfference between early and late season mean asymptote of body weight was significant ($P \le 0.05$). Mean was reported as mean±SD

	No. of broods	Body weight		Tarsus length	
		Growth rate (g/hour)	Asmyptote (g)	Growth rate (mm/hour)	Asymptote (mm)
Brood size					
Small	13	0.0227±0.0008	60.7±1.7	0.0167±0.0004	37.5±0.8
Large	14	0.0215±0.0007	58.1±1.6	0.0163±0.0004	37.7±0.8
Season					
Early	7	0.0213±0.0010	62.2±2.0	0.0169±0.0005	37.0±1.0
Late	20	0.0229±0.0006	56.7±1.2	0.0162±0.0003	38.3±0.6

Figure 1. Estimated curves from logistic equation fitted to growth data for 7 early and 20 late season broods of nestling American Robins. The first body weight for each nestling was recorded between 0 to 24 hours after hatching

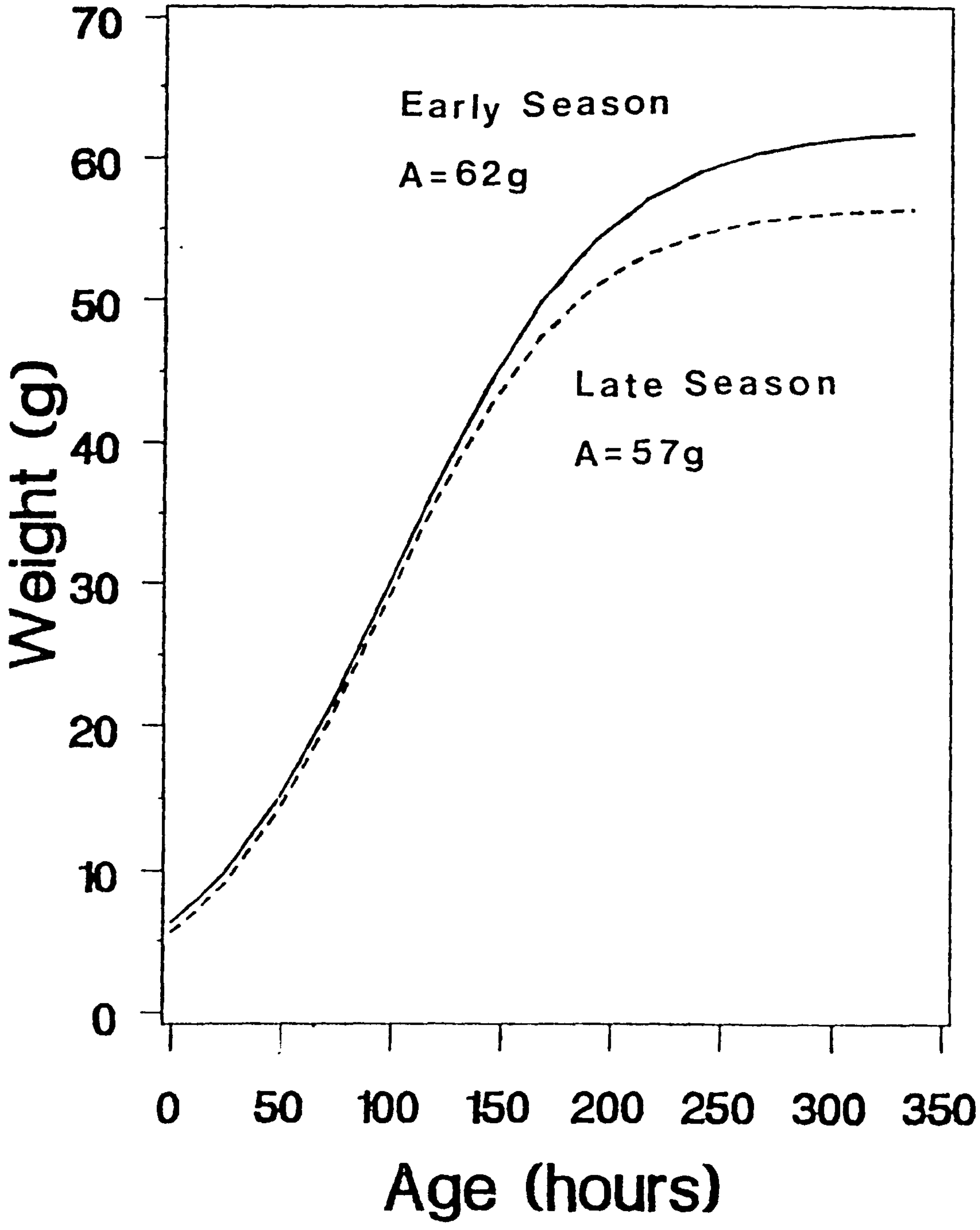
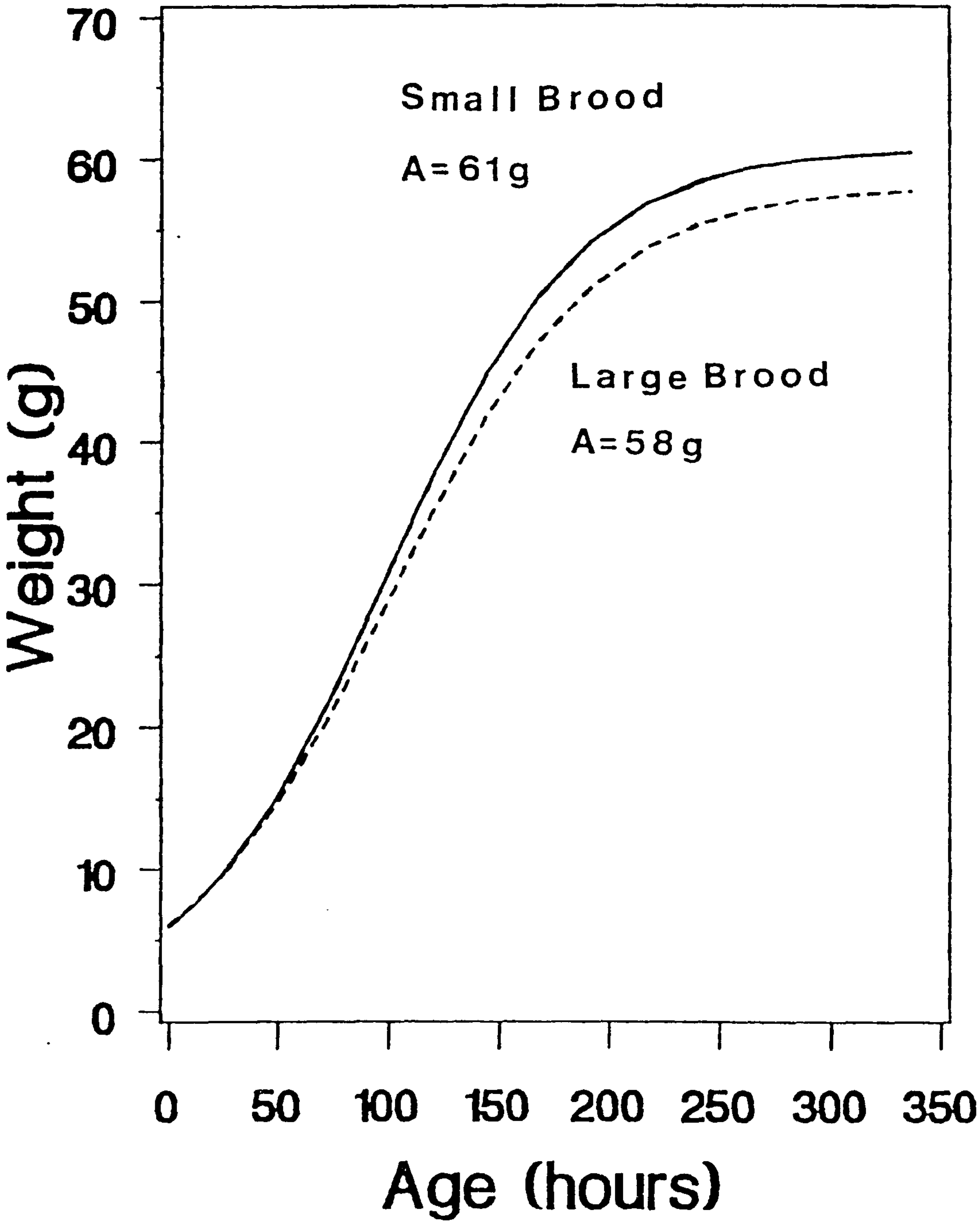

70
60
50
40
30
20
10
0
Weight (g)
0
50
100
150
200
250
300
350
Age (hours)
Early Season
A=62g
Late Season
A=57g

Figure 2. Estimated curves from the logistic equation fitted to growth data of 13 small and 14 large broods of nestling American Robins. The first body weight for each nestling was measured between 0 to 24 hours after hatching


Small Brood
A=61g
Large Brood
A=58g
Weight (g)
0
10
20
30
40
50
60
70
0
50
100
150
200
250
300
350
Age (hours)

LITERATURE CITED

Ankeney, C. D. 1980. Egg weight, survival and growth of Lesser Snow Goose Goslings. J. Wildl. Manage. 44:174-182.

Best, L. B. 1977. Nestling biology of the Field Sparrow. Auk 94:308-319.

Brookes, M., and K. U. May. 1982. The influence of temperature on bone growth in the chick. J. Anat. 111:351-363.

Bryant, D. M. 1975. Breeding biology of House Martins Delichon urbica in relation to aerial insect abundant. Ibis 117:180-216.

Bryant, D. M. 1978. Environmental influences on growth and survival of nestling House Martins (Delichon urbica). Ibis 120:271-283.

Case, T. J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. Q. Rev. Biol. 53:243-273.

Cronmiller, J. R., and C. F. Thompson. 1980. Experimental manipulation of brood-size in Red-winged Blackbirds. Auk 97:559-565.

Dunn, E. K. 1973. Changes in fishing ability of terns associated with windspread and sea surface condition.

Nature 244:520-521.

Dunn, E. K. 1975. The role of environmental factors in the growth of tern chicks. J. Anim. Ecol. 44:743-754.

Hahu, D. C. 1981. Asynchronous hatching in the Laughing Gull: Cutting losses and reducing rivalry. Animal Behaviour 29:421-427.

Howe, H. F. 1976. Egg size, hatching asynchrony, sex and brood reduction in Common Grackle. Ecology 57:1195-1107.

Howe, H. F. 1978. Initial investment, clutch size, and brood reduction in the Common Grackle (Quiscalus quiscula L.). Ecology 59:1109-1122.

Howell, J. C. 1942. Notes on the nesting habits of the American Robin. Am. Midl. Nat. 28:529-603.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuem, London, England. 409 pp.

Murphy, M. T. 1983. Clutch size in the Eastern Kingbird: Factors affecting nestling survival. Auk 100:326-334.

Parsons, J. 1970. Relationship between egg size, and post-hatching chick mortality in the Herring Gull, Larus argentatus. Nature 228:1221-1222.

Petersen, K. L., L. B. Best, and B. M. Winter. 1986. Growth of nestling Sage Sparrows and Brewer's Sparrows. Wilson Bull. 98:535-546.

Ricklefs, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology 48:978-983.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithson. Contr. Zool. 9:1-48.

Ricklefs, R. E. 1973. Patterns of growth in birds. II. Growth rate and mode of development. Ibis 115:177-201.

Ricklefs, R. E. 1976. Growth rates of birds in the humid New World Tropics. Ibis 118:179-207.

Ricklefs, R. E. 1979. Patterns of growth in birds. V. A comparative study of development in the Starling, Common Tern, and Japanese Quail. Auk 96:10-30.

Ross, H. A. 1980. Growth of nestling Ipswich Sparrows in relation to season, habitat, brood size, and parental age. Auk 97:721-732.

SAS Institute Inc. 1985. SAS user's guide: Statistics, Version 5 edition. SAS Institute Inc., Cary, NC.

Satchell, J. E. 1983. Earthworm ecology. Chapman and Hall Ltd. 495pp.

Schifferli, L. 1973. The effect of egg-weight on the subsequent growth of nestlilng Great tits, Parus major L. Ibis 115:549-558.

Skoglund, W. C., K. C. Seegar, and A. T. Ringrose. 1952. Growth of broiler chicks hatched from various sized eggs when reared in competition with each other. Poult. Sci. 31:796-799.

Skowron, C., and M. Kern. 1980. The insulation in nests of selected Noth American songburds. Auk 97:816-824.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. 2nd edition. W. H. Freeman and Company. 859 pp.

Van Balen, J. H. 1973. A comparative study of the breeding ecology of the Great Tit Parus major in different habitats. Ardea 61:1-93.

Wheelwright, N. T. 1986. The diet of American Robins: An analysis of U. S. biological survey records. Auk 103:710-725.

Weller, M. W. 1971. Robin mortality in relation to Dutch elm disease control programs on the Iowa State University campus. Iowa. State. J. Sci. 45:471-475.

Willson, G. D. 1978. Reproductive biology of American Robins following a Dutch elm disease control program. Proc. Ia. Acad. Sci. 85:91-96.

SUMMARY AND CONCLUSIONS

Nesting success, site selection and nestling growth of the American Robin were studied in 1987 on the Iowa State University campus. Overall nest success estimated by the Mayfield method was 41.2 % and success for the 12-day neslting period (77.5 %) was significantly higher ($P < 0.05$) than 13-day incubation period (53.6 %). Daily survival rates of nests did not differ between small and large clutches, but nests on buildings had a significantly lower survival rates than nests placed in vegetation. Nearly all nests on buildings were active in the early part of the season, but early season nests placed in trees and shrubs were also less successful than late season nests. Predation was the major source of mortality for eggs, whereas predation and starvation caused most of the losses of nestlings.

Robins nested on buildings and in a wide variety of trees and shrubs. Buildings and evergreens were used more often in the early half of the season whereas deciduous trees were chiefly used in the late half the season. Principal component analysis indicated that tree size and foliage cover immediately surrounding the nest were variables that consistantly characterized robin nest sites.

Discriminant function analysis detected significant differences in nest site characteristics of successful and failed nests and of early and late season nests. Robins did not orient their nests in vegetation in any special direction from the plant's main trunk, and nest success was independent of orientation, building configuration and the nature of the nest support. Although shade was not measured and analyzed as a nest site variable, it can be inferred from the data and general observation that shade may be very important in seasonal variation in nest site selection.

The growth pattern of robin nestlings can best be explained by a logistic equation. Asymptotic weight was significantly higher among early season broods than late season broods. The seasonal observed difference was possibly caused by reduced rainfall and high air temperatures which affected availability of food and foraging efficiency of parents. Variation in clutch and brood size had no effect on growth in body mass. Tarsus length did not vary with season, clutch size, or brood size, which suggests that skeletal size is controlled more by genetic than by environmental factors.

ACKNOWLEDGEMENTS

I am grateful to Dr. Erwin E. Klaas, my major professor, for his guidance, support, encouragement, and assistance in every phase of this study. I thank Drs. Louis Best and Kenneth Shaw for their service on my graduate committee; also Dr. David Cox provided helpful advice on statistical analysis. I thank Steve Ruthbun for his patience and many hours of statistical advice and insight into avian ecological study. Many thanks go to the animal ecology graduate students who provided stimulating conversation and lasting friendship. Thanks also to Susan Davis for reading my manuscript.

I am grateful to my husband, Kam, who has provided invaluable understanding and help throughout my graduate program. I couldn't have done it without his companionship. Above all, I thank my parents, Ming-Fu and Jin-Wei, my sister, Chiung-Ru who provided constant support for my interest. Also, my grandmother, now 88, a strong lady who has given me countless encouragement.

ADDITIONAL REFERENCES

Brady, E. 1962. A partial woody flora of Iowa State Univeristy campus. Unpub. Nat. Sci. Found. Proj, Washington, D. C.

Howell, J. C. 1942. Notes on the nesting habits of the American Robin (Turdus migratorius). Am. Midl. Nat. 28:243-247.

Kemper, D. L., and J. M. Taylor. 1981. Seasonal reproductive changes in the American Robin (Turdus migratorius L.) of the Pacific Northwest. Can. J. Zool. 59(2):211-217.

Klimstra, W. D., and W. O. Stieglitz. 1957. Notes on reproductive activities of robins in Iowa and Illinois. Wilson Bull. 69:333-337.

Mayfield, H. 1961. Nesting success calculated from exposure. Wilson Bull. 73:255-261.

Mayfield, H. 1975. Suggestion for calculating nesting success. Wilson Bull. 87:456-466.

Nickell, W. P. 1944. Studies of habitats, location and structural material of nests of the Robin. The Jack-Pine Warbler 22(2):48-64.

Weller, M. W. 1971. Robin mortality in relation to Dutch elm disease control programs on the Iowa State

University campus. Iowa State J. Sci. 45:471-475.

Willson, G. D. 1978. Reproductive biology of American Robins following a Dutch elm disease control program. Proc. Ia. Acad. Sci. 85(3):91-96.

Young, H. 1955. Breeding behavior and nesting of Eastern Robin. Am. Midl. Nat. 53:329-352.