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ROBERTSON, RALEIGH JOHN
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OPTIMAL NICHE SPACE
OF THE
REDWINGED BLACKBIRD

by

Raleigh J. Robertson

A DISSERTATION PRESENTED TO THE FACULTY OF
THE GRADUATE SCHOOL OF YALE UNIVERSITY
IN CANDIDACY FOR THE DEGREE OF
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1971

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SUMMARY

The survival value of different parts of the fundamental niche of the Redwinged Blackbird was determined by comparing nesting success and the factors that affect it in marsh and upland breeding habitats. The results support the hypothesis that where sympatric, Redwings are being excluded from their optimal niche space by Yellowheaded Blackbirds.

I. Nesting success in marsh and upland habitat. Marsh nesting populations had greater nest success than those in uplands due to a larger proportion of nests destroyed by predators in upland habitats. Predation pressure on marsh nests was negatively correlated with the depth of water beneath the nest.

The structure and phenology of marsh vegetation plays an important role in providing an abundance of song perches, structural reference for delineating territories, and nest support early in the spring thus making possible dense and synchronous nesting. Upland nesting is delayed and protracted as spring growth makes the necessary structure available sequentially.

It is considered unlikely that genetic separation exists between marsh and upland populations. It is proposed that habitat selection involves a degree of site tenacity by adults and selection for optimal habitats by first time breeders.

The relationships between density, nest success, and the function of territoriality lead to the conclusion that territorial behavior limits breeding density.

II. Spatial and temporal patterns of nesting activity and success. Nesting colonies of Redwings in marshes are larger and tend to be more synchronous than colonies in upland habitats of comparable area. These variations in timing are probably correlated with the phenology of the vegetation and not with the size of the breeding colony. Earlier nesting may be selectively advantageous due to a seasonal trend of increasing predation.

The survival value of large colony size and synchronous nesting, for Redwings in the colonies studied, was a reduced predation rate on a percentage basis due to the presence of a large number of prey. The Holling predation model is applied as a possible interpretation of predation rates on different sized nesting colonies.

III. Growth rate and food of nestlings in marsh and upland habitats. Growth rate and the incidence of starvation are similar for Redwing nestlings in marsh and upland habitats. It is suggested that the relative abundance of food is approximately the same for nestlings in either marshes or uplands, but that a higher absolute abundance of food in marshes makes large dense nesting colonies possible. The relationship between nesting density and food supply is not simple because obvious differences in the phenology of vegetation used as nest support are also correlated with colony size and density.

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OPTIMAL NICHE SPACE OF THE REDWINGED BLACKBIRD

I. NESTING SUCCESS IN MARSH AND UPLAND HABITAT

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Competition between species is often credited with playing a major role in determining the structure of ecological communities. The natural control, distribution, and evolution of populations, species diversity and community structure are often considered to be greatly influenced by, if not a product of, competitive interactions. Yet there are relatively few documented examples of interspecific competition in natural communities (Miller 1967); most evidence of interspecific interactions being indirect, derived from observations on distribution patterns inferred as an effect of competition (Hutchinson 1957).

To establish that competition is a factor influencing the spatial distributions of two species, it is first necessary to demonstrate that there is significant overlap in their fundamental niches and that the realized niches of one or both species represents less niche space than that species can potentially occupy (Miller 1967). When competitive exclusion does occur, often by interference with access to a resource, it imposes some limitation on the population size and distribution of the excluded species. The extent of this limitation must be some function of the relative volume and survival value of the niche space from which the species is excluded compared with that of the realized niche space. Therefore, in order to fully understand the conditions of competition between species and the effect of competitive exclusion on limiting population size, the survival value of different parts of the

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species' fundamental niche must be appraised.

Niche Space

The model of a fundamental niche proposed by Hutchinson (1957) provides a useful conceptual framework for evaluating the competitive relationships between species. The fundamental niche of a species can be considered as an n-dimensional hypervolume existing in an abstract N space. Each dimension of the hypervolume covers that range of an environmental variable which permits survival of the species S_1. The n environmental variables correspond to those ecological factors that affect S_1. Described in this way, every point in the hypervolume N_1 corresponds to a state of the environment which would permit species S_1 to exist indefinitely. If N_1 and N_2 are the fundamental niches of species S_1 and S_2 respectively, they may be separate, having no points in common. Intersecting fundamental niches, in which $N_1 \cdot N_2$ is the subset of points common to N_1 and N_2 include those in which (1) N_2 is the proper subset of N_1 and (2) $N_1 \cdot N_2$ is the proper subset of both N_1 and N_2 (Figure 1). The former case has been described as an "included niche" and the latter as an "overlapping niche" (Miller 1967).

Intersecting niches provide the necessary conditions for competitive interactions. The outcome of interactions for case 1 and case 2 depends on the competitive ability of the species involved and includes the possibilities

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Figure 1. Relationships between fundamental niches that provide the neccessary conditions for competition (after Miller 1967). These niche diagrams should be conceptualized as a projection of an n-dimensional hypervolume on a two-dimensional plane.

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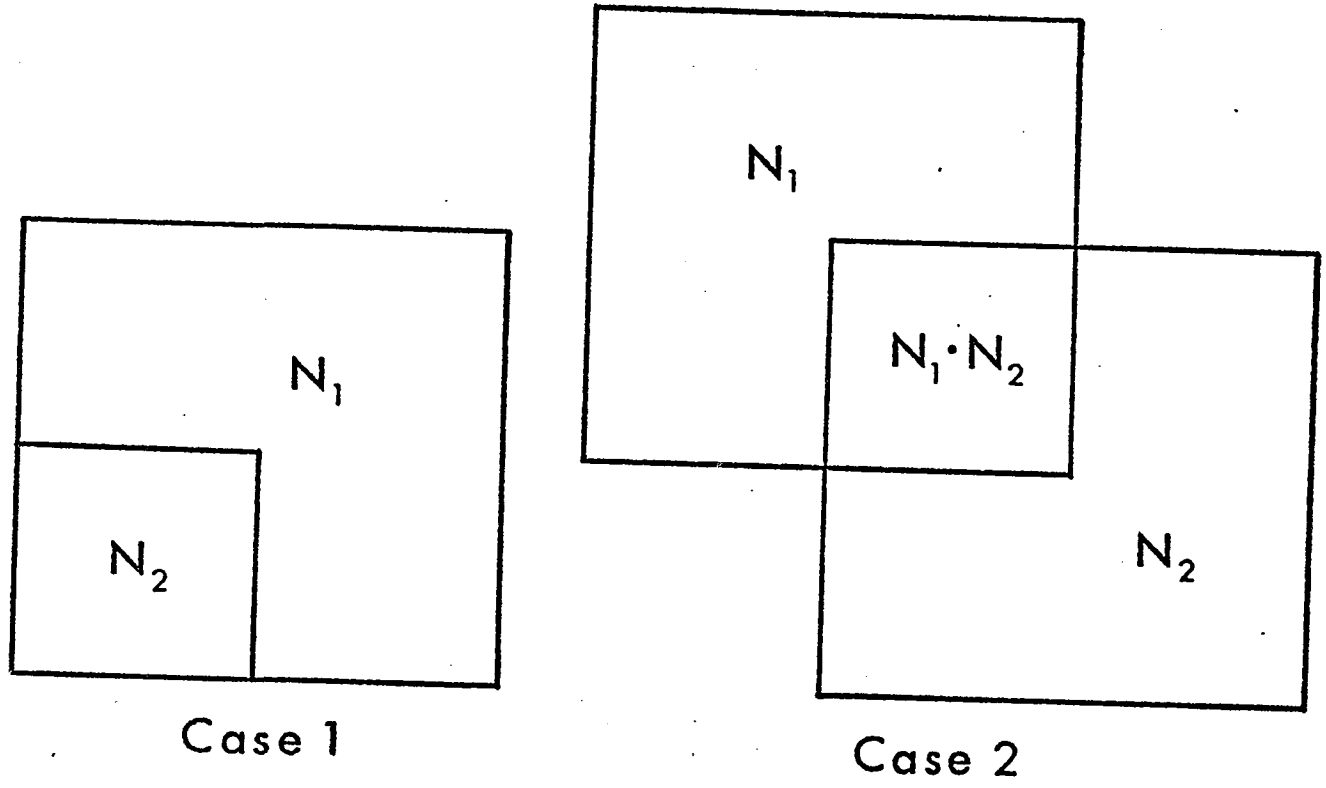

shown in Table 1.

One of the limitations of the set-theoretic model is that all points in each fundamental niche imply equal probability of survival and all points outside each niche imply zero probability of survival of the relevant species. However, as a rule there will be an optimal part of the niche with markedly suboptimal conditions near the boundaries (Hutchinson 1957). A more realistic concept of the niche might therefore have abstract boundaries determined by probabilities of survival, the chance of survival varying between different subunits within the hypervolume. Slobodkin (1961) considers such a "probability of survival" space in n-dimensions and Levins (1968) referred to this concept of the niche as a "fitness measure on an environmental space." In a two-dimensional projection, the niche hypervolume would be comprised of gradients from optimum to suboptimum conditions for survival with respect to the various niche parameters. Such an n-dimensional "topographic volume" would have isoclines of suitability of the niche space to the species. This would be the counterpart of "Sewall Wright Diagrams" in which the isoclines are of the adaptiveness of the species to the environment (Wright 1932).

Competitive interactions or direct interference can diminish the volume of niche space that a species realizes. Conversely, population pressure, resulting from either inter- or intraspecific competition, can constitute a

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Table 1. Outcome possibilities for competitive interactions of species with included or overlapping fundamental niches

Case	Species	Fundamental Niche	Competitive Relationship	Realized Niche
1.	S_1	N_1	$S_1 > S_2$	N_1
	S_2	N_2		Excluded
	S_1	N_1	$S_2 > S_1$	$N_1 - N_2$
	S_2	N_2		N_2
2.	S_1	N_1	$S_1 > S_2$	N_1
	S_2	N_2		$N_2 - (N_1 \cdot N_2)$
	S_1	N_1	$S_2 > S_1$	$N_1 - (N_1 \cdot N_2)$
	S_2	N_2		N_2

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selective force causing the extension of occupancy into suboptimal parts of the niche (Svärdson 1949) and favoring the expansion of the boundaries of the realized or fundamental niche.

The direction of the outcome of competitive interactions often depends on the survival value of the niche space in which competition occurs (cf. Lack 1947, Park 1954). The variable influence of different combinations of niche parameters on the outcome of competition is an expected consequence of the fact that the ability to endure conditions which are unfavorable with respect to one environmental factor may be modified by the action of another factor (Moore and Kitching 1939, Hutchinson and Deevey 1949). This would imply that a species is competitively superior in the optimal part of its niche space because a species will be better able to withstand competition in that habitat for which it is best suited. Thus Svärdson (1949) suggested that interspecific competition would cause species to retreat to their respective adaptive peaks and concluded that exclusion would usually be from a marginal part of the excluded species' habitat range. Hutchinson (1959) considered it most likely that an invader would compete successfully only for a marginal part of the established species' fundamental niche. This would almost certainly be the case when the optimal parts of the niches of competing species do not coincide, but it is not possible for both species to "retreat to their

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adaptive peak" when their optimal niche space or adaptive peaks do coincide. Accordingly, Willis (1966) found, in testing Svärdson's hypothesis, that the directions and force of interspecific competition and the opportunities available to a species probably determine whether the species narrows its niche to include only the optimal niche space, shifts to another adaptive peak, widens its niche space, or is completely excluded.

Niche relationships that fit the model of the "included niche" usually suggest a coincidence of optimal niche space of the two species involved. Although the frequency of occurrence in nature of a truly included niche is not known, since for no species have all niche parameters been defined, there are a number of cases that fit the included niche model when only the few niche parameters apparently significant in competitive interactions are considered. Many of these have been reviewed by Miller (1967) and in most cases the relationships indicate that the included portion of the larger fundamental niche has higher survival value to the excluded species than those parts of the niche space to which the species is excluded. Yet the relative survival value of different parts of a fundamental niche is usually only inferred by observations of habitat preference. Very little attention has been given to quantitative measures of the comparative survival value of different parts of a species' niche hypervolume.

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Niche Space of Redwings and Yellowheads

Studies of competitive interactions between Redwinged Blackbirds (Agelaius phoeniceus) and Yellowheaded Blackbirds (Xanthocephalus xanthocephalus) have shown that in the zone of sympatry, Yellowheads exclude Redwings from breeding habitats which correspond to the included fundamental niche of the Yellowhead (Miller 1968). Competition by interference with access to a resource in the form of interspecific territoriality results in the exclusion of the Redwing by the Yellowhead from central parts of large marshes (Linsdale 1938, Fautin 1940, Willson and Orians 1963, Orians and Willson 1964, Weller and Spatcher 1965, Willson 1966, Miller 1968, Burt 1970). This nesting habitat and its associated niche parameters is represented by N_2 in case 1 in Figure 1. Under these conditions, the realized niche of the Redwing is the difference subset (N_1-N_2) of the fundamental niches of the two species. In terms of habitat, this niche space (N_1-N_2) corresponds to the marsh edge, riparian situations, and upland fields, those nesting situations suitable for Redwings but apparently unsuitable for Yellowheads.

This included niche relationship implies (1) that the niche space of the Redwing corresponding to the subset N_2 is preferred and (2) that in allopatric populations of Redwings this niche space would have higher survival value. These implications are supported by observations on nesting density and the chronology of territory establishment.

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The Redwing has long been considered to prefer nesting in marsh habitat (Bent 1958) and comparisons reveal higher nesting density in marsh than upland habitat (Graber and Graber 1963, Case and Hewitt 1963). In the zone of sympatry Redwings arrive in the spring prior to Yellowheads and establish territories on marshes, providing further evidence of a preference for marsh habitat (Miller 1968). However, upon the arrival of the Yellowheads, the Redwings are displaced.

In order to understand the conditions of competition between Redwings and Yellowheads, it is important to know whether the two species use different parts of the niche space in the absence of competition (Miller 1968). Also, to evaluate the effect of the competitive exclusion on the distribution and abundance of Redwings it is necessary to appraise the survival value of different parts of the fundamental niche of the Redwing.

The objectives of this study were to (1) determine what nesting habitat represents the optimal part of the fundamental niche of the Redwing with respect to nesting and production of young and (2) delineate those niche parameters responsible for the survival value of nesting in a particular habitat.

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METHODS

Marsh nesting habitat and its associated niche parameters was used to represent the included portion (N_2) of the Redwing fundamental niche and upland habitat and the associated niche parameters represented the difference subset (N_1-N_2). Survival value was measured using several indices of nesting success; various factors resulting in egg and nestling mortality were considered as niche parameters affecting the survival value of niche space. Differential mortality of adult birds, or of young birds after fledging, are also factors that affect the survival value of a nesting habitat. No data were obtained on these aspects of the nesting ecology of Redwings, however, there is no evidence to suggest that patterns of mortality for adults or fledglings would be different than for nestlings in marsh and upland habitats respectively.

The study was done in Connecticut, outside the zone of sympatry of Redwings and Yellowheads, where Redwings can express their full range of nesting habitat preference without interference from Yellowheads. The principal study areas were two fresh-water cattail marshes and three upland hayfields, all of which supported breeding colonies of Redwings. Observations were made during the nesting seasons of 1968, 1969, and 1970. Throughout the nesting season, an attempt was made to visit each nesting habitat every three days. This schedule was maintained except during cold rainy weather when flushing a brooding female might

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increase mortality of nestlings. Visits by observers had no noticeable effects in terms of causing egg or nestling mortality. Marsh nests were reached by wading except in the deep parts of Clarkes Pond where a canoe was used. As new nests were located, usually during nest construction or egg laying, they were marked by placing a numbered bamboo pole at a distance of 3-4 m in a known direction from the nest. This allowed easy relocation, and placing the pole at a distance from the nest was thought to reduce the likelihood of predators using the markers as clues for finding nests. Water depth, nest height, and the type of vegetation used as nest support were recorded for each new nest. On subsequent visits each nest was checked and the following data were recorded; (1) state of nesting progress, (2) number of eggs or nestlings, (3) nestling weight, (4) nestling tarso-metatarus length (1970 only), (5) occurrence of mortality and its cause, and (6) occurrence of successful fledging. Individual recognition of nestlings was achieved by marking combinations of anterior or posterior, right or left tarsi with a permanent waterproof felt tip marking pen. Weights, to the nearest gram, were measured by placing the nestling in a plastic cup (10 g tare weight) and weighing with a 100 g capacity Pesola spring balance. Tarso-metatarsus length to the nearest 0.1 mm was measured with vernier calipers using the method described by Kalma (1970).

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During the 1968 and 1969 nesting season measurements of egg dimensions were made for the purpose of examining the relationships between clutch size and egg volume (Robertson and Miller in prep.).

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NESTING HABITAT

Marsh

1. Clarkes Pond, a man-made impoundment on the Mill River in Hamden, Connecticut, covers an area of 4.65 ha of which 1.92 ha is occupied by emergent vegetation and 2.73 ha is open water with some pond lily (Nymphaea), pickerelweed (Pontederia), and arrowhead (Sagittaria). The 1.92 ha of emergent vegetation consists of several recognizable units. Two species of cattail, 0.53 ha of Typha latifolia and 0.54 ha of T. angustifolia, form contiguous but discrete patches. An additional patch of 0.39 ha of T. latifolia forms a very dense stand and except during periods of high water the substrate in this area is quite dry. Along the shore opposite the large stands of cattail are narrow strips of cattail patches totaling 0.14 ha. There is also a small part of the marsh, 0.32 ha, separated from the main part by the channel of the Mill River. The cattail stands are bordered by open water on the pond side and mixed deciduous woodlands on the shore. Within 500 m of Clarkes Pond is a mature plantation of white pine, a small horse pasture, a large mowed field, and extensive stands of mixed deciduous woodland, all of which served as sources of either food or nesting material.

The water depth in Clarkes Pond gradually decreased during the nesting season but was occasionally raised by heavy rains. The average depth of water under nests in

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emergent vegetation was about 42 cm.

2. All Saints Marsh, located about 10 miles northeast of New Haven, Connecticut, is a cattail marsh in the late stages of pond succession. It has an area of 1.09 ha, all of which is occupied by emergent vegetation. Typha latifolia forms a moderately dense stand interspersed with patches of open water. Buttonbush (Cephalanthus occidentalis) forms a dense tangle in some areas and there are scattered bushes throughout the marsh. These are often used for nest support.

All Saints Marsh has no flowing inlet, but in spring and early summer there is a trickling outflow apparently fed by springs in the marsh. During the nesting season, the water depth in the marsh averaged 30-40 cm. In some years the marsh dries up in August. This may account for an apparently low abundance of emergent aquatic insects in this marsh compared with Clarkes Pond. All Saints Marsh is surrounded on two sides by quite extensive stands of mixed deciduous woodland, and on two sides by weedy fields in early stages of old field succession.

In both marshes muskrats have a significant influence on the pattern of vegetation by opening channels and preventing the formation of extremely dense stands of cattail. They may actually improve the quality of the habitat for Redwing nesting (Weller and Spatcher 1965). Comparisons

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of nesting density indicate the patchy stands of cattail with interspersed patches of open water are preferred over dense homogeneous stands of cattail.

The structure of the marsh vegetation is an important feature in the breeding ecology of Redwings. The visual and vocal communication used in maintaining the Redwing's nesting system of grouped territories (Lack 1968) or neighborhoods (Crook 1964) is adapted to a habitat with a relatively uniform height of vegetation with an open view over the top (cf. Crook 1964). In undisturbed marshes the height and structural configuration of the vegetation is constant throughout the nesting season. Prior to the growth of new vegetation in the spring, the dead but sturdy cattail growth from previous seasons provides structure for delineating territories, for use as song perches, and for nest support. The growth of new vegetation does little to change the basic structure of the marsh, the most significant change being an increase in the density of the structure and better camouflage of nests.

Upland

1. Hyland Farm is an upland hayfield with an area of 2.68 ha on the property of Mr. Clarence Hyland in North Branford, Connecticut. The field has been in a government crop diversion program for several years so that, with the cooperation of Mr. Hyland, this hayfield was not mowed until mid-July, after the last young Redwings had fledged.

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bordered on the two long sides by hayfields with good stands of "hay" species and few "weed" species. One short edge is bordered by a road and the other by a golf course. Across one of the adjacent hayfields, at a distance ranging from about 100-400 m from any point in the study area, is a large stand of mixed deciduous trees bordering a small stream.

The poor quality of hay and the cooperation of Mr. Lyman made it possible to leave this field undisturbed until mid-July. At this time the field was mowed for hay causing the destruction of only the one last active nest.

3. Augur Jr. is an upland hayfield with an area of 9.85 ha on the property of Mr. George Augur, Jr. in Northford, Connecticut. The vegetation on most of the field is a perennial hay crop of timothy, bromegrass, orchard grass, alfalfa and clover forming a uniform dense stand. Scattered dock plants provided nest support in several instances, but in general this field was less "weedy" and more homogeneous than the two previously described. An open grown hickory (Carya ovata) is in the center of the field and a row of about six hickory border the field on the west, separating it from a field of planted rye. The field is bordered on the south by a fence row with deciduous shrubs and trees, on the east by a large tract of mixed deciduous woods, and on the north by a road and mowed lawn. A small man-made pond of about 60 m^2 is near

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the north edge of the field. A thistle (Cirsium arvense) patch of about 50 m^2 contained one nest and a boggy portion of the field, about 1 ha in extent, supported one nest. The remaining nests were in the tillable, dry portion of the hayfield. This hayfield was not mowed until early August, at least two weeks after the last nestling had fledged.

During the course of this study, several additional upland sites were under occasional observation and found to support small numbers of nesting Redwings. Hausman's Old Field is an old field successional site, probably cut over and abandoned 20 years ago, with typical successional species now present. Gross Farm is a Christmas tree plantation with several species of spruce and fir, all 3-4 m tall. Lyman Sod is an upland field from which sod was harvested for landscaping. The field was not replanted and has grown up with a dense stand of dock and other sturdy weeds with some timothy and clover. Nests in these sites that were visited frequently enough to provide reliable data are included in the upland averages.

The structure of the vegetation on upland sites is in some ways quite similar to the structure of the marsh vegetation. Many of the sturdy herbaceous "weeds" used for nest support provide a vertical configuration of stems and allow a pattern of nest building similar to that found in cattails. Both habitats have the vegetation structure

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concentrated in a relatively narrow belt with an open view over the top of vegetation that is quite homogeneous in height and type.

In other respects, the structure and phenology of vegetation on the upland sites is markedly different from that of the marshes. The upland hayfields were mowed in late summer and made little growth prior to winter frosts. Consequently, in early spring the upland fields had no standing vegetation structure prior to the growth of the various herbaceous perennial hay and weed species. The growth of this vegetation begins in mid- to late-April, but does not provide sufficient concealment or support for nests until about May 10. Around May 10 is also the time when deciduous trees and shrubs are leafing and the earliest these would afford nest concealment. After this time, growth continues to change the structural configuration of the upland vegetation and new nest sites, song perches, and territorial reference points become available sequentially.

The lack of standing vegetation structure in early spring in upland hayfield nesting habitats, in contrast to marshes, results in nesting being deferred until the spring growth makes available the vegetation support and concealment required for nesting. It is also likely that the absence of song perches and structural "markers" for delineating territories would hinder the establishment of clearly defined territories until the spring growth

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made this vegetation structure available.

The hayfield type of upland habitat, and to some extent old field successional sites, may represent unnatural habitats for nesting Redwings in that there were probably no strictly comparable habitats of great extent in pre-agricultural North America. However, prairies and savannahs would be comparable to agricultural hayfields in many respects and may have supported upland nesting populations of Redwings. Disturbed areas such as burned woodland would also provide habitats similar to old field successional sites.

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RESULTS

Breeding populations of Redwings respond to the differences in vegetation structure, phenology, and other associated niche parameters by nesting earlier, more synchronously, and in greater density in marsh than in upland habitat. The chronology of nesting and its effect on nest success is the subject of another paper (Robertson in prep. a).

Nesting Density

Nesting density of Redwings in marshes is about 10 times as great as in upland habitats. In either habitat the aggregations of nesting birds are best described as a grouped territory (Lack 1968) or neighborhood (Crook 1964) nesting system, but these are commonly referred to as colonies in Redwings (Mayr 1941, Smith 1943). The nesting densities for individual sites and for habitat types are shown in Table 2. Case and Hewitt (1963) and Graber and Graber (1963) have previously noted that Redwing nesting density is greater in marsh than upland habitat, although the magnitude of the difference previously reported was not as great as that found in this study. Redwings are occasionally known to raise two broods and will often renest if the first nest is destroyed early in the season (Fankhauser 1964). The nesting densities shown in Table 2 are therefore greater than the actual number of females. Renesting might be more common in

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Table 2. Nesting density of Redwings in marsh and upland habitats

Site	Area (ha)	Number of Active Nests 1969	1970	Nests/ha/yr
Marsh				
Clarkes Pond	1.92	202	167	96.1
All Saints Marsh	1.09	108	128	108.3
Total	3.01			100.5
Upland				
Hyland Farm	2.68	35	32	12.7
Lyman Golf	2.99	-	32	10.7
Augur Jr.	9.85	-	41	4.2
Total	15.52			7.7

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uplands, where the percentage of nests predated is higher than in marshes, but second nesting is more likely in marshes where initiation of nesting activity is earlier. In any case, the magnitude of the difference in the number of females per unit area is probably very similar to the difference in nesting density between the two habitats.

Observations on Redwing nests in three additional upland sites indicate the nesting density in general for upland areas supporting colonies or solitary nesting pairs is even lower than reported in Table 2. Hausman's Old Field had 10 nests in 1969 and 5 in 1970; Lyman Sod had 6 nests in 1970; and Gross Farm had 1 nest in 1969. Large areas were searched to find these few nests. An estimate of nesting density would be about 3/ha for Hausman's Old Field; 2/ha for Lyman Sod; and 0.1/ha for Gross Farm.

Nest Success and Causes of Mortality

Nesting success was consistently greater in marsh than in upland habitats during 1969, 1970, and the combined years of this study. The percentage of active nests (nests in which at least 1 egg was laid) that were successful (fledged at least 1 young) (Table 3) and the mean number fledged per active nest (cf. Table 5) were significantly greater in marshes than in upland areas. Some of the individual upland sites had greater nest success than the less favorable of the two marshes, but with the

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Table 3. Nest success for individual sites and marsh and upland summaries, measured by the percentage of nests successful (fledged ≥1). The number of active nests for each site is shown in parentheses

Site	1968	1969	1970	Mean
Marsh				
Clarkes Pond	66.2(133)	40.6(202)	41.3(167)	47.6(502)
All Saints Marsh		67.6(108)	61.7(128)	64.4(236)
Total	66.2(133)	50.0(310)	50.2(295)	53.0(738)
Upland				
Hyland Farm		25.7(35)	21.9(32)	23.9(67)
Lyman Golf			50.0(32)	50.0(32)
Augur Jr.			19.5(41)	19.5(41)
Hausman's Old Field		40.0(10)	100.0(5)	60.0(15)
Lyman Sod			83.3(6)	83.3(6)
Gross Farm		100.0(1)		100.0(1)
Total		30.4(46)	35.3(116)	33.9(162)
χ^2 for Marsh-Upland totals		5.39 P<.05	6.78 P<.01	18.49 P<.001

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exception of Lyman Golf, these sites supported very small colonies or a few solitary pairs. The mean number fledged per successful nest was not significantly different in the two habitats (cf. Table 5). This suggests that the difference in success is due to mortality factors that result in total nest destruction rather than partial brood reduction.

A variety of factors were responsible for mortality of eggs and nestlings. As indicated in Table 4, nest predation was the single most common cause of mortality to both eggs and nestlings in both marsh and upland habitats. Combining the figures for egg and nestling mortality, in marshes 30.2% of the active nests were destroyed by predation and in uplands 45%. In both habitats, predation accounted for more egg losses than all other types of egg mortality combined. In marshes, predation accounted for 42% of all nestling mortality, and in uplands 63%. Racoons (Procyon lotor) were responsible for a large portion of the predation in marshes; of 80 Redwing nests in marshes predated in the nestling phase, 54 were typical of racoon predation. From a blind in Clarkes Pond, a racoon was seen in the process of nest predation, reaching up and pulling down one edge of the nest and then raking out the contents. Late in the season in 1969, traps were set near some nests in Clarkes Pond and two racoons were captured on 27 and 30 June respectively. While these two racoons were certainly responsible for some nest predation,

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Table 4. Factors accounting for mortality of eggs and nestlings, and hatching and fledging success in marsh and upland

	Marsh				Upland			
	Nests		Individuals		Nests		Individuals	
	No.	%[c]	No.	%	No.	%[c]	No.	%
Nests with Eggs								
Total Active	738	-	2416	-	162	-	516	-
After Manipulations	738	-	2426	-	162	-	524	-
Mortality by[a]								
Predation	143	19.4	407	16.8	38	23.5	118***	22.5
Abandonment	61	8.3	129	5.3	18	11.1	40*	7.6
Unhatched Eggs	123	16.7	155	6.4	26	16.1	33	6.3
Egg Breakage	17	2.3	17	0.7	3	1.9	4	0.8
Disappearance	26	3.5	39	1.6	4	2.5	5	0.9
Vegetation Failure	14	1.9	38	1.6	7	4.3	19**	3.6
Breakage by Observer	14	1.9	14	0.6	1	0.6	1	0.2
Human Interference	0	0	0	0	2*	1.2	6***	1.2
Hatched	516	69.9	1627	67.1	99*	61.1	298***	56.9

(Continued on following page)

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Table 4. (Cont.)

	Marsh				Upland			
	Nests		Individuals		Nests		Individuals	
	No.	%[c]	No.	%	No.	%[c]	No.	%
Nests with Nestlings								
After Manipulations	516	-	1619	-	99	-	295	-
Mortality by[b]								
Predation	80	15.5	236	14.6	35***	35.3	100***	33.9
Starvation-Diarrhea	97	18.8	175	10.8	17	17.2	22	7.5
Disappearance	57	11.1	73	4.5	8	8.1	10	3.4
Vegetation Failure	8	1.5	24	1.5	1	1.0	2	0.7
Miscellaneous	13	2.5	36	2.2	7*	7.1	15**	5.1
Human Interference	10	1.9	14	0.8	3	3.0	9***	3.1
Fledged	391	75.8	1061	65.5	55***	55.6	137***	46.4
% Active Nests, Eggs Fledged	391	53.0	1061	43.7	55***	33.9	137***	26.1

*P<.05 **P<.01 ***P<.001 probability that difference between upland and marsh counterpart is due to chance

[a]Mortality expressed as % nests with eggs and % eggs
[b]Mortality expressed as % nests with nestlings and % nestlings
[c]% nests totals >100 because more than 1 mortality factor can act on a single nest

their capture did not markedly change the pattern of predation, or the predation pressure, during the subsequent 18 days while there were still active nests on the marsh. In the 10 days immediately prior to the capture of the first racoon there were 495 nest days and 13 nests destroyed by predation or 0.0263 nests predated per nest day. In the 10 days after the capture of the second racoon there were 196 nest days and 5 nests predated or 0.0255 nests predated per nest day. Nest predation in marshes that was not accompanied by significant nest destruction was likely done by birds or perhaps water snakes (Natrix sipedon). Blue jays, grackles, crows, green heron, hawks, and owls are potential predators on Redwing nests. Many of these species illicited alarm calls and mobbing from Redwings suggesting that they pose a threat of some kind. Although long billed marsh wrens (Telmatodytes palustris) nested in Clarkes Pond in 1968 and 1969 there was no evidence they destroyed Redwing eggs as has previously been noted (Bent 1958). Muskrats have also been mentioned as potential predators of marsh nests (Bent 1958, in Miller 1968), but there was no evidence of muskrat predation during this study. That Redwings did not mob or give alarm calls when muskrats were present indicates they are not recognized as a predator. Patterns of predation were less discernable in the uplands, perhaps indicating a greater variety of predators. With the exception of water snakes, all of the potential marsh nest predators mentioned above could be found

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in upland habitats. In addition, foxes, skunks, opossums, feral cats, weasels, and snakes are potential predators on Redwing nests in upland habitat.

A detailed analysis of all the causes of mortality affecting Redwing eggs and nestlings and the relative frequency of occurrence is shown in Table 4. During the egg phase of the nesting cycle, the factors that result in egg mortality cause greater losses in upland than in marsh nesting populations. None of the egg mortality factors alone has a significantly greater effect on whole clutches (nests) in one habitat than the other, but the summation of these factors results in a significantly ($P<.05$) greater proportion of the marsh clutches hatching. Egg predation, abandonment, destruction of eggs due to failure of the nest support vegetation, and human interference all cause significantly greater mortality in uplands when comparing individual eggs in the two habitats. Thus, although none of these factors alone diminishes the success of females as measured by hatching some eggs, they do decrease the success of upland nesting as measured by the proportion of eggs that hatch.

Mortality of individual nestlings and whole broods due to predation is significantly ($P<.001$) greater in upland areas than marshes; the proportion of broods and nestlings predated in uplands being more than double that in marshes. Mortality due to human interference and to

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miscellaneous unexplained factors is also greater in upland than marsh, but these causes of mortality account for relatively few deaths. The combination of all types of nestling mortality results in a larger proportion of marsh broods and individuals surviving to fledging than survive in uplands. The end result of egg and nestling mortality combined is that in marshes, a greater proportion of nests are successful and a greater proportion of individuals starting as eggs survive to fledging.

As indicated in Table 4, mortality during the nestling phase is greater than during the egg phase in both marsh and upland habitats. This is more clearly illustrated in a curve of survivorship as shown in Figure 2. This curve is expressed on a semi-log scale so that a uniform rate of survival (or its inverse, mortality) would result in a straight line from day 0 to fledging. Day 0 is the day of clutch completion. Some egg losses occur prior to clutch completion and this mortality was assigned to day 0. Thus the apparently heavy mortality from day 0 to day 1 is actually all the mortality that occurs between clutch initiation and day 1, usually a period of three to five days. From day 1 to hatching at day 11 both marsh and upland populations show a constant rate of egg mortality with the rate in upland habitat being greater than in marshes. At hatching the rate of mortality increases as shown by the change in slope of both curves, the rate in uplands increasing more dramatically than in marshes.

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Figure 2. Survivorship curves of Redwing eggs and nestlings. The marsh curve is based on data from 738 nests starting with 2426 eggs, the upland curve from 162 nests, 524 eggs.

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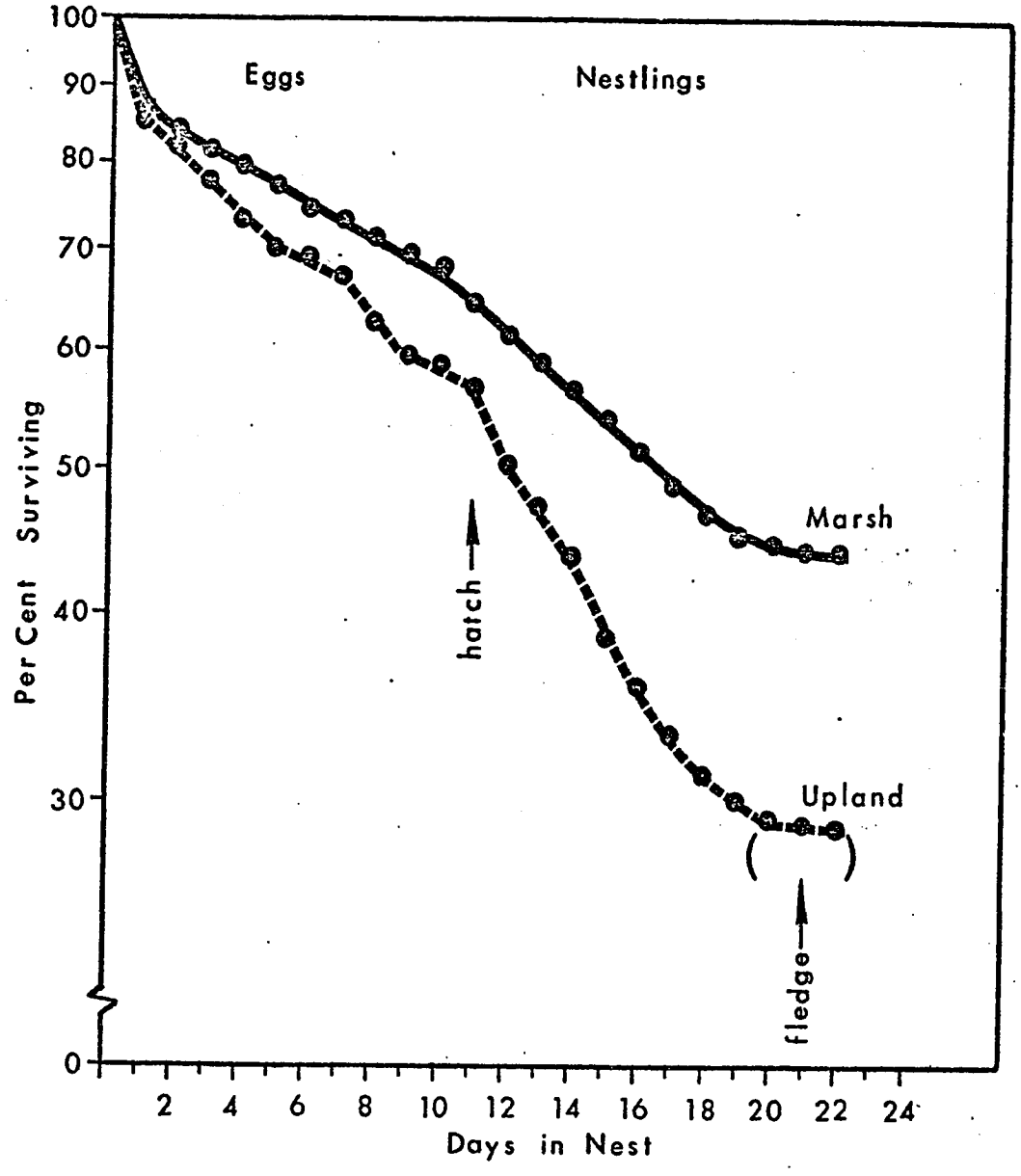

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These curves show survivorship of nestlings until fledging which, if the nest is disturbed, may occur as early as day 19 (when the nestlings are 8 days old). Survival is uniformly high among the nestlings that remain in the nest past day 19, but this should not be interpreted as a measure of true survival. If it were possible to obtain data on post-fledging survival, continuation of the curve past day 19 would likely show a sharp increase in the rate of mortality during the first week out of the nest.

The mortality rate of nestlings appears to be quite uniform from hatching to day 19. A more sensitive method of examining age specific mortality rate, as seen in Figure 3, indicates high mortality at hatching (day 11), decreased mortality shortly after hatching, then a trend of increasing mortality to day 14-16 (nestling age 3-5 days) and a declining mortality rate thereafter. Starvation is the single factor most responsible for this trend, usually affecting nestlings at this age. Figure 3 also shows that the rate of egg mortality in general is lower than nestling mortality, and that throughout the nesting period the mortality rate is greater in uplands than in marshes.

Productivity of Redwings in Marsh and Upland

The combined results of several aspects of Redwing breeding ecology lead to a much greater productivity of fledged young per hectare in marshes than uplands. Initial productivity, measured by clutch size, is slightly greater

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Figure 3. Age specific mortality showing the percentage of those surviving on day n that do not survive until day n+1. Based on the same data as Figure 2.

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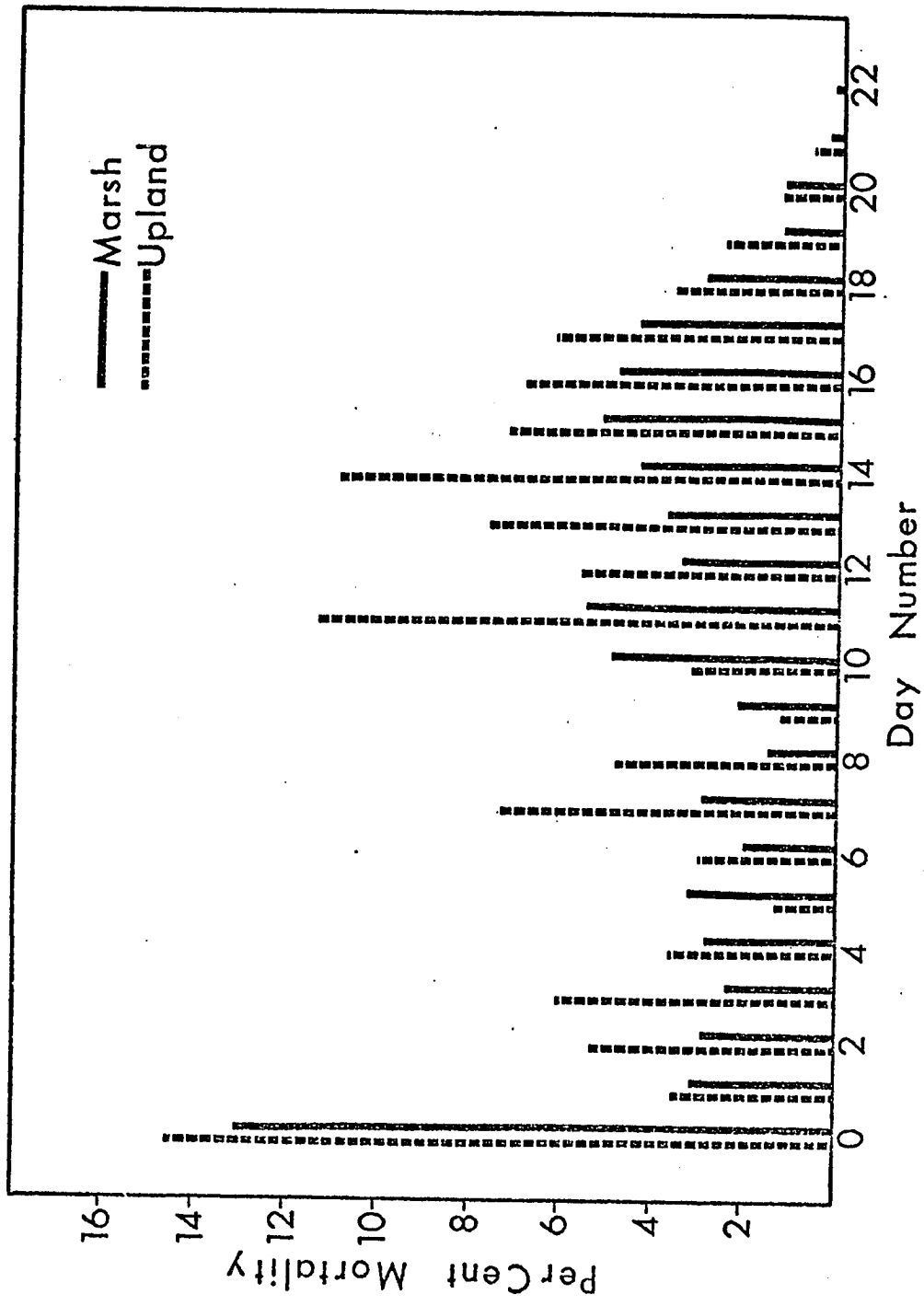

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for marsh than upland nesting females (Table 5). In marsh populations, 4 is the most common clutch while in uplands, 3 and 4 egg clutches are equally common (Robertson in prep. b). This initial difference may make some contribution to productivity as measured by number of fledglings since, on average, there is a slightly larger number of young fledged per successful nest in marshes than in uplands (Table 5). That this difference is not statistically significant is due to a smaller sample size and greater variability for number of fledglings than for clutch size. The combination of higher nesting density and a larger proportion of nests successful results in the productivity in fledged young per hectare being much greater in marshes than uplands.

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Table 5. Productivity of marsh and upland, measured per egg, per nest, per hectare

	Marsh		Upland
Eggs			
No. Eggs	2426		524
Fledged/Egg	0.44	***	0.26
Nests			
Full Clutches	654		145
Mean Clutch Size[a]	3.50±.02	*	3.37±.06
Fledged/Active Nest	1.44±.06	**	0.85±.10
Fledged/Successful Nest	2.71±.05	ns	2.49±.13
Area			
No. Active Nests/ha/yr	100.5		7.7
Fledged/ha/yr	132.7		5.4

[a]mean of clutches known to be complete (full clutches)

*P<.05 **P<.01 ***P<.001 ns = not significant

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DISCUSSION

Nesting Success in Marsh and Upland Habitats

The niche space of the Redwing corresponding to marsh nesting and its associated niche parameters (N_2) has significantly higher survival value than the niche space corresponding to upland nesting (N_1-N_2) (Figure 4). Survival value, as measured by percentage of active nests that were successful, number fledged per active nest, number fledged per egg, and number fledged per unit area, averaged consistently higher in marsh than in upland habitat during the two years in which comparisons were made. Case and Hewitt (1963) also found Redwings nesting in marshes to be generally more successful than those in uplands, and Orians (1961) made similar but non-quantitative observations.

Several aspects of Redwing breeding ecology that could have an influence on nesting success differ between marshes and uplands. Some of these include structural features of the environment; configuration, height, density, and phenology of the vegetation, and presence of water beneath the nest. Others are biotic factors such as diversity and abundance of predators, distribution, abundance, and type of food available. Others are features of the nesting ecology itself; initiation, synchrony, and density of nesting, and breeding colony size.

Since all of these factors are interrelated it would

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Figure 4. Survival value of different parts of the fundamental niche of the Redwing. The niche diagram represents a two-dimensional projection of an n-dimensional niche hypervolume, some of the dimensions of which are generalized below.

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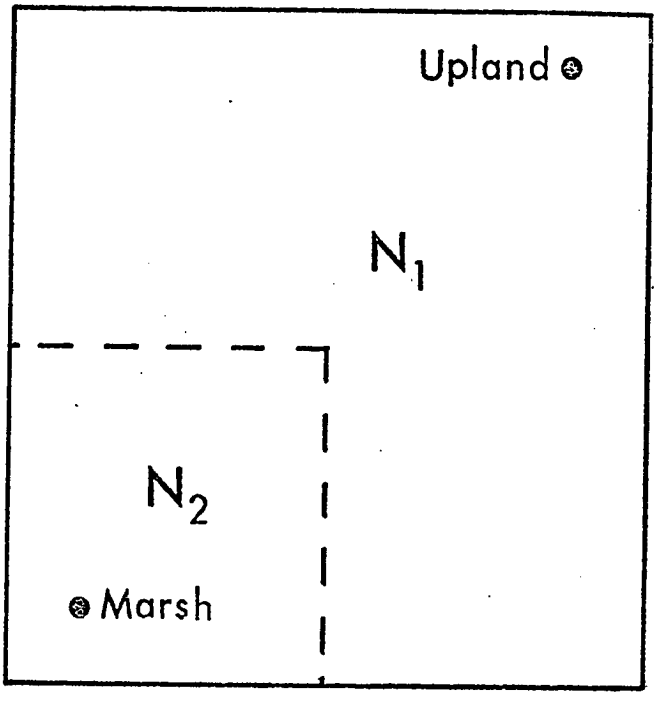

Habitat Type	Aquatic	Terrestrial
Nesting Density	High	Low
Synchrony	High	Low
Predation	Low	High
Food Productivity	High	Low
Survival Value	High	Low

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be misleading to specify a single niche parameter as being most important in contributing to or diminishing the survival value of a given niche space. The high proportion of nests destroyed by predation is the immediate cause of higher mortality, hence lower survival value, in upland than marsh nesting habitat. However, the different predation rates are due to a number of factors. The presence of water beneath nests probably renders marsh nests inaccessible to all but a few predators. That water is a deterrant to nest predation is indicated in Table 6 which shows a negative correlation between water depth and the percentage of nests predated. In contrast, upland nests are readily accessible to a wide variety of predators.

The combination of high nesting density and more synchronous nesting also plays a role in diminishing the proportion of nests predated in marshes. Predation is a highly local and temporal phenomenon, with the type and capacity of predator populations varying greatly between habitat types, habitats of the same type, and seasonally within a given habitat. In some cases, the high density and synchrony of nesting activity tend to "swamp" local predator populations; the number of nests predated per day remaining constant while the density of nests increases (Robertson in prep. a). In other cases, a swamping effect is not evident, but a proportional effect results in a lower percentage of nests being destroyed

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Table 6. Percentage of nests predated in relation to the depth of water beneath the nest. The number of nests in each category is in parentheses. Clarkes Pond had different predation rates during the three years studied and is analyzed annually. All Saints Marsh had consistent and lower predation rates and 1969 and 1970 are lumped

Nesting Site	Water Depth (cm) 0-25	26-50	51-75	76-100	101-200	201+
Clarkes Pond 1968	20.8(48)	12.7(71)	7.7(13)	0(1)	-	-
Clarkes Pond 1969	70.9(55)	36.8(95)	33.3(24)	32.8(22)	33.3(6)	-
Clarkes Pond 1970	51.8(54)	46.0(63)	44.8(29)	42.9(21)	-	-
All Saints Marsh 1969 and 1970	27.1(59)	9.7(154)	8.7(23)	-	-	-

at high nesting densities. If equal levels of predator activity, measured by nests destroyed per day, were assumed in nesting colonies in two habitats, then the habitat with the larger number of active nests would have a smaller proportion destroyed. Fautin (1941) observed that the percentage of eggs predated was twice as great in a small colony of Yellowheads as in a large colony and suggested that the greater number of available predatees would tend to reduce the total percentage taken by predators. A similar effect was observed for different sized colonies of Redwings (Robertson in prep. a).

High density and synchrony of nesting are possible in marshes because the structural and phenological nature of the vegetation provides an abundance of suitable nest sites early in the season. The structure of cattails, though dead, remains sturdy for at least a year following active growth and is frequently used as the sole or principal nest support (Table 7). The success of nests using some form of old Typha was generally greater than those using some other type of nest support, but this may have been a coincidental seasonal phenomenon; nest success decreased after mid-season while the availability and use of new growth increased. In the hayfield type of upland habitat, late summer mowing, little autumnal growth, and matting of the vegetation by snow, all contribute to the absence of standing vegetation in early spring. All upland nests, with the exception of those in old field habitats where

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Table 7. Relative use of vegetation types for nest support in marshes and uplands ranked in order of nest success

Nest Support	Number of Nests	Number Fledged per Active Nest
Marsh		
Old *Typha angustifolia*	8	1.88
Old *T. latifolia* and Marsh Woody	45	1.78
Old *T. latifolia*	220	1.73
Miscellaneous[a]	36	1.40
Old and New *T. latifolia*	253	1.36
Sagittaria	17	1.35
Old and New *T. angustifolia*	91	1.18
Marsh Woody	38	1.03
New *T. latifolia*	4	1.00
New *T. angustifolia*	6	0.67
Marsh Grasses	20	0.65
Upland		
Alfalfa	3	3.33
Upland Woody	17	1.94
Other Upland Herbaceous	9	1.11
Campion	10	0.90
Miscellaneous[a]	15	0.73
Dock	79	0.67
Upland Grasses	25	0.44
Dock and Campion	1	0
Alfalfa and Grass	3	0

[a]This category includes various combinations of the single vegetation support types listed, as well as certain infrequently used species.

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nests are often built in woody shrubs, use for nest support and concealment herbaceous vegetation that becomes available with spring growth (Table 7). The relatively high success of nests in upland woody vegetation, such as that found in old field successional habitats, would suggest that these are favorable nesting areas and that consequently they should frequently be used by nesting Redwings. That Redwings do not nest in abundance in such sites may be because they are poorly suited for the grouped territorial nesting pattern to which Redwings are adapted.

Initiation of nesting activity began at least 10 days later in uplands than in marshes. In 1969 the first nest was begun 17 April in marshes and 8 May in uplands; in 1970, 27 April in marshes and 7 May in uplands. Case and Hewitt (1963) and Holcomb and Twiest (1968) also found the initiation of nesting activity to be later in upland habitat. The delay in upland nesting is likely due to the absence of suitable nest support and concealment until 5-10 May when new spring growth provides the necessary structure. Phenological observations recorded on 5 May 1970 indicate that vegetation on upland hayfields was too short and sparse to afford cover for a nest, and on old fields the deciduous shrubs and trees were not leafed out enough to conceal a nest. Holcomb and Twiest (1968), in following nest building in relation to phenology, report that prior to new vegetation growth on upland sites the only available support for nests was old goldenrod,

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wheatgrass, and sweet clover stems and that these were widely scattered and would have made poor cover for nests. Consequently, nest initiation is delayed until the necessary support is available. Continued growth of vegetation on upland fields makes additional nest sites available sequentially, thus contributing to a protracted rather than synchronous pattern of nesting activity.

An alternative hypothesis to explain the earlier and more synchronous nesting in the large colonies as found in marshes was proposed by Darling (1938). Darling found that larger colonies of gulls showed (a) earlier beginning of laying (b) greater synchronization of breeding and (c) higher reproductive success. He suggested that synchronized breeding had survival value and that it was accomplished in large colonies because ". . . the social group and its magnitude, in birds which are gregarious at the breeding season, are themselves exteroceptive factors in the development and synchronization of reproductive condition in members of individual pairs of birds and throughout the flock." (Darling 1938, p. 3)

Mayr (1941) concluded from a study of Redwings breeding in 4 different swamps that differences in the timing of nest initiation were due to differences in the suitability of vegetation at the sites studied rather than the "Darling effect." Mayr's study was probably not a good test of the Darling hypothesis, however, since the sizes of the colonies observed were all at the small end of the spectrum of

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colony size known to occur in Redwings. In a more complete test of Darling's hypothesis, Smith (1943) found that Redwings breeding in a very large marsh colony were no more synchronous in their nesting and had no greater nesting success than an equal number of birds distributed among 24 small colonies in marshes and ponds of restricted size. Orians (1961) found that variations in timing and synchrony of breeding in Redwings were correlated with the nature of the marsh and its surrounding vegetation and not with the size of the breeding population. Data from Goddard and Board (1967) showed no apparent correlation between the number of active nests and nest success. These examples indicate that the "Darling effect" does not apply to Redwing colonies and the earlier and more synchronous nesting of marsh colonies in this study was not simply a result of greater social group stimulation in the larger marsh colonies than in the smaller upland colonies.

This does not imply that large colony size has no survival value. As mentioned previously, high nesting density and synchrony are probably important in lowering the proportion of nests predated. The point here is not the survival value of synchrony nor the mechanism by which it is achieved, but rather the factors that prevent it in uplands. I would suggest that high density and synchrony are possible with the simultaneous abundance of nest support early in the season in marshes and not possible with the sequential development of new nest support in

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uplands.

The survival value of synchronous nesting in dense colonies afforded by a swamping of predators and proportionately lower predation would be offset if the abundance of food were not sufficient to support large numbers of breeding birds. The relative abundance of food was apparently similar for females nesting in either habitat because the rates of growth were nearly the same and the mean weight at fledging was equal among nestlings from marshes and uplands (Robertson in prep. b). Marsh habitat probably has a much greater absolute abundance of food than uplands (Orians pers. comm., Haigh 1968) and it is therefore possible that the availability of food limits density and synchrony of upland nesting at a lower level than in marshes. However, if breeding populations assess the food resources and adjust the density of active nests accordingly by means of territoriality, then such a limitation would not be evident from comparisons of nestling growth (cf. Brown 1969, Fretwell and Lucas 1970).

Genetic Separation between Marsh and Upland Populations

The possibility exists that marsh and upland breeding populations of Redwings are genetically separate and that differences in nest success result from divergent adaptations of two genotypes. Dyer (1964, p. 79) found no overlap in the mean ±2S.E. culmen length between breeding male Redwings taken from marsh and upland habitats; the upland population having the longer mean culmen length. These and

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other data showing differences between sample means of marsh and upland breeding populations (p. 105) led Dyer to conclude that "there is little or no genetic interchange between these two breeding types despite the fact that they are barely separated spatially." (p. 146). However, some of Dyer's data indicate morphometric differences between different marsh populations as great as those between marsh and upland. More recently, Dyer (1968) found a significant difference in respiratory quotient (R.Q.) between Redwing nestlings from uplands and marshes for both homeo- and hypothermic responses, nestlings from uplands having the lower R.Q. Dyer suggested that this difference could be a result of either genetic differences or acclimatization to different habitats. Parker (1968) also found Redwing nestlings from upland habitats to have a lower R.Q. than nestlings from marshes. In addition, he found that upland nestlings showed greater metabolic resistance to cold stress than did marsh young, but suggested the differences were causally related to differences in the climatic and nutritional conditions of the two breeding habitats rather than to genetic differences. The question of morphometric, physiological, behavioral, and perhaps genetic differences between marsh and upland breeding Redwings is currently being investigated by Stone (1969). Although statistical analyses are incomplete, Stone (pers. comm.) has "detected little difference in marsh and upland populations of redwings."

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Stone (1969) suggested earlier that Redwings may be partially imprinted to either terrestrial or marsh vegetation, and that the population is not subdivided genetically.

Habitat Selection

The mechanism of breeding habitat selection would in large part determine whether genetic separation and divergence of marsh and upland populations of Redwings would occur. Strong site tenacity, as reported common in many species of birds (Hildén 1965), would contribute to such separation. Banding returns reported by Nero (1956) indicate strong site tenacity in adult Redwings, and Beer and Tibbits (1950) observed some Redwing males banded as nestlings to hold territories on their natal marsh as two year olds. Fankhauser's (1964) observation of a female nesting in a marsh after having raised one brood and had a second nest destroyed in a nearby upland hayfield indicates site tenacity is not perfect.

At least three alternative hypotheses can be suggested to explain habitat selection in Redwings: (1) Site tenacity of adults, and habitat imprinting of nestlings resulting in their faithful return to the natal area or at least the natal habitat type. (2) Preference for the "optimal" (marsh) breeding habitat by all individuals, resulting in a great deal of mixing between populations since younger birds would probably be forced to nest in suboptimal habitats and older, competitively superior birds would breed in the more optimal habitats. (3) Site

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tenacity of adults breeding for the second or more time, and habitat selection for the "optimal" breeding habitat by first-time breeders, resulting in some exchange between optimal and suboptimal habitats.

Alternatives 2 and 3 require that individual birds be capable of assessing the survival value of a nesting habitat. Since survival value is most likely correlated in some way with density (Lack 1966) this assessment involves recognition of both environmental cues and behavioral or other cues that yield information about population density. The observations of Kluyver and Tinbergen (1953) suggested that such assessment occurs and that territoriality serves as the density cue (Fretwell and Lucas 1970). They found that titmice exhibited habitat selection for a favorable mixed wood, settling earlier and in greater density than in pine wood. However, as density increased, the suitability of the mixed wood decreased and it became more advantageous to settle in the suboptimal but uncrowded pine wood. Reproductive success was similar in the two habitats indicating an accurately assessed balance between environmental favorability and population density.

Alternative 1 allows provision for assessment of neither environmental nor density cues because it involves an all or none response to a habitat stimulus. Selection would probably act against this because it precludes the possibility of achieving an "optimum mix" of density between habitats that Brown (1969) suggests would maximize

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population productivity. Maximum population productivity results from the "optimum mix" because individual birds nesting in uncrowded suboptimal habitats have higher reproductive success than if they were to settle in a crowded optimal habitat. Natural selection would thus favor those individuals that respond to density cues and achieve an "optimum mix". Without the possibility of an exchange between habitat types, periodic overpopulation of local breeding habitats or non-breeding males and females would result. Non-breeding males are known to occur (Orians 1961, Peek 1969) and first year males rarely breed, but this is probably a result of polygyny. Non-breeding females have not been reported.

Alternative 2, while providing the opportunity to achieve a balance between the survival value of a crowded optimal and uncrowded suboptimal habitat, affords none of the advantages gained by site tenacity of adults that have become familiar with a particular breeding habitat. Alternative 3 provides this advantage and at the same time maintains the flexibility to allow a density and environmental favorability assessment in the initial habitat selection of a given individual. The pattern of habitat selection in Great Tits is appropriately described by alternative 3. Krebs (1971) found that when territories were made vacant in an optimal habitat, yearling male Great Tits were more likely to move from a suboptimal to the optimal habitat than were adult males that had once

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bred in the suboptimal habitat. A program for testing these hypotheses with regard to the Redwing is planned.

Territoriality and Nesting Success

Fretwell and Lucas (1970) have suggested that if territorial behavior is functioning to limit density (the ideal dominance distribution), the suitability (eg. nest success) of two different nesting habitats will be unequal and positively correlated with density. This situation occurs because, due to the risks involved in establishing a territory in a crowded habitat, the apparent suitability (an assessment of potential success) of a densely populated habitat to newly settling individuals is lower than the actual suitability to already established individuals. In an uncrowded habitat, the apparent suitability is higher but the actual suitability lower than in the crowded habitat. Removal experiments of territorial male Redwings by Orians (1961) and Peek (1969) show that vacated territories are rapidly reoccupied by previously unestablished males, suggesting that territorial behavior is in fact limiting density on breeding habitats. Given this fact, the argument of Fretwell and Lucas would predict that the more densely populated marsh breeding habitat would have higher suitability (survival value) than less densely populated uplands. Comparisons of nest success in the two habitats support this hypothesis. Ignoring the evidence of removal experiments on the role of

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territoriality, the fact that nest success is not equal for Redwings breeding in marsh and upland and that success is positively correlated with density would, according to Fretwell and Lucas (1970), indicate that territoriality is functioning to limit density. The data of Orians (1961) and Peek (1969) could then be used as confirmatory evidence for the ideal dominance distribution hypothesis of Fretwell and Lucas (1970). The Allee type of ideal dominance distribution is probably applicable in this case since Redwings are colonial and may show a predator swamping effect at high densities.

Observations on sex ratios in marsh and upland habitats also support Fretwell and Calver's (1970) argument that the female/male ratio would be positively correlated with the suitability of different habitats. Case and Hewitt (1963) found a sex ratio of 2.17 in marshes and 1.85 in uplands and my observations indicate a substantially higher sex ratio in marshes than uplands. Thus, in Redwings, sex ratio is positively correlated with suitability since marshes were shown to have higher suitability as measured by nest success than uplands.

It should be emphasized that, although territorial behavior is limiting breeding density in local habitats, it is not necessarily limiting population size. As Brown (1969) suggested, if reproductive output decreases with increased population density beyond some point, territoriality may result in an optimum mix between

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crowded optimal and uncrowded suboptimal habitats and thus maximize the reproductive rate.

Competition and Niche Space

The optimal part of the fundamental niche of the Redwing during the breeding season is represented by marsh nesting habitat and its associated niche parameters, having significantly higher survival value than upland habitat. Interspecific territoriality resulting in the exclusion of Redwings by Yellowheads from the central part of marshes (Orians and Willson 1964) therefore prevents the Redwing from realizing the optimum part of its niche space where the two species are sympatric. This suggests that the competitive exclusion by Yellowheads would have a severe limiting effect on Redwing population size. Significant limitation probably does occur in local areas of sympatry. However, on a large scale, the zone of Redwing-Yellowhead sympatry is relatively small compared with the geographic range of Redwing nesting. Also, throughout the geographic range of the Redwing, the suboptimal nesting habitat is much more extensive in area than the optimal marsh habitat. Therefore, a large portion of population recruitment in the Redwing, both within and outside the zone of sympatry with Yellowheads, may originate in suboptimal habitats (cf. Giltz and Stockdale 1960, Graber and Graber 1963).

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SUMMARY

The survival value of different parts of the fundamental niche of the Redwinged Blackbird was determined by comparing nesting success and the factors that affect it in marsh and upland breeding habitats. The results support the hypothesis that where sympatric, Redwings are being excluded from their optimal niche space by Yellowheaded Blackbirds.

Nest initiation was earlier, and colony size, breeding density, and synchrony were greater in marsh than upland habitat. Marsh nesting populations had greater nest success as measured by the proportion of active nests that were successful, number of young fledged per active nest, and number fledged per egg.

A larger proportion of nests destroyed by predators resulted in the lower reproductive success of upland populations. Predation pressure on marsh nests was negatively correlated with the depth of water beneath the nest, the presence of water providing an anti-predator barrier that upland populations are unable to achieve. The synchrony and greater density of nesting in marshes in some cases has a swamping effect on local predator populations, further reducing predation pressure on marsh Redwing populations.

Growth rates, weight at fledging, and the number fledged per successful nest were similar in the two habitats indicating the relative abundance of food resources

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was also similar. The higher density and success of nests resulted in a much greater productivity of marsh in fledged young per hectare. This suggests the absolute abundance of food is substantially greater in marsh than upland.

The structure and phenology of marsh vegetation is considered to play an important role in providing an abundance of song perches, structural reference for delineating territories, and nest support early in the spring thus making possible relatively dense and synchronous nesting. Upland nesting is delayed and protracted as new spring growth makes the necessary structure available sequentially.

It is considered unlikely that genetic separation exists between marsh and upland populations. It is proposed that habitat selection involves a degree of site tenacity by adults and selection for optimal habitats, assessing both environmental favorability and population density, by first-time breeders.

The relationships between density, nest success, and the function of territoriality lead to the conclusion that territorial behavior limits breeding density.

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LITERATURE CITED

Beer, J.R., and D. Tibbitts. 1950. Nesting behavior of the red-wing blackbird. Flicker 22: 61-77.

Bent, A.C. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. Bull. U.S. National Museum 211: 1-549.

Brown, J.L. 1969. The buffer effect and productivity in Tit populations. Amer. Naturalist 103: 347-354.

Burt, D.E. 1970. Habitat selection and species interactions of some marsh passerines. M.S. Thesis. Iowa State University. 75 p.

Case, N.A., and O.H. Hewitt. 1963. Nesting and productivity of the red-winged blackbird in relation to habitat. Living Bird 2: 7-20.

Crook, J.H. 1964. The evolution of social organization and visual communication in the weaver birds (Ploceinae). Behavior, Suppl. 10: 1-178.

Darling, F.F. 1938. Bird flocks and the breeding cycle. Cambridge University Press. England. 124 p.

Dyer, M.I. 1964. Radar and morphometric studies on transient Red-winged Blackbird populations. Ph.D. Dissertation. University of Minnesota. 156 p.

_____. 1968. Respiratory metabolism studies on red-winged blackbird nestlings. Can. Jour. Zool. 46: 223-233.

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Fankhauser, D.P. 1964. Renesting and second nesting of individually marked Redwinged Blackbirds. Bird-Banding 35: 119-121.

Fautin, R.W. 1940. The establishment and maintenance of territories by the Yellowheaded Blackbird in Utah. Great Basin Naturalist 1: 75-91.

_____. 1941. Incubation studies of the Yellowheaded Blackbird. Wilson Bull. 53: 107-122.

Fretwell, S.D., and J.S. Calver. 1970. On territorial behavior and other factors influencing habitat distribution in birds. II. Sex ratio variation in the Dickcissel. Acta Biotheoretica 19: 37-44.

Fretwell, S.D., and H.L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica 19: 16-36.

Giltz, M.L., and T.M. Stockdale. 1960. The redwinged blackbird story. Ohio Agr. Exper. Sta. Special Circular 95, 18 p.

Goddard, S.V., and V.V. Board. 1967. Reproductive success of Redwinged Blackbirds in North Central Oklahoma. Wilson Bull. 79: 283-289.

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

Haigh, C.R. 1968. Sexual dimorphism, sex ratios and polygyny in the Red-winged Blackbird. Ph.D. Dissertation. Univ. of Washington. 116 p.

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Hildén, O. 1965. Habitat selection in birds. Ann. Zool. Fenn. 2: 53-75.

Holcomb, L.C., and G. Twiest. 1968. Ecological factors affecting nest building in Redwinged Blackbirds. Bird-Banding 39: 14-22.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harb. Symp. Quant. Biol. 22: 415-427.

_____. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? Amer. Naturalist 93: 145-159.

Hutchinson, G.E., and E.S. Deevey, Jr. 1949. Ecological studies on populations. Survey of Biol. Prog. 1: 325-359.

Kalma, D.L. 1970. Some aspects of the breeding ecology and annual cycle of three populations of the Rufous-Collared Sparrow (Zonotrichia capensis) in Western Panama. Ph.D. Dissertation, Yale University. 218 p.

Kluyver, H.N., and L. Tinbergen. 1953. Territory and the regulation of density in titmice. Arch. Neerl. Zool. 10: 265-289.

Krebs, J.R. 1971. Territory and breeding density in the Great Tit, Parus major L. Ecology 52: 2-22.

Lack, D. 1947. Darwin's Finches. Cambridge University Press. England. 208 p.

_____. 1966. Population studies of birds. Clarendon Press, Oxford. 341 p.

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Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen and Co. London. 409 p.

Levins, R. 1968. Toward an evolutionary theory of the niche. in Evolution and environment, ed. E.T. Drake. Yale Univ. Press, New Haven. p. 325-340.

Linsdale, J.M. 1938. Environmental response of vertebrates in the Great Basin. Amer. Midland Naturalist 19: 1-206.

Mayr, E. 1941. Redwing observations of 1940. Proc. Linnaean Soc. New York. 52-53: 75-83.

Miller, R.S. 1967. Pattern and process in competition. Adv. Ecol. Res. 4: 1-74.

_____. 1968. Conditions of competition between Redwings and Yellowheaded Blackbirds. J. Animal Ecol. 37: 43-61.

Moore, H.B., and J.A. Kitching. 1939. The biology of Chthamalus stellatus (Poli). J. Marine Biol. Assoc. Unit. Kingdom 23: 521-541.

Nero, R.W. 1965. A behavior study of the redwinged blackbird. I. Mating and nesting activities. Wilson Bull. 68: 5-37.

Orians, G.H. 1961. The ecology of blackbird (Agelaius) social systems. Ecol. Monogr. 31: 285-312.

Orians, G.H., and M.F. Willson. 1964. Interspecific territories of birds. Ecology 45: 736-745.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Park, T. 1954. Experimental studies of interspecies competition. II. Temperature, humidity, and competition in two species of Tribolium. Physiol. Zool. 27: 177-238.

Parker, G.H. 1968. On the development of temperature regulation in Red-Winged Blackbird (Agelaius phoeniceus) nestlings from two habitats. M.S. Thesis. Univ. Guelph. 34 p.

Peek, F.W. 1969. An experimental study of territorial behavior in the Red-Wing Blackbird. Ph.D. Dissertation. The Pennsylvania State University. 111 p.

Robertson, R.J. in prep. a. Optimal niche space of the Redwinged Blackbird. II. Spatial and temporal patterns of nesting and success.

_____. in prep. b. Optimal niche space of the Redwinged Blackbird. III. Growth rate and food of nestlings in marsh and upland habitat.

Robertson, R.J., and R.S. Miller. in prep. Clutch size and egg volume in Redwinged Blackbirds.

Slobodkin, L.B. 1961. Growth and regulation of animal populations. Holt, Rinehart, and Winston, New York. 184 p.

Smith, H.M. 1943. Size of breeding populations in relation to egg-laying and reproductive success in the eastern Redwing (Agelaius p. phoeniceus). Ecology 24: 183-207.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Stone, C. P. 1969. Phenetic variation of breeding red-winged blackbirds in Ohio. Ohio Cooperative Wildlife Research Unit. Quarterly Report. 23: 1-33.

Svärdson, G. 1949. Competition and habitat selection in birds. Oikos 1: 157-174.

Weller, M.W., and C.S. Spatcher. 1965. Role of habitat in the distribution and abundance of marsh birds. Special Report No. 43. Iowa State Univ. Agr. and Home Econ. Exp. Sta. 31 p.

Willis, E.D. 1966. Interspecific competition and the foraging behavior of plain-brown woodcreepers. Ecology 47: 667-672.

Willson, M.F. 1966. Breeding ecology of the yellow-headed blackbird. Ecol. Monogr. 36: 52-77.

Willson, M.F., and G.H. Orians. 1963. Comparative ecology of red-winged and yellow-headed blackbirds during the breeding season. Proc. XVI Int. Congr. Zool. 3: 342-346.

Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. Proc. 6th Int. Cong. Genetics 1: 356-366.

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OPTIMAL NICHE SPACE OF THE REDWINGED BLACKBIRD

II. SPATIAL AND TEMPORAL PATTERNS OF NESTING ACTIVITY AND SUCCESS

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Spatial and temporal patterns of dispersion of nesting in birds are adaptations, evolved through natural selection, which enable each species to raise, on average, the greatest possible number of young (Lack 1968). The survival value of many patterns has been discussed (Lack 1954, 1966, 1968), but quantitative data on comparative survival value are difficult to obtain because we normally find in nature only the successful products of evolution and not the failures (Lack 1968). However, some spatial and temporal differences in nesting dispersion exist within species so that comparisons between them can yield insight into the survival value of a given pattern.

The survival value of colonial nesting and the significance of colony size and breeding synchrony have received much attention since Darling's (1938) observations on the reproductive success of gulls nesting in different sized colonies. The importance of the "Darling effect" of group social stimulation in achieving synchrony and greater reproductive success has been seriously questioned (cf. Lack 1954, Orians 1961a), and alternative mechanisms responsible for achieving colonial and synchronous nesting have been discussed (cf. Coulson and White 1960, Hailman 1964, Horn 1970).

Survival value to individuals nesting in colonies has been attributed to a variety of factors listed by Smith (1943) including (1) tolerance for near neighbors in the face of a shortage of suitable nesting sites,

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(2) mass protection supplied by the "mobbing" of potential predators, (3) added protection on a percentage basis from the presence of larger numbers of prey and (4) heightened synchronization which shortens the more vulnerable egg and nestling stages. Colonial nesting may also represent an efficient system for exploiting a food source that is spacially and temporally variable (Horn 1968).

Redwinged Blackbirds (Agelaius phoeniceus), although perhaps not colonial in the strict sense of the word (Orians 1961a), have a breeding system of neighborhoods (Crook 1964) or grouped territories (Lack 1968) and these aggregations are usually considered colonies (Mayr 1941, Smith 1943). Data on the nesting success of Redwings breeding in different habitats and in colonies of different size and density provide an opportunity to evaluate the adaptive significance of the different spatial and temporal patterns of nesting. Comparisons of nesting success of Redwings breeding in marsh and upland habitats indicate that, due largely to differences in the proportion of nests predated, Redwings nesting in marshes are more successful than those in upland habitat (Robertson in prep. a). The purpose of this paper is to examine the effect of spatial and temporal patterns of nesting on nest success in general and on mortality by predation in particular.

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METHODS

Nesting success and the factors responsible for egg and nestling mortality were recorded for individual Redwing nests in two large colonies and three small colonies. All of the nesting colonies studied were within 25 miles of New Haven, Connecticut. The study was done during the 1968, 1969, and 1970 nesting season; Table 2 indicates the years during which each colony was observed. The two large colonies occupied fresh-water cattail marshes and the small colonies were in upland hayfields that had a number of sturdy "weed" species that provided nest support.

Throughout the nesting season an attempt was made to visit each nesting colony every three days. Periods of cold rainy weather, when flushing a brooding female might increase mortality of nestlings, occasionally disrupted this schedule. Nests were usually located during construction or egg laying and marked with a numbered bamboo pole. On subsequent visits, each nest was checked and its state of progress or cause of failure recorded. Further details of the field methods and habitat descriptions are recorded in Robertson (in prep. a).

Temporal analysis of nesting activity, success, and mortality involved assigning a day number to each event. The day number of clutch completion was the basis for assigning a given nest to a time span cohort. Mortality was considered to have occurred on the day mid-way between

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visits by the observer unless evidence of the exact day of mortality was available. Data were coded for analysis which was done with an IBM 7040/7094 computer. Statistical analyses included Chi-square tests for determining the significance of the difference between two proportions and Student's t-tests for differences between means.

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RESULTS

Spatial and Temporal Patterns of Nesting

The average density of nests in breeding colonies of Redwings was about 10 times as great in marsh habitats as in upland habitats of comparable land area (Table 1). Although larger colony size might occur in either habitat if the area suitable for nesting were larger, the nesting densities for the colonies studied represent the maximum for those observed in marsh and upland habitats respectively in southern Connecticut.

The temporal patterns of nesting activity for individual colonies of Redwings during the 1970 breeding season are shown in Figure 1. Nesting activity begins earlier in marsh than in upland habitat and continues for at least as long, resulting in a slightly longer nesting season. In 1970, the date of completion of the first clutch laid in the marsh habitats was 10 days earlier than for the first clutch in upland habitats, and the last clutch laid was completed on the same day in both habitats (Table 2). The period of greatest nesting activity in marsh colonies was consistently from about May 16-19 to May 26-30, relatively early in the season. Hyland Farm had its peak of nesting activity during this period also, but the other two upland sites reached a peak of activity much later (Figure 1 and Table 2).

The distinct peak of nesting activity in the two marsh habitats (Figure 1) suggests that nesting activity

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Table 1. Breeding colony size and nesting density of Redwings in marsh and upland habitats. Active nests are those in which at least one egg was laid

Site	Area (ha)	Colony Size (No. Active Nests) 1969	1970	Average Nesting Density Nests/ha/year
Marsh				
Clarkes Pond	1.92	202	167	96.1
All Saints Marsh	1.09	108	128	108.3
Upland				
Hyland Farm	2.68	35	32	12.7
Augur Jr.	9.85	-	41	4.2
Lyman Golf	2.99	-	32	10.7

Figure 1. Nesting chronology of individual marsh and upland colonies of Redwings for 1970.

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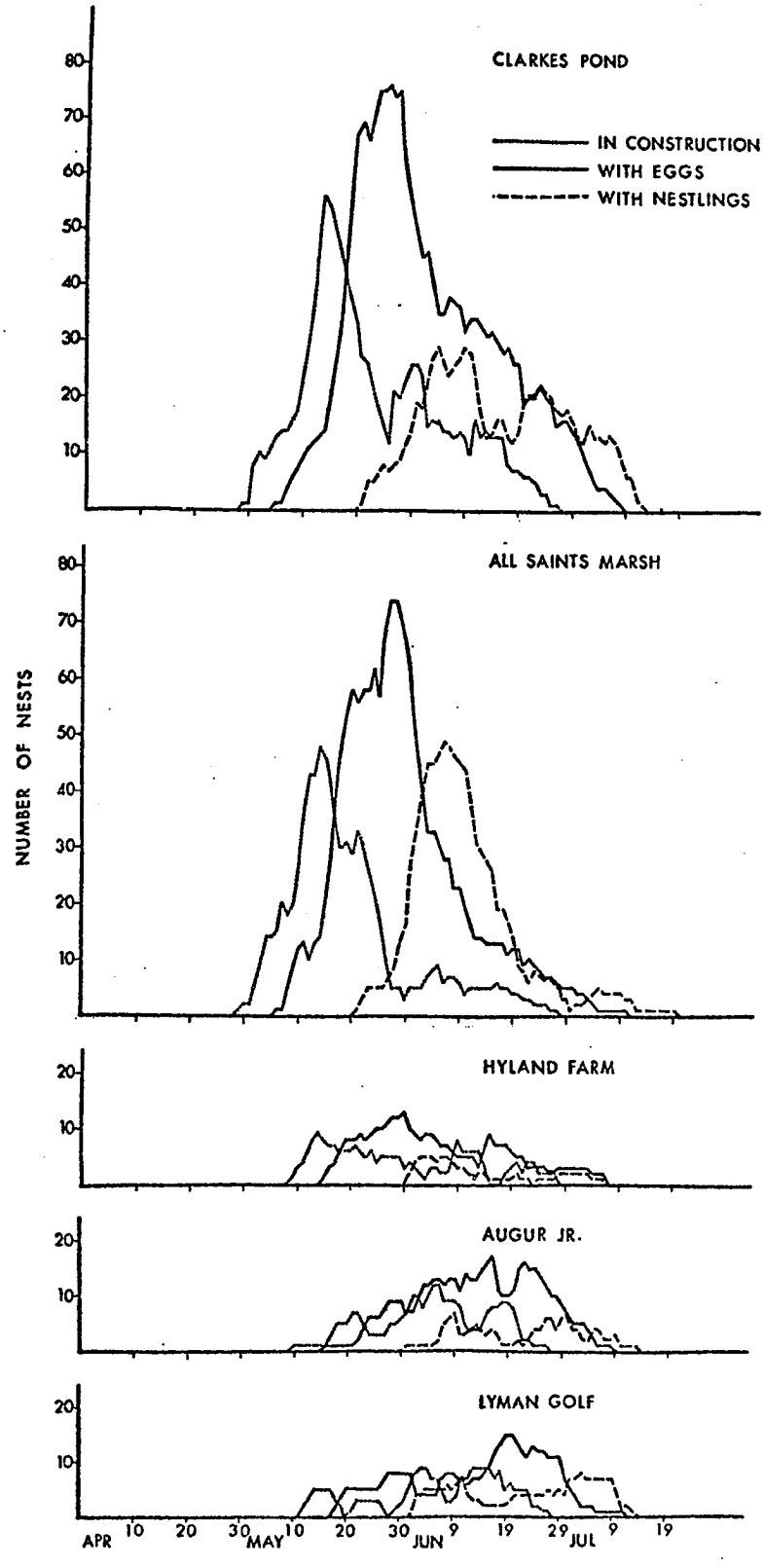

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Table 2. Duration of egg laying activity and nesting synchrony as measured by (1) the variance of the date of clutch completion for each active nest, and (2) the smallest number of consecutive days required to include 50% of the nests built in each colony. Nests were assigned a day number corresponding to the day of clutch completion

Site	No. Active Nests	Date of First-Last Clutch Completion	Duration (Days-inclusive)	Variance	Dates Including 50% of Clutches	Duration (Days-inclusive)
Marsh						
Clarkes Pond 1968	133	May 3-July 4	62	104	May 18-May 26	9
Clarkes Pond 1969	202	May 4-July 1	58	164	May 16-June 1	17
Clarkes Pond 1970	167	May 8-June 30	53	145	May 18-May 30	13
All Saints Marsh 1969	108	May 9-June 16	38	69	May 19-May 27	9
All Saints Marsh 1970	128	May 9-June 30	52	128	May 18-May 28	11
Upland						
Hyland Farm 1969	35	May 18-June 22	35	105	May 19-May 31	13
Hyland Farm 1970	32	May 19-June 30	42	164	May 19-May 31	13
Augur Jr.1970	41	May 19-June 27	39	104	June 5-June 17	13
Lyman Golf 1970	32	May 21-June 29	39	150	June 9-June 21	13

in the larger marsh-breeding colonies, although spread over a longer span of time, is more synchronous than in the smaller colonies found in the uplands. A single measure of synchrony is somewhat unsatisfactory however, as at least two elements are involved; total time span of activity and distribution of activity within the time span. The variance of the date of clutch completion (cf. Horn 1970) is a measure that includes both elements, but the presence of only a few very early or late nests has the effect of markedly increasing the variance. According to this index, the degree of synchrony of nesting in large colonies in marshes is about the same as in small colonies in uplands, even though the nesting activity is spread over a longer time span in the marsh habitats (Table 2). Another measure of synchrony, a version of the quartile method, was used to analyze for the distribution of nesting activity regardless of the length of the nesting season. The smallest number of consecutive days that included 50% of the nests, assigned by date of clutch completion, is an index of the degree of synchrony occurring within any part of the nesting season. A time span that included 50% of the nests was arbitrarily chosen because it best illustrated the differences in synchrony that seemed to occur in Figure 1. Differences in synchrony measured by this index, while not necessarily statistically significant, are biologically interesting because they give a direct comparison of the time span during which a majority

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of females are engaged in nesting activity, an important factor when considering predation pressure.

Measured by this index, 3 out of 5 large colonies in marshes were more synchronous than the small colonies in uplands (Table 2). Clarkes Pond in 1968 and All Saints Marsh in 1969 and 1970 had greater synchronization of nesting activity within the season than any of the colonies in uplands, but Clarkes Pond in 1969 and 1970 was equally or less synchronous than the upland sites. The upland sites were very uniform between sites and years in the number of consecutive days required to include 50% of the nests.

Predation Pressure

Predation pressure, measured as the average number of nests predated per day for the duration of the nesting season, was quite similar between some colonies in marshes and those in upland habitat despite the difference in colony size and synchrony (Table 3). In 1969 and 1970 Clarkes Pond was exceptional when it had much higher predation pressure than in 1968 or All Saints Marsh in either 1969 or 1970. However, similar predation pressure on colonies of different size meant that the predation pressure per individual nest was much lower in the large marsh nesting colonies than in the small upland colonies. Comparisons of the number of nests predated per nest day show that in 3 of the 5 large marsh nesting colonies the chance

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Table 3. Predation pressure measured on a per day, per nest day, and percentage basis. Nest days were calculated using the method of Mayfield (1961). The number of active nests in each colony is in Table 2

Site	Nests Predated Per Day	Nests Predated Per Nest Day ($x10^{-2}$)	Percent Nests Predated			
Marsh						
Clarkes Pond 1968	0.23	0.72	15.0	**		
Clarkes Pond 1969	1.20	2.56	45.0		*	++
Clarkes Pond 1970	1.13	2.76	47.3			++
All Saints Marsh 1969	0.19	0.50	11.1	**		
All Saints Marsh 1970	0.27	0.81	16.4	**		
Upland						
Hyland Farm 1969	0.26	2.64	45.7	**		
Hyland Farm 1970	0.35	4.39	59.3	**		
Augur Jr. 1970	0.45	4.30	65.8	**	*	
Lyman Golf 1970	0.10	1.04	18.7			++

*P<.05; **, ++P<.01 Probability that the difference between similarly marked pairs in marsh and upland are due to chance, determined by χ^2.

of a given nest being predated was much less than in the smaller upland colonies (Table 3). In Clarkes Pond in 1969 and 1970, with its much higher absolute predation pressure, the predation pressure per nest was still less than in two of the upland nesting colonies. The result of the lower predation per nest day was that the percentage of nests destroyed by predation in the large colonies of Redwings nesting in marshes was on average significantly lower ($P<.001$) than in the small colonies in uplands.

The average rate of predation was not uniform throughout the season. In most colonies, there was a gradual increase in the average number of nests predated per day as the number of active nests increased. This trend of increasing predation often continued past the peak of nesting activity while the number of available nests was beginning to decline. Thereafter, the predation rate declined but at a proportionately lower rate than the decline in nesting activity. In Figure 2, the average number of active nests per day for consecutive 10-day periods throughout the nesting season is a measure of the number of nests susceptable to predation. The average number of nests predated per day during each 10-day period shows a trend of increasing predation until one or two 10-day periods past the peak of nesting activity. Predation in the Clarkes Pond nesting colony in 1969 and 1970 exhibited a different trend, with predation markedly increasing with an increase in the number of active nests

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Figure 2. Seasonal pattern of nesting activity during consecutive 10-day periods and the average number of nests predated per day and per nest day for each period. The nine 10-day periods begin on April 30, May 10, 20, 30, June 9, 19, 29, July 9, 19.

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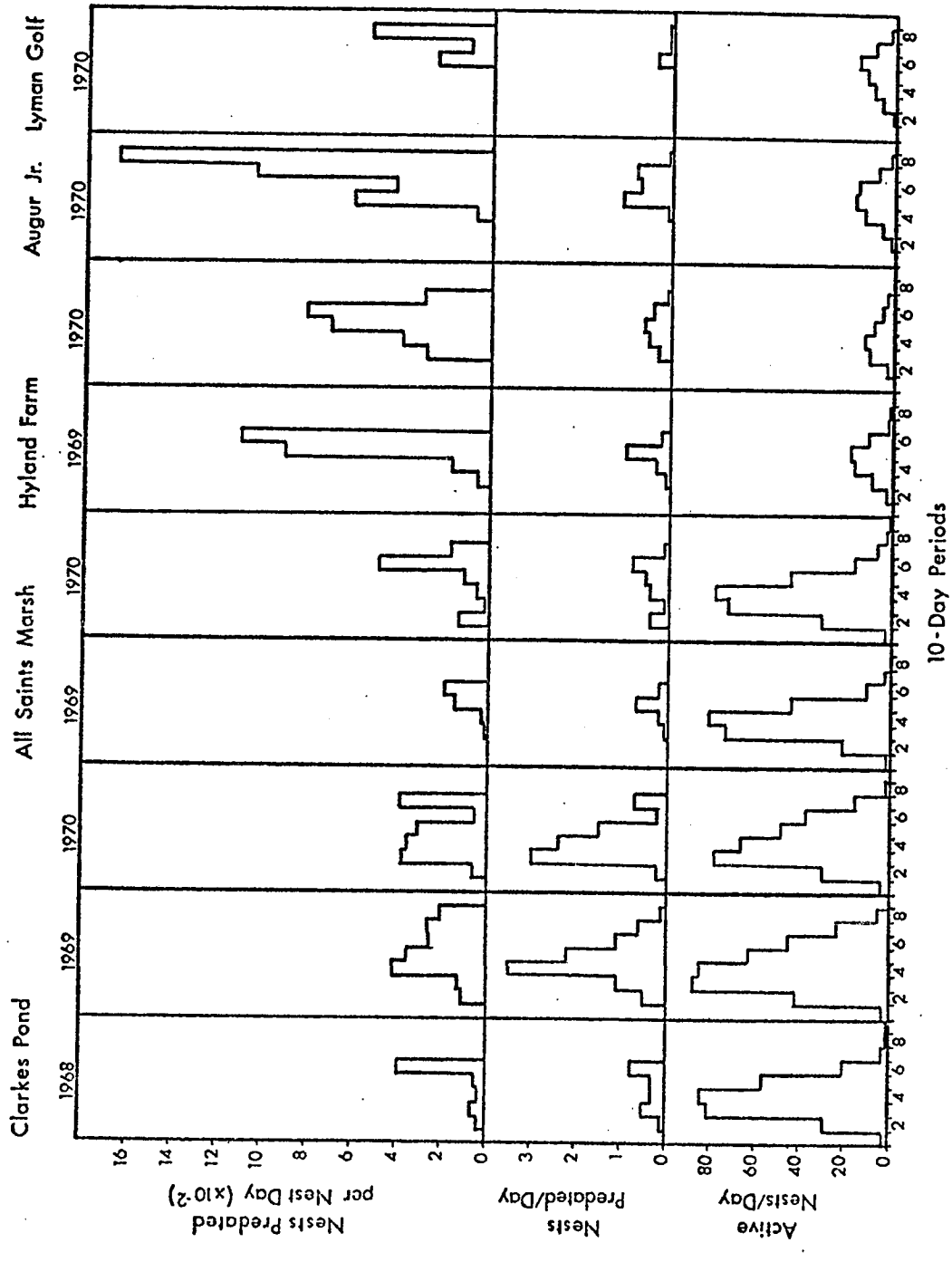

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and declining immediately after the peak of nesting activity. With the exception of Clarkes Pond in 1969 and 1970, the result of the increasing predation beyond the peak of nesting activity was that the average number of nests predated per nest day increased throughout the nesting season (Figure 2). Thus, the probability of a given nest being predated was lower during the peak of nesting activity than at some time after the peak. In two colonies, Clarkes Pond 1968 and All Saints Marsh 1970, the chance of a nest being predated during the peak of activity was also lower than for the period prior to the peak. In the other colonies, the predation pressure on individual nests was slightly lower during the early part of the nesting season than during the period of peak nesting activity or later.

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DISCUSSION

Redwings nesting in large dense colonies in marshes began nesting earlier and were more synchronous by some measures than those nesting in small, less dense colonies in upland habitats. Darling's (1938) hypothesis suggests that these results would be due to greater social stimulation in the larger colonies. It seems more likely, as concluded previously by Orians (1961a), that the variations in timing and synchrony were correlated with the nature of the nesting habitat and its vegetation and not with the size of the breeding colony. In cattail marshes, the dead cattails from previous years provide a favorable structure for nest support and concealment, song perches, and territorial reference points early in the spring prior to the growth of new vegetation. This may promote early nesting, and the abundance of suitable nest sites makes greater synchrony possible. In upland hayfield nesting habitats, the structural features of standing vegetation necessary for nest support and concealment, which are possibly important also for song perches and territorial reference points, are not available until the growth of new vegetation in mid-May. Seasonal growth of vegetation makes nest sites available sequentially in this type of nesting habitat, and consequently reduces the chance of achieving synchrony early in the nesting season in the Redwing's grouped territory or colonial

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nesting system.

Nesting Season Length

A longer period of nesting activity occurred in the larger colonies. Although different from Darling's (1938) observations on gulls, this is in agreement with the observations of Coulson and White (1960) on colonies of the Kittiwake and of Smith (1943) and Orians (1961a) on different sized breeding populations of Redwings. This difference in length of nesting season was due largely to earlier beginning rather than to later finishing of nesting activity in marshes compared with uplands. In view of the phenology of the vegetation, it seems obvious why marsh populations can begin nesting activity earlier in the spring than upland populations. Why they actually do begin earlier requires explanation.

The longer period of nesting activity in the large compared with the small colonies decreases the effect of the lowered predation pressure per nest that is achieved by the saturation of predators due to synchronous nesting. The longer nesting period would therefore increase the total number of nests predated per colony so that natural selection would be expected to favor those individuals breeding during the peak of nesting activity. This would lead to a shortened nesting period which could be achieved by beginning nesting later or terminating earlier or both. Large colony size is even more important than short nesting season in reducing the predation pressure per individual

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nest, so selection would also favor those individuals that joined large colonies. Horn (1970) has suggested that large colony size might decrease the likelihood of a short nesting season; if a colony recruits birds that are in the same reproductive state as those already established in the colony (cf. Orians 1961a, Hailman 1964), then the more birds in the colony, the greater the chance of attracting extreme nesters. The product of these selective forces might be large colonies with long nesting seasons in the habitats that would support them and smaller colonies and shorter seasons elsewhere.

A shorter nesting season might occur in a large colony if recruitment to colonies did not follow the pattern suggested by Orians (1961a). However, a delay in the initiation of nesting in large colonies is unlikely for several reasons. Since Redwings occasionally raise two broods in a single season (Fankhauser 1964), those individuals that breed early in the season would have a better chance at raising a second brood. These individuals would be favored by selection if early breeding and the possibility of a second brood increased the reproductive output during the lifetime of a given bird. Nesting in marshes is known to have higher survival value for Redwings than nesting in uplands (Robertson in prep. a). If selection of breeding habitat by individual birds proceeds from most to least favorable habitats, those birds physiologically most ready to breed in early spring would likely occupy

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the optimal habitats. This would lead to earlier initiation of nesting in marshes than uplands.

Early nesting is also favored by seasonal patterns of predation. Comparisons of predation rates throughout the nesting season consistently indicate that an early nest has a much lower chance of being predated than a late nest; there is a trend of increasing predation pressure per nest as the season progresses (cf. Figure 2). Such a trend would constitute a selective force that would lead to early nesting and decrease the frequency of late nesting. A trend of increasingly heavy predation on tern nests by frigate birds as the season progressed was noted by Ashmole (1963). As he pointed out, a trend of increasing predation that continues at a high level after the peak of abundance has passed will penalize breeding at any time after the first peak. This seasonal trend in predation is probably quite common, with predators becoming aware of a prey population when the prey are abundant, and retaining the pattern of searching after the number of prey has decreased. With selection acting against nesting activity at a time when the risks involved outweigh the potential reproductive output, the probable result of the seasonal trend in predation would be initiation of nesting activity as early in the season as weather and food supply permit, and termination of nesting activity at a time when weather and food are apparently still suitable for raising a brood.

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Further selection pressure, with the same logical conclusion, could be exerted by the relative rates of survival of individual fledglings at different levels in the population dominance hierarchy (Fretwell 1969). Individuals fledged early in the season might achieve higher dominance positions in winter feeding flocks and hence have a better survival rate than individuals fledged later in the season.

Timing of nesting activity to coincide with the period of greatest food abundance may be another reason for early nesting. The proportion of nests with some nestlings dying from starvation was in most cases higher after the peak of nesting activity than during or before the peak (Robertson in prep. b).

Termination of nesting activity at an earlier date is another alternative for achieving a shorter nesting period. While weather might permit a longer nesting season, a combination of factors, including a dominance hierarchy (Fretwell 1969) and seasonal increases in predation and starvation, diminishes the probability of successfully raising a brood late in the season. Consequently, selection would probably lead to a shortened nesting season achieved by this alternative rather than by later initiation. That nesting activity does stop in mid-summer suggests that this is the case.

Synchrony

The causes of a slightly higher degree of synchrony

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in the larger colonies of Redwings are not obvious. Observations were not directed toward the interpretation of these mechanisms, and each of the possible mechanisms discussed by Hailman (1964) and Horn (1970) (see also Schreiber and Ashmole 1970) are potentially applicable. However, caution is needed in interpreting these results to be a consequence of colony size or nesting density alone, since important differences in habitat were correlated with colony size and density. Moreover, it is possible that the same mechanisms are at work in both large and small colonies in the two habitats, but that the phenology of the vegetation in upland habitats precludes the achievement of greater synchrony.

Colony Size, Synchrony, and Predation

For Redwings in the colonies studied, the survival value of synchrony, and especially of large colony size, lies in the reduced predation rate on a percentage basis due to the presence of a large number of prey. While the number of nests predated per day was about the same in some large and small colonies, the percentage of nests predated was lower in the large colonies. This relationship does not necessarily indicate that the local predator population is satiated in the large colonies, because increases in the number of nests in either colony might result in an increased number of nests predated per day. This could occur if increasing colony size in either habitat

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increased the number of nests that were built at the edge of the colony or in other situations that made the nests more susceptable to predation. Clearly, factors other than colony size alone are involved here; at any nesting density nests in uplands are more susceptable to predation than those in marshes. An additional protection from predation would occur in large colonies if the local predator population was satiated so that additional increases in nesting density would not be accompanied by further increases in the number of nests predated. Since local predator populations vary greatly in size, predation capacity, and their ability to locate and destroy nests, the level of nesting density at which predator saturation is reached will vary greatly with habitat, site, and season. A plot of the average number of nests predated per day at different densities of active nests (Figure 3) shows that, in Clarkes Pond 1968 and All Saints Marsh in 1969 and 1970, beyond a certain level, the number of nests predated did not increase with increases in nesting density. For these sites, the chance of a nest being predated decreased as the number of active nests increased. A contrasting pattern, one of density-dependent predation, was observed in Clarkes Pond in 1969 and 1970 where predators continued to show a functional response (Holling 1959) to increased density of prey without reaching a saturation level. As the number of nests increased, the number of nests predated increased proportionately faster and the probability

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Figure 3. Relation of the average number of nests predated per day to the number of active nests in the colony.
CP = Clarkes Pond, AS = All Saints Marsh

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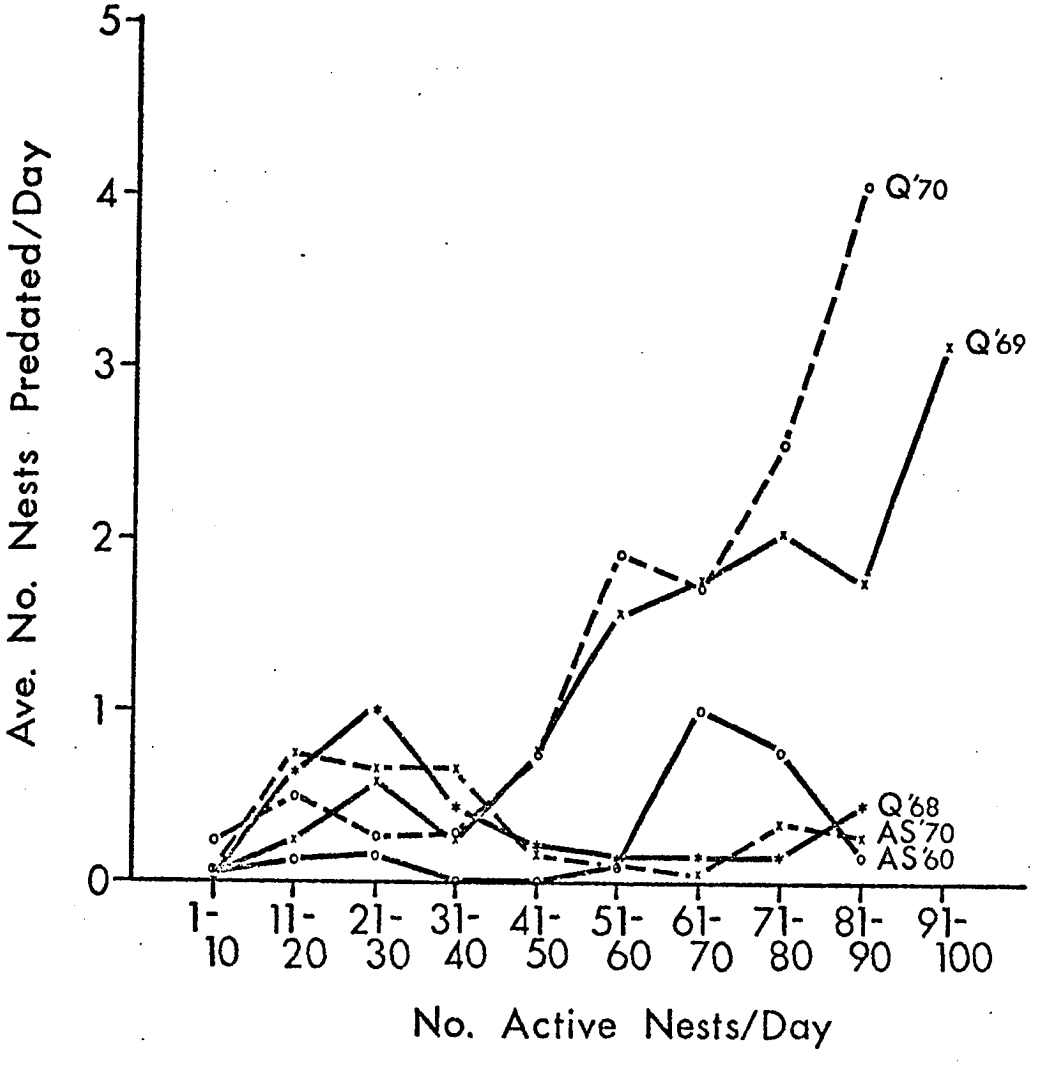

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of a nest being predated was greater. Krebs (1970 and 1971) found a similar pattern of density-dependent predation on nests of the Great Tit (Parus major).

Fautin (1941) suggested that the inverse relationship between colony size and the percentage of nests predated was an important factor contributing to a higher degree of nesting success in large colonies of Yellowheaded Blackbirds (Xanthocephalus xanthocephalus) and Cullen (1960), Kruuk (1964) and Patterson (1965) have observed this relationship for various colonial nesting sea-birds. Smith (1943), in comparing nesting success in different sized colonies of Redwings nesting in marshes, found a significantly larger proportion of eggs predated in small than in large colonies, but the relationship was reversed for nestling predation. The total proportions predated was similar in colonies of different size.

In a colony of any size, if synchrony results in a peak of nesting activity, further protection from predators might be gained by nesting during the peak. As shown in Table 4, in 7 of 9 colonies studied the nests included in the peak of activity (designated as the smallest number of consecutive days required to include 50% of the nests) had a smaller percentage predated than nests after the peak. While only three of these differences are statistically significant, the consistency of the trend suggests that there is survival value in reducing the probability of predation by nesting during the peak of activity.

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Table 4. Percentage of nests predated as a function of time of egg-laying. Peak category includes the nests with clutch completion dates falling within the smallest number of consecutive days required to include 50% of the active nests in each colony. Early and late categories include nests with clutch completion before and after the peak respectively. The number of active nests in each category is shown in Table 5

Site	Percent Nests Predated Early	Peak		Late
Marsh				
Clarkes Pond 1968	4	10	**	30
Clarkes Pond 1969	56	43		46
Clarkes Pond 1970	44	55		38
All Saints Marsh 1969	0	10		23
All Saints Marsh 1970	18	4	**	38
Upland				
Hyland Farm 1969	0	24	*	71
Hyland Farm 1970	0	56		63
Augur Jr. 1970	33	68		90
Lyman Golf 1970	0	31		17

*P<.05 **P<.01

Also, except in Clarkes Pond 1969 and All Saints Marsh 1970, those nests that preceded the peak had less predation than those during the peak. However, nesting success in general, in 6 of the 9 colonies, was greater during the peak than either before or after (Table 5). Of the 3 exceptions, 2 were upland sites (Augur Jr. and Lyman Golf) that had the peak of nesting late in the season. Those nests active before the peak of activity, while perhaps subject to lower predation pressure, are probably affected by uncertain weather conditions early in the season. Patterson (1965) found that in Blackheaded Gulls, pairs laying during the peak had a higher breeding success than pairs laying either earlier or later in the season.

The results of this study, and those of Smith (1943), can probably be interpreted according to Holling's (1959) predation model. In this model, the result of a functional, and in some cases numerical, response by predators to prey density is that "the proportion of prey destroyed increases from zero to some finite prey density and thereafter decreases" (Holling 1959, p. 310). A schematic representation of Holling's model is shown in Figure 4. With the possible exception of some immigration of predators as the season progressed, there is probably no numerical response by predators of Redwing nests. Holling's type 3-b model (Holling 1959) most accurately represents these conditions. Since there is variation in the size

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Table 5. Percentage of nests fledging at least one young as a function of time of egg-laying. Categories are as described for Table 4. The number of active nests in each category is in parentheses

Site	Percent Nests Successful Early	Peak		Late
Marsh				
Clarkes Pond 1968	65(23)	79(70)	**	45(40)
Clarkes Pond 1969	33(18)	47(103)		35(81)
Clarkes Pond 1970	44(18)	33(84)	*	51(65)
All Saints Marsh 1969	77(22)	82(60)	**	27(26)
All Saints Marsh 1970	59(22)	68(69)		51(37)
Upland				
Hyland Farm 1969	0(1)	29(17)		24(17)
Hyland Farm 1970	0(0)	25(16)		19(16)
Augur Jr. 1970	44(9)	14(22)		10(10)
Lyman Golf 1970	70(10)	56(16)		0(6)

*P<.05 **P<.01

Figure 4. A schematic representation of the Holling type predation model as applied to predation on nesting colonies of Redwings. See text for explanation.

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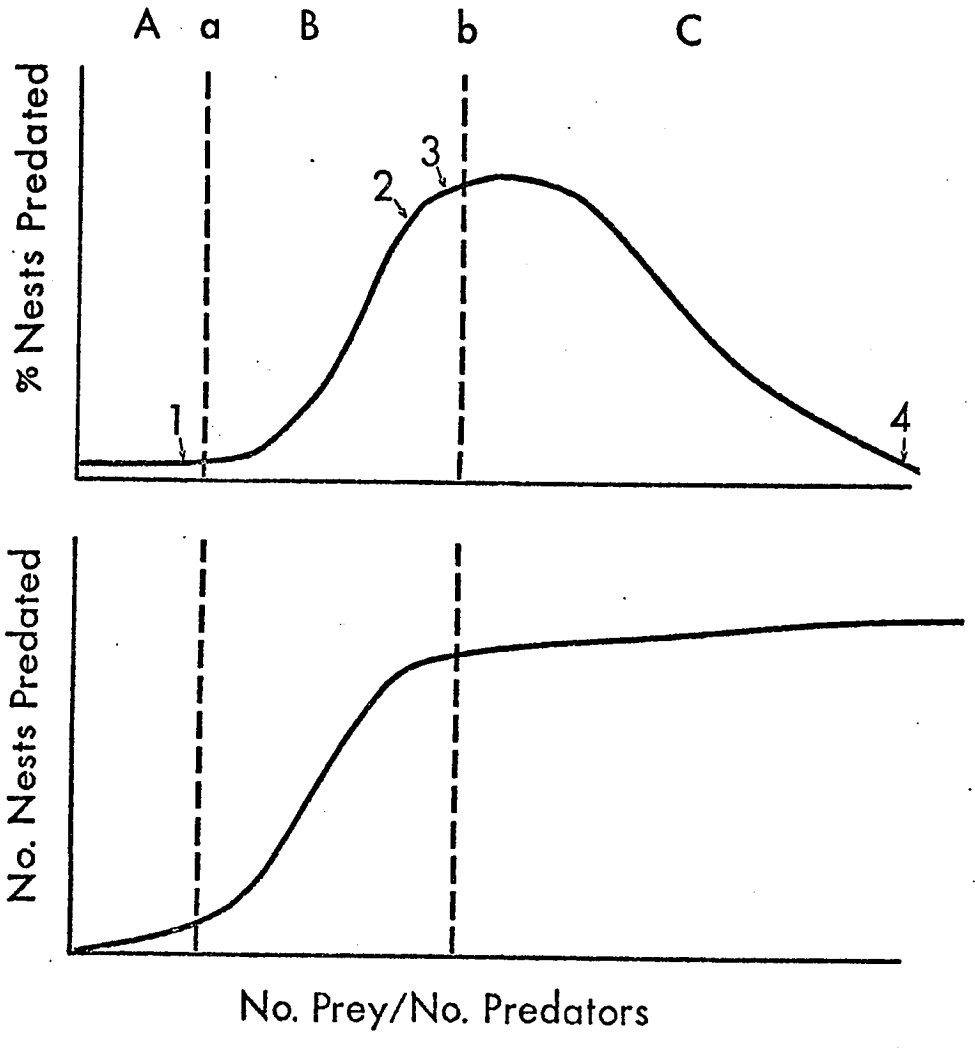

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and capacity of local predator populations between the sites studied, prey density is expressed in relation to predator density so that the different colonies can be represented on a single curve.

In the low prey/predator ratio part of the curves (A), the prey resource is not sufficiently abundant for a predator to specialize on. The proportion of nests predated remains constant while more frequent random finds occur as the prey/predator ratio increases. Most of the small "colonies" of Redwings studied by Smith (1943) consisted of only 1-3 males and females and would perhaps fall within this part of the curve (1). At some prey/predator ratio (a) prey become sufficiently abundant to allow predator specialization. At this threshold, it becomes advantageous for predators to form a search image or develop a searching pattern, and a period of density-dependent predation follows (B). In this prey/predator density range the probability of a nest being predated increases as density increases. The upland Redwing populations, with moderate nesting density, fall within this range (2), and Clarkes Pond in 1969 and 1970, with high nesting density but also high predator populations, perhaps fall somewhere near the end of this range (3). At a relatively high prey/predator ratio (b) another threshold is reached where the predator population approaches satiation. Further increases in prey density result in a decreasing percentage of the nests being destroyed (C).

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All Saints Marsh in 1969 and 1970, Clarkes Pond in 1968 (4), and Smith's (1943) large colony would fall in this range. Smith, by sampling populations of different density extremes, might have found equal predation in both, due to the peaked nature of the predation-prey density curve.

According to this interpretation, increasingly large colonies in either marshes or uplands would be advantageous. However, in a breeding habitat of limited area, breeding density and hence colony size is limited by territoriality (Orians 1961b, Krebs 1971, Robertson in prep. a). In both marsh and upland habitat, territory size is probably related to the abundance of some resource such as food or nest sites. Consequently the marsh and upland nesting colonies observed in this study may represent the maximum size possible for habitats of their respective size and type.

If the interpretation of Smith's (1943) results are correct and the low prey/predator ratio part of the Holling type model is realistic, upland nesting birds could experience lower predation pressure by nesting in smaller colonies or in solitary pairs. However, the upland nesting birds may represent a spill-over from more optimum marsh habitats where colonial nesting is advantageous. There is also a limit to the size of territory that can be defended and the large territories that would be necessary for achieving lower nesting density and smaller colony

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size in uplands may exceed this limit. This assumes all available upland nesting habitats are filled, which probably is not the case. Yet genetic exchange with marsh nesting populations may be responsible for maintaining a grouped territory nesting system in upland habitats.

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SUMMARY

Nesting colonies of Redwings in marshes are larger and tend to be more synchronous than colonies in upland habitats of comparable area, but the duration of nesting activity is longer in large colonies. These variations in timing are probably correlated with the phenology of the vegetation in the nesting habitat and not with the size of the breeding colony. Earlier nesting may be selectively advantageous due to a seasonal trend of increasing predation.

The survival value of large colony size and synchronous nesting, for Redwings in the colonies studied, was a reduced predation rate on a percentage basis due to the presence of a large number of prey. With equal predation pressure, the percentage of nests predated was lower in large colonies. In most large and small colonies, the percentage of nests predated was lower during the peak of nesting activity than later.

The Holling predation model is applied as a possible interpretation of predation rates on different sized nesting colonies.

Larger colonies in uplands might reduce predation on individual nests, but colony size is probably limited by a territorial system that insures adequate abundance of certain resources. Solitary pairs or smaller colonies might also suffer less predation, but genetic exchange

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with marsh populations, where colonial nesting is advantageous, may prevent their occurrence.

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LITERATURE CITED

Ashmole, N.P. 1963. The biology of the Wideawake or Sooty Tern Sterna fuscata on Ascension Island. Ibis 103b: 297-364.

Coulson, J.C., and E. White. 1960. The effect of age and density of breeding birds on the time of breeding of the Kittiwake Rissa tridactyla. Ibis 102: 71-86.

Crook, J.H. 1964. The evolution of social organization and visual communiciation in the weaver birds (Ploceine). Behavior, Suppl. 10: 1-178.

Cullen, J.M. 1960. Some adaptations in the nesting behavior of Terns. Proc. XII Intern. Ornithol. Congr., Helsinki, 153-157.

Darling, F.F. 1938. Bird flocks and the breeding cycle. Cambridge University Press. 124 p.

Fankhauser, D.P. 1964. Renesting and second nesting of individually marked Redwinged Blackbirds. Bird-Banding 35: 119-121.

Fautin, R.W. 1941. Incubation studies of the Yellow-headed Blackbird. Wilson Bull. 53: 107-122.

Fretwell, S.D. 1969. The adjustment of birth rate to mortality in birds. Ibis 111: 624-627.

Hailman, J.P. 1964. Breeding synchrony in the equatorial Swallow-tailed Gull. Amer. Naturalist 98: 79-83.

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Holling, C.S. 1959. The components of predation as revealed by a study of small mammal predation of the European Pine Sawfly. Can. Entomol. 91: 293-320.

Horn, H.S. 1968. The adaptive significance of colonial nesting in the Brewer's Blackbird (Euphagus cyanocephalus). Ecology 49: 682-694.

_____. 1970. Social behavior of nesting Brewer's Blackbirds. Condor 72: 15-23.

Krebs, J.R. 1970. Regulation of numbers in the Great Tit (Aves: Passeriformes). J. of Zool. 162: 317-333.

_____. 1971. Territory and breeding density in the Great Tit, Parus major. Ecology 52: 2-22.

Kruuk, H. 1964. Predators and anti-predator behavior of the Blackheaded Gull (Larus ridibundus L.). Behavior, Suppl. 11: 1-129.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford. 343 p.

_____. 1966. Population studies of birds. Clarendon Press, Oxford. 341 p.

_____. 1968. Ecological adaptations for breeding in birds. Methuen & Co. London. 409 p.

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

Mayr, E. 1941. Redwing observations of 1940. Proc. Linnaean Soc. New York 52-53: 75-83.

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Orians, G.H. 1961a. Social stimulation within blackbird colonies. Condor 63: 330-337.

_____. 1961b. The ecology of blackbird (Agelaius) social systems. Ecol. Monogr. 31: 285-312.

Patterson, I.J. 1965. Timing and spacing of broods in the Black-headed Gull (Larus ridibundus). Ibis 107: 433-459.

Robertson, R.J. in prep. a. Optimal niche space of the Redwinged Blackbird. I. Nesting success in marsh and upland habitat.

_____. in prep. b. Optimal niche space of the Redwinged Blackbird. II. Growth rate and food of nestlings in marsh and upland habitat.

Schreiber, R.W., and N.P. Ashmole. 1970. Sea-bird breeding seasons on Christmas Island, Pacific Ocean. Ibis 112: 363-394.

Smith, H.M. 1943. Size of breeding populations in relation to egg laying and reproductive success in the Eastern Red-wing (Agelaius phoeniceus). Ecology 24: 183-207.

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OPTIMAL NICHE SPACE OF THE REDWINGED BLACKBIRD

III. GROWTH RATE AND FOOD OF NESTLINGS IN MARSH AND UPLAND HABITAT

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Comparisons of the survival value of different parts of the fundamental niche of the Redwinged Blackbird (Agelaius phoeniceus) indicate that marsh nesting habitats and their associated niche parameters represent a more optimal niche space than upland habitats (Robertson in prep. a). The difference in survival value between the two habitats is largely due to differences in the proportion of nests destroyed by predators. However, the relative abundance of food for nestlings might also be expected to play an important role in determining the survival value of a nesting habitat. Marshes are usually more productive than upland habitats and have a food source, in the form of emergent aquatic insects, that is rapidly and continually renewed (Orians 1969). The purpose of this paper is to examine the role of food supply in determining the survival value of a nesting habitat by comparing the types and source of food brought to nestlings, the growth rate of nestlings, and the incidence of starvation in nestling populations of Redwings in marsh and upland habitats.

Food Habits

The food habits of adult Redwings have been extensively studied because of crop depredations associated with their flock feeding behavior (Allen 1914). During the breeding season, animal matter forms a substantial part of the diet (Neff and Meanley 1957, Bird and Smith 1964, Brenner

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1967, Stone 1969), but after the breeding season there is a decrease in the proportion of animal matter and an increase in weed seeds and agricultural grain crops in the diet (Hintz and Dyer 1970). Grain crops used as a food source include sweet corn (Dyer 1967), field corn (Giltz and Stockdale 1960), peanuts (Meanley 1962), grain sorghum, oats, and rice (Neff and Meanley 1957, Orians 1961b).

The food brought to nestlings is usually 100% animal matter, with a preponderance of insects and occasional arachnids, mollusks, and miscellaneous items (Allen 1914, Neff and Meanley 1957, Bird and Smith 1964, Snelling 1968, Orians and Horn 1969, Voigts 1970). In most cases, only the female feeds the nestlings, but occasionally a male assists (Orians 1961b, Case and Hewitt 1963). After the young have fledged, the male regularly feeds them (Beer and Tibbits 1950, Orians 1961b). Some of the food for nestlings is obtained in the vicinity of the nest, but much food is gathered from areas outside the male's territory (Beecher 1942) and in many cases outside the nesting habitat at some distance from the nest (Orians 1961a, Case and Hewitt 1963, Wiens 1965, Snelling 1968).

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METHODS

Two marsh colonies and three upland colonies of Redwings were studied during the breeding seasons of 1968, 1969, and 1970. Table 5 (p. 19) lists the names and years studied for each of the nesting habitats. All of the study areas are within a 25 mile radius of New Haven, Connecticut (see Robertson in prep. a).

Both marsh habitats are freshwater cattail marshes bordered on at least two sides by large stands of deciduous woodland and in close proximity to pasture or early stages of old field succession. Clarkes Pond is an impoundment on the Mill River that covers an area of 4.65 ha; 1.92 ha is occupied by cattails (Typha latifolia and T. angustifolia) and the remaining 2.73 ha is open water with some pond lily (Nymphaea), pickerelweed (Pontederia), and arrowhead (Sagittaria). The flow of the Mill River keeps the water at a fairly constant level year-round. All Saints Marsh covers an area of 1.09 ha, all of which is occupied by a moderately dense stand of Typha latifolia interspersed with small patches of open water. Buttonbush (Cephalanthus occidentalis) forms a dense tangle in some areas. This marsh has no flowing inlet, but in spring and early summer there is a trickling outflow, apparently fed by springs in the marsh. In some years the marsh dries up in late summer. This may account for an apparently low abundance of emergent aquatic insects in this marsh compared with Clarkes Pond.

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The upland sites all consist of rather poor quality hayfields supporting a mixture of timothy (Phleum pratense), bromegrass (Bromus sp.), orchard grass (Dactylis glomerata), red clover (Trifolium pratense) and alfalfa (Medicago sativa). Sturdy "weed" species such as dock (Rumex sp.) are quite abundant and frequently were used as nest support. Hyland Farm (2.68 ha) and Augur Jr. (9.85 ha) are bordered on at least two sides by stands of deciduous woodlands and hedge-rows. Lyman Golf (2.99 ha) is bordered by hayfields and is located about 200 m from a large stand of mixed deciduous trees bordering a small stream. More complete habitat descriptions are recorded in Robertson (in prep. a).

Throughout the nesting season, except during periods of rainy weather, each colony was visited once every three days. Nests were usually located during construction or egg laying and marked with a numbered bamboo pole. On subsequent visits each nest was checked and the following data were recorded: (1) state of nesting progress, (2) number of eggs or nestlings, (3) nestling weight, (4) nestling tarso-metatarsus length (1970 only), (5) occurrence of mortality and its cause, and (6) occurrence of successful fledging. Individual recognition of nestlings was achieved by marking combinations of anterior or posterior, right or left tarsi with a water-proof felt-tipped marking pen. Weights, to the nearest gram, were measured by placing the nestling in a plastic cup (10 g tare weight) and

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weighing with a 100 g capacity Pesola spring balance. Tarso-metatarsus length to the nearest 0.1 mm was measured with vernier calipers using the method described by Kalma (1970). Nestlings were assigned a day number corresponding to the date of hatching, and weight and tarso-metatarsus measurements were recorded by day number. Data were punched on computer cards and analysis of growth rates was done using an IBM 7040/7094 computer.

Samples of the types of food brought to nestlings were obtained using the pipe-cleaner neck collar technique (Willson 1966). Collars were placed on all nestlings in a nest for a period of 30 to 60 minutes, during which the female delivered food. The unswallowed food was then removed from the throat of the nestlings, stored in 70% alcohol for later identification, and the collar removed. A given brood was sampled no more than every three days. The effect of food deprivation for one hour every third day on nestling growth was considered negligible. Many nests were never sampled and many were sampled only once. A total of 169 brood samplings were made and food was obtained in samples from 110 nests. Some females reacted negatively to the collars and tried to remove them rather than feeding the nestlings. In some cases, when food was not swallowed, the female would remove it and, if no nestling would swallow it, eat it herself. This technique is not reliable, therefore, as an absolute measure of feeding rates. However, it is assumed that the food items obtained

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in the samples are representative of the type of food brought to the nestlings, so the technique is very useful for comparative purposes (cf. Orians 1966, Orians and Horn 1969). Food sampling was done throughout the nesting season and at times ranging from early morning to evening. Observations from portable blinds were made to determine the habitat origin of food items brought to nestlings.

In 1969 and 1970, several clutch and brood size manipulations were made to determine whether birds in one habitat were more closely faced by food limitation than the other. It was expected that females would be most capable of raising artificially enlarged broods in the habitat that had the highest relative abundance of food. Transfers of eggs or nestlings were made only between nests known to be of exactly the same stage in the nesting sequence.

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RESULTS

Growth Rate

The mean weight of nestlings at 9 days of age, the last day before fledging when most nestlings were still available for weighing, was 32.39 ± .34 g (±1S.E.) for nestlings from marshes and 32.19 ± .86 g for those from uplands. This similarity in mean weight at fledging suggests the growth rate of nestlings in the two habitats is the same. Comparisons of composite growth curves for all years of the study and for all nestlings of both sexes from marshes and uplands (Figure 1) reveal that the form of the curve for the first 7 days is similar, but that the mean daily weight of nestlings from upland habitats is consistently greater than that for nestlings from marshes. If mean daily weights are treated as paired samples, upland nestlings are significantly ($P<.05$; Wilcoxin Matched Pair Signed Rank Test) larger than marsh nestlings until the time of fledging. Comparison of growth rates, as measured by tarso-metatarsus lengths, gives the same result (Figure 2). However, mean weight and mean tarso-metatarsus length are not significantly different for marsh and upland nestlings at age 9 days. A decrease in mean weight of upland nestlings from day 7 to day 8, and a period of slow tarso-metatarsus growth from day 7 to day 8, result in the previously larger upland nestlings fledging at about the same weight and tarso-metatarsus length as marsh nestlings. Growth

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Figure 1. Growth of Redwing nestlings shown by mean daily weights. Growth curves are composites including nestlings of both sexes for all years of the study.

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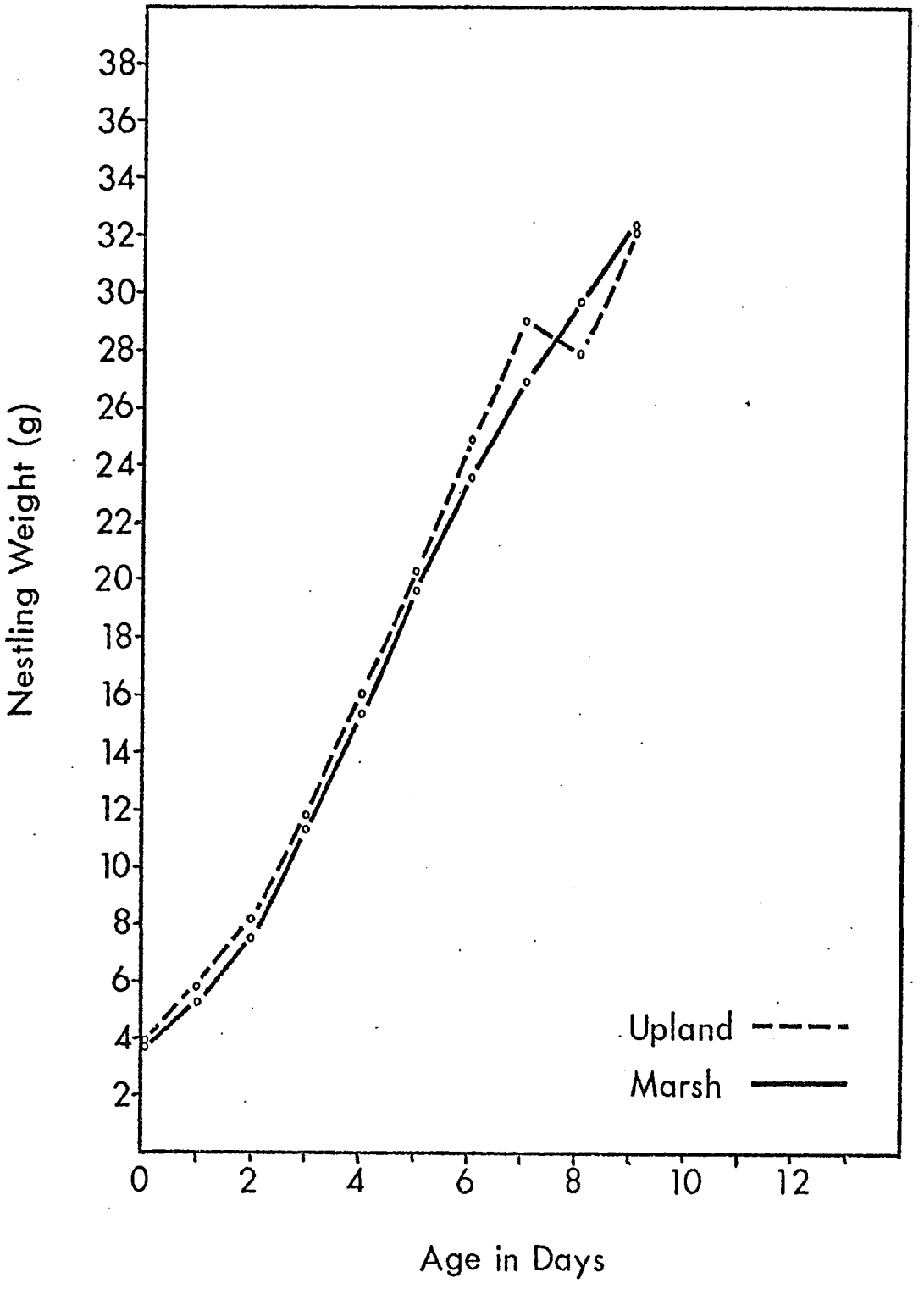

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Figure 2. Growth of Redwing nestlings in 1970 as shown by mean daily tarso-metatarsus lengths (male and female combined).

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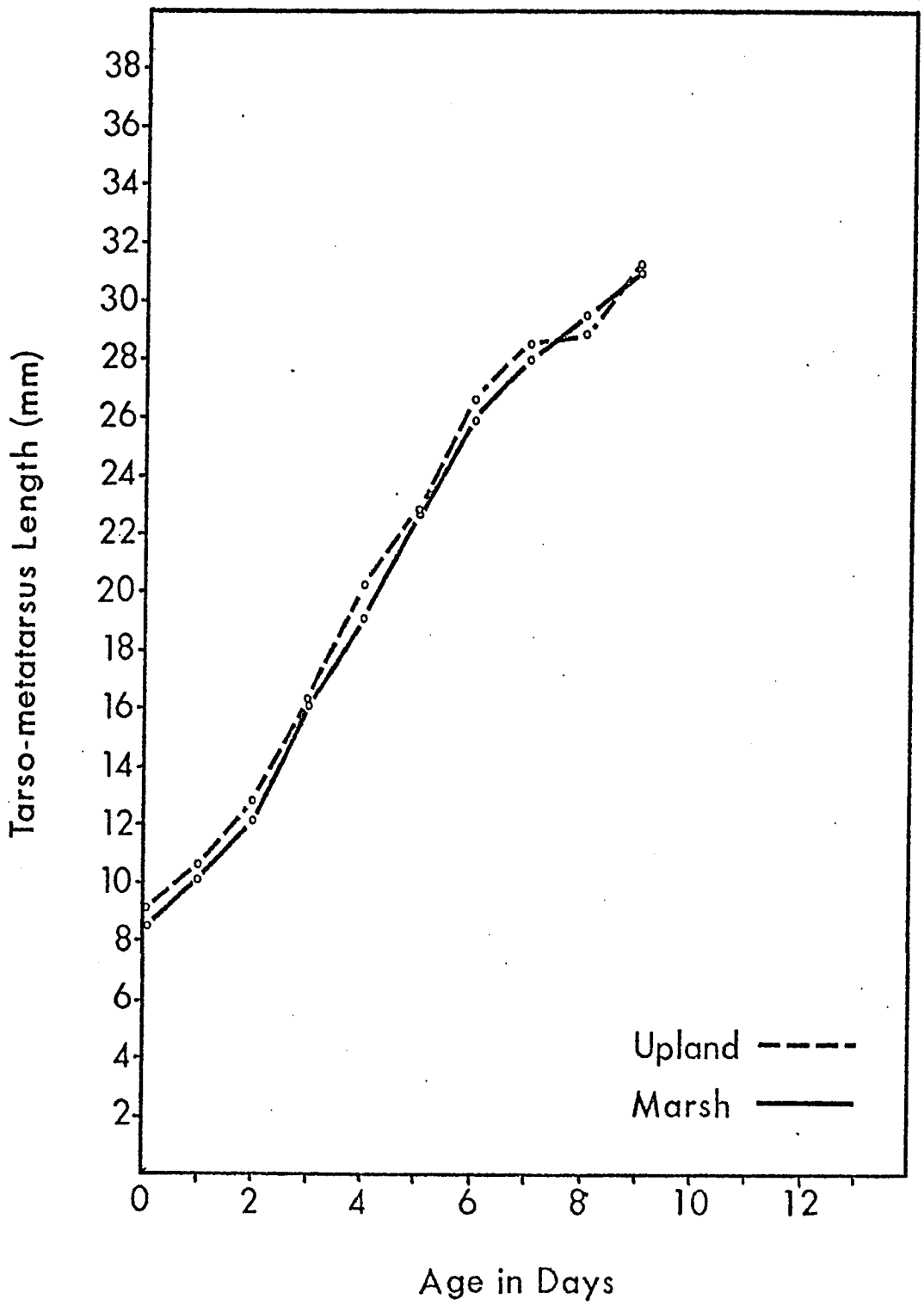

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curves for 1969 and for 1970 analyzed separately have the same form as the combined curve for both years, with the mean daily weight of upland nestlings consistently greater than for marsh nestlings until day 8. In both years, upland nestlings show a decrease in mean weight from day 7 to day 8, resulting in their weight near fledging on day 9 being the same as for marsh nestlings.

To compare the rate of nestling growth in different parts of the nesting season, the season was divided into early, middle, and late portions. Separate analyses indicated that within habitat types there were no significant differences in over-all growth rates, nor between growth rates of nestlings of a given brood size, for nestlings hatched in different parts of the season. Within a given habitat, there were no consistant or significant differences in growth rate or mean weight at fledging between individuals in different sized broods (Table 1).

Redwing Productivity

The initial productivity of individual Redwing females, as measured by clutch size, is on average significantly ($P<.05$) greater in marsh than upland habitats (Table 2). The larger mean clutch size in marshes results from a frequency distribution in which 4 is the most common clutch size (Table 3). In uplands, clutches of 3 and 4 are equally common and clutches of 2 are more common than in marshes. Ignoring the clutches of 1 because of small

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Table 1. Mean weight (in grams ±1 S.E.) on alternate days of all Redwing nestlings from different brood sizes in marsh (m) and upland (u) habitats. The designated brood sizes refer to the number of nestlings in the brood at the time of the first post-hatching observation, when nestling age was 1-3 days

Day		Brood Size 1	2	3	4	5	6
0	m	3.38±.26	3.50±.10	3.62±.06	3.55±.06	3.56±.12	3.80±.13
	u	3.56±.18	2.80±.49	3.92±.10	3.62±.08	3.17±.31	-
2	m	7.56±.56	7.22±.27	7.79±.15	7.47±.12	7.33±.33	7.20±.58
	u	9.25±1.25	8.67±.67	8.30±.27	8.24±.29	6.67±.33	-
4	m	16.43±1.43	16.59±.65	15.20±.35	15.36±.33	15.00±.53	14.57±.90
	u	23.00±3.46	15.00±1.15	15.33±.78	15.94±.69	-	-
6	m	23.59±1.13	23.39±.72	23.64±.47	24.10±.38	20.13±1.57	22.10±1.11
	u	26.00±3.70	25.22±1.15	24.38±1.08	25.21±1.18	-	-
8	m	32.40±1.38	30.89±1.21	29.95±.56	29.72±.54	30.23±1.34	23.94±1.16
	u	29.80±2.82	26.33±.88	26.80±1.40	28.58±.99	-	-

Table 2. Redwing productivity in marsh and upland

	Marsh		Upland
Nests			
No. Full Clutches	654		145
Mean Clutch Size	3.50±.02	*	3.37±.06
Fledged/Successful Nest	2.71±.05	ns	2.49±.13
Area			
No. Active Nests/ha/yr	100.5		7.7
Fledged/ha/yr	132.7		5.4

*P<.05 ns = not significant

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Table 3. Frequency distribution and success of various clutch sizes in marsh and upland. Manipulated clutches are not included

	Clutch Size				
	1	2	3	4	5
Percent(No.)					
Marsh	0.3(2)	4.7(28)	43.0(254)	50.0(295)	2.0(12)
Upland	0.7(1)	10.1(14)	43.5(60)	43.5(60)	2.2(3)
% Successful					
Marsh	100.0	50.0	59.8	61.7	41.7
Upland	0.0	57.1	31.7	43.3	33.3
Fledged/Suc. Nest					
Marsh	1.00	1.64	2.33	3.09	3.80
Upland	0.00	1.38	2.11	3.08	4.00
Fledged/Egg					
Marsh	1.00	0.41	0.46	0.48	0.32
Upland	0.00	0.39	0.22	0.33	0.27

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sample size, the most common clutch size in marshes (4) is also most successful both in the proportion of nests that fledge at least one young and the number fledged per egg laid. However, for those nests that fledged at least one nestling, clutches of 5 are more productive than clutches of 4; the mean fledged per successful nest is directly related to clutch size. In upland habitats, clutches of 2 have a greater percentage successful and fledge a larger proportion of eggs than the more common 3 or 4 egg clutches. As in marshes, the number fledged per successful nest is directly related to clutch size.

The initially larger mean clutch size of marsh nesting Redwings may make some contribution to the productivity as measured by mean number fledged per successful nest (Table 2). Although this figure is not different statistically between the two habitats, because of higher variability and smaller sample size of fledging nests than clutch sizes, marsh nests tend to have a larger number fledged per successful nest than those in uplands.

The combination of greater nesting density and larger number of young fledged per active nest results in productivity measured by the number of young Redwings fledged per hectare being much greater in marshes than in upland habitats (Table 2).

Starvation

Mortality of a small and nearly equal portion of nestlings in both marsh and upland habitats was attributed

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to starvation or a starvation-diarrhea syndrome. The nestlings dying from starvation showed a lower rate of growth than those that eventually fledged (Figure 3). Many of them also failed to form fecal sacs and as a result the nest became fouled (see also Haigh 1968). This sometimes led to a deterioration of condition of the entire brood. Bacterial culture analyses from gastro-intestinal tracts of nestlings that failed to form fecal sacs were done at the University of Connecticut Department of Animal Pathology. These tests provided no evidence of pathogens responsible for the diarrhea aspects of this syndrome (S. Wyant pers. comm.), but this possibility cannot be ruled out. However, since this condition was often preceded by poor weight gain, nestlings in this condition were combined with those dying of starvation per se into a starvation-diarrhea syndrome category, subsequently referred to as "starvation".

Starvation occurred in 18.8% of the broods in marshes and in 17.2% of those in uplands (cf. Table 5). 10.8% of the marsh nestlings and 7.5% of the upland nestlings died of starvation (cf. Robertson in prep. a). Neither of these proportions are significantly different between habitats. Comparisons of the proportion of broods having some starvation also reveal no differences between habitat for each brood size, and no statistically significant differences within habitat between broods of 1, 2, 3, 4, and 5 (Table 4). Broods of 6, which have not been found to

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Figure 3. Comparison of growth (mean daily weight) of nestlings that eventually fledge and those that die of starvation for all marsh nestlings in 1970.

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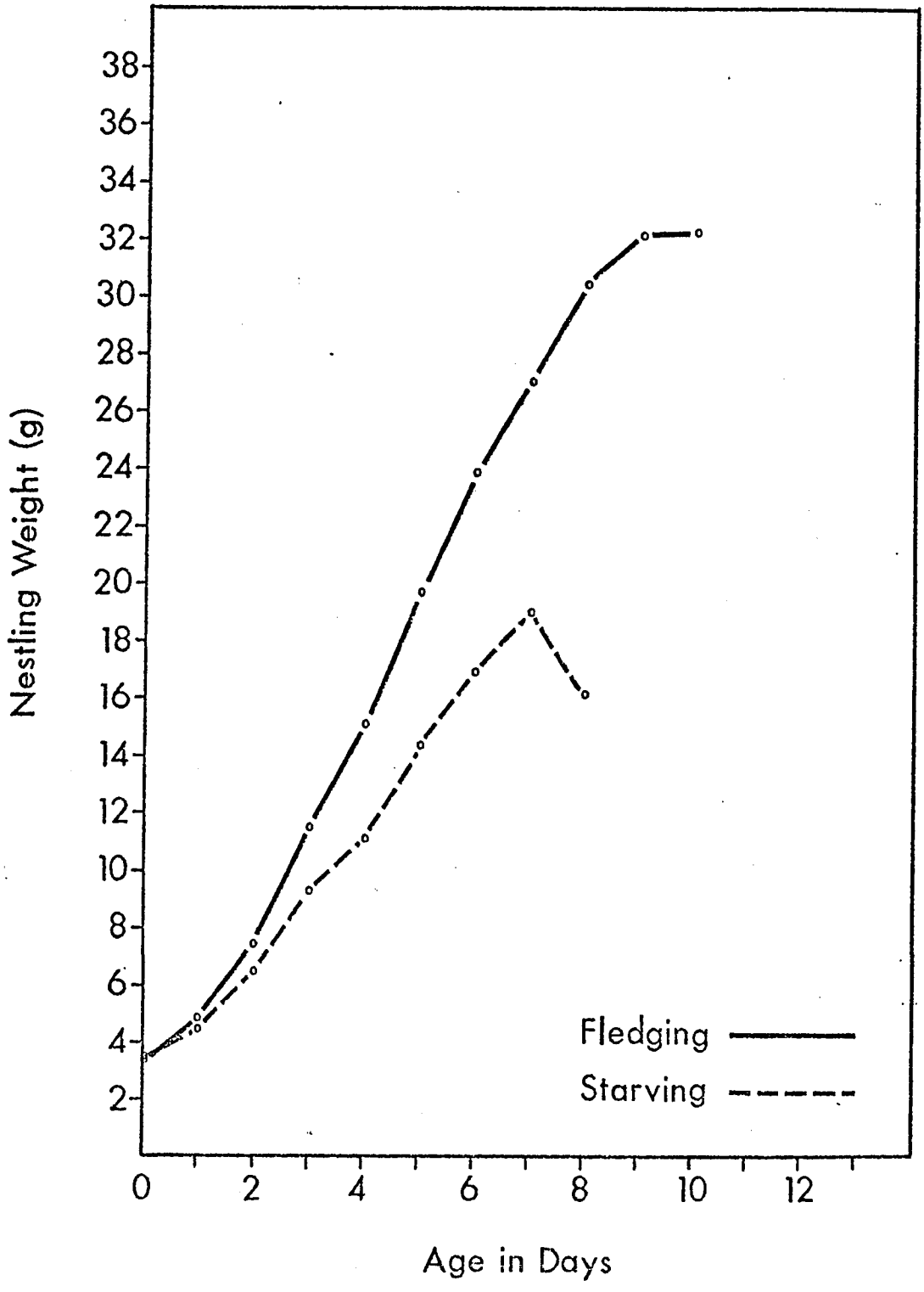

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Table 4. Occurrence of starvation in different sized broods in marsh and upland habitats. All of the broods of 6, and some of the 1's, 2's, and 5's, are products of clutch or brood size manipulations

	Brood Size					
	1	2	3	4	5	6
Number of Broods						
Marsh	33	78	206	171	13	6
Upland	13	14	34	34	1	1
% Broods with some Starvation						
Marsh	0	12	19	22	15	** 100
Upland	0	0	24	26	0	0
% Individuals Starving						
Marsh	0	7	9	6	2	32
Upland	0	0	8	10	0	0

**P<.01 that difference between B6 and smaller broods is due to chance. No other differences between brood size, or between habitats for a given brood size, are significant (χ^2 test).

occur naturally in Connecticut, were obtained by clutch or brood size manipulations. In marshes, a significantly higher proportion of broods of 6 had some mortality by starvation than the smaller brood sizes.

Although the rate of growth and size of nestlings at fledging is the same in different parts of the nesting season, the incidence of starvation increases throughout the season (Table 5). All 9 colonies studied showed a trend of a larger proportion of nests with starvation during the peak of activity (cf. Robertson in prep. b) than before, and 7 of 9 colonies had a larger proportion of nests with starvation after the peak than during the peak of activity.

Type and Source of Food

The proportionate distribution of food types by sample and by food item in the diet of nestling Redwings in marsh and upland habitats is shown in Table 6. Lepidopteran larvae were found in about the same proportion of samples from the two habitats, but they comprised a greater proportion of the individual food items brought to marsh than to upland nestlings. A smaller proportion of marsh than upland samples contained miscellaneous items such as arachnids, spittle insects, and beetles that were known to have a terrestrial origin; these items made up a significantly smaller portion of the marsh nestling's diet. Conversely, a larger proportion of marsh than

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Table 5. Percentage of broods with some nestlings starving as a function of time of egg-laying. Peak category includes nests with clutch completion dates falling within the smallest number of consecutive days required to include 50% of the active nests in each colony. Early and late categories include nests with clutch completion before and after the peak respectively. The number of broods in each category is in parentheses

Site	Percent Nests with Some Starvation					
	Early		Peak		Late	Total
Marsh						
Clarkes Pond 1968	0 (18)		3.5(57)		4.0(25)	3.0(100)
Clarkes Pond 1969	0 (12)		2.9(69)	**	43.7(48)	17.8(129)
Clarkes Pond 1970	0 (14)		0 (46)	**	24.4(41)	9.9(101)
All Saints Marsh 1969	5.9(17)		23.2(56)	**	76.5(17)	30.0(90)
All Saints Marsh 1970	0 (14)	*	35.9(53)		51.7(29)	35.4(96
Total						18.8(516)
Upland						
Hyland Farm 1969	0 (1)		11.1(9)		25.0(12)	18.2(22)
Hyland Farm 1970	0 (0)		0 (6)		25.0(4)	10.0(10)
Augur Jr. 1970	0 (8)		18.2(11)		0 (6)	8.0(25)
Lyman Golf 1970	12.5(8)		50.0(14)		0 (2)	33.3(24)
Total						17.2(99)+

*P<.05 **P<.01
+Total includes 18 nests from other upland sites

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Table 6. Proportionate distribution of food types by sample and food item in the diet of nestling Redwings in two habitats. A sample includes the food delivered to all individuals in a brood during a sampling period

	Samples		Items	
	Marsh	Upland	Marsh	Upland
Number	89	21	500	135
Percent with Terrestrial food source				
Lepidopteran larvae	74	71	42	26
Misc. terrestrial	29	71	13	72
Total	-	-	55	98
Aquatic food source				
Odonata	37	5	21	1
Misc. aquatic	31	0	12	0
Total	-	-	33	1
Unidentified food source				
Misc.	40	5	12	1

All pairwise proportionate differences are significant ($P<.01$) determined by χ^2, except samples of Lepidopteran larvae.

upland samples contained odonates and other food items of aquatic origin, as well as items of uncertain habitat origin, and these items also comprised a significantly larger portion of the diet of marsh nestlings. Many single samples from marsh nests contained both items from aquatic and terrestrial habitats. At least 54% of the items in the diet of marsh nestlings were obtained from terrestrial habitats and 33% were from aquatic habitats. Ninty-eight percent of the food items in the upland nestling's diet were from terrestrial habitats.

There were also differences in the proportionate distribution of nestling food items between individual marshes. Lepidopteran larvae comprised a significantly ($P<.01$) larger proportion of individual food items brought to nestlings in All Saints Marsh (57%) compared with Clarkes Pond (34%), and odonates comprised a larger proportion ($P<.01$) in Clarkes Pond (31%) compared with All Saints Marsh (1%). No differences in proportionate distribution of food items occurred between upland habitats.

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DISCUSSION

The growth rates of nestlings from marsh and upland habitats are slightly different in that, until day 7, upland nestlings are consistently larger than marsh nestlings. These growth curves, with minor differences in form at various stages of nestling development, may have a physiological basis that is related to acclimatization to different microclimatic conditions in marshes and uplands. Parker (1968) found that Redwing nestlings from upland habitats developed the capability of thermoregulation at an earlier age than marsh nestlings, and suggested that more frequent cold stress in the uplands stimulated hormonal controls that result in this developmental change. Parker (1968) and Dyer (1968) also found upland nestlings to have a lower respiratory quotient than marsh nestlings. Although the pattern of weight difference found in this study is inconsistent with expectations based on differences in the development of homeothermy as found by Parker (1968), the fact that physiological differences may occur between nestlings from marshes and uplands gives some basis for expecting slightly different forms in the growth curve.

The decrease in mean nestling weight from day 7 to day 8 that was observed in upland habitats, while consistent between years and sites, did not occur in marsh nestlings. It is possible that this marked change in growth rate is related to rapid feather development at this age

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(Holcomb and Twiest 1970), but it is not clear why a similar change was not observed in marsh nestlings. If upland nestlings were under more stress for food than marsh nestlings, a rapid developmental change might be accompanied by weight loss. However, since there was no more starvation in one habitat than the other and the mean weight at fledging and the number fledged per brood was nearly the same between habitats, there is no evidence to suggest that nestlings in one habitat were under greater food stress than in the other.

The growth rates of nestlings in marshes and uplands are similar in that they result in the same average weight at fledging for nestlings in both habitats. Since weight at fledging is probably correlated with post-fledging survival (cf. Lack 1968), the slight differences in the size of nestlings during the early part of the nestling phase are probably not important in terms of subsequent survival. That nestlings from both habitats fledge at the same weight and stage of development, as shown by tarso-metatarsus length, indicates that their growth to fledging is ecologically similar and that the probability of subsequent survival, as related to developmental stage, is similar. This suggests that the relative abundance of food is roughly equal for females nesting in marshes and uplands. Holcomb and Twiest (1970) also reported that there was no difference in growth of Redwings raised in either marsh or upland habitat, but they noted some

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brood reduction in uplands that was apparently attributed to starvation (cf. Parker 1968). Although there was no differential starvation or brood reduction between habitats in this study, there was an increase in the occurrence of starvation late in the season (cf. Table 5) while the growth rate showed no seasonal trends. Rate of growth, and mean weight at fledging, when used alone, are therefore not necessarily good indicators of the availability of food for nestlings. A difference between habitats in the proportion of broods with some nestlings starving is a better indicator of the relative abundance of food.

Measured by either index, the relative abundance of food was apparently equal for nestlings in marsh and upland habitats. The fact that there was no differential starvation between habitats in broods of a given size, especially large broods, is also indicative of similarity in relative abundance of food.

Within a given habitat, the growth rate and incidence of starvation were the same for broods of different size (cf. Royama 1966, Ricklefs 1968). Brenner (1964) made similar observations and also noted a constancy of growth rate throughout the season. This relationship, and the fact that, compared with smaller broods, a significantly larger ($P<.01$) proportion of the artificially enlarged broods of 6 had some nestlings starve, suggest the brood size of females is adapted to the number of offspring that the parents can nourish (Lack 1954).

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Starvation resulted in the mortality of about 10% of the nestlings in both marsh and upland habitats. Predation accounted for a greater proportion of mortality in both habitats, but especially in uplands where 34% of the nestlings were taken by predators (Robertson in prep. a). In a study of Redwings nesting in marshes in Illinois, starvation accounted for the mortality of less than 1% of the nestlings (Smith 1943). In Wisconsin, Young (1963) recognized no starvation; however, some of the mortality where nestlings were found dead in the nest (5.2%) or had disappeared (24.1%) may have been due to starvation (Haigh 1968). During a three year study in eastern Washington, Haigh (1968) found that between 40.7% and 58.6% of the nestlings died of starvation, the most common single cause of nestling mortality.

The difference in the incidence of starvation between marsh habitats in eastern Washington and habitats in Illinois or Connecticut may be ultimately due to competitive interactions between Redwings and Yellowheaded Blackbirds (Xanthocephalus xanthocephalus) in western North America where the two species are sympatric. Marshes in general are more productive in the arid and semiarid regions of the West than in the humid regions of central and eastern North America (Orians and Horn 1969), and the geographic range of the Yellowhead is limited to those regions where the productivity of lakes and marshes is high (Willson and Orians 1963). In the zone of sympatry, Redwings are

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excluded by Yellowheads from the most productive marshes, or at least are forced to nest near wooded shores (Willson and Orians 1963, Orians 1966, Miller 1968). Therefore, Redwings are not able to take advantage of the food supply of the most productive western marshes and must rely on upland habitats as a source of a large portion of their food (Orians and Horn 1969). Since the upland foraging areas in the West are probably not as productive as the eastern deciduous forests, where Redwings obtain large numbers of lepidopteran larvae, the relative availability of food is perhaps lower, and the incidence of starvation higher, in the arid regions of the Redwing's geographic range.

In both marshes and uplands, female Redwings spend a large portion of their foraging time in the stands of mixed deciduous woodland that border the nesting habitat. Observations revealed these woodlands to be the source of lepidopteran larvae that occurred in over 70% of the food samples from nests in either habitat. Wiens (1965) found that Redwings nesting on Lake Wingra in Wisconsin obtained the bulk of their food (lepidopteran larvae) in the hardwood forests bordering the marsh, and Snelling (1968), on the same marsh, reported that female Redwings spent 16% of their time foraging on the marsh and 45% of their time off the marsh, presumably foraging a large portion of this time. This would suggest that marsh nesting Redwings have little advantage over upland birds in terms

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of the availability of food within the nesting territory. However, the time and energy expenditure for food gathering would perhaps be lower for marsh than upland nesting females because the largest food items (odonates) are obtained near the nest site. Also, comparisons between two marshes of different productivity indicate the emergent insects, especially odonates, are an important component of the diet in the dense marsh nesting colonies. Odonates comprised a significantly larger portion of the diet of nestlings in Clarkes Pond than in All Saints Marsh. Both marshes are bordered by deciduous woodlands that are probably equally productive of Lepidoptera, but subjective observations of the abundance of adult odonates indicate All Saints Marsh was less productive of Odonata than Clarkes Pond. This difference in marsh productivity is likely responsible for a larger proportion ($P<.01$) of the nests having some mortality due to starvation in All Saints Marsh than in Clarkes Pond (cf. Table 5).

It was suggested the relative abundance of food is similar for nestlings in marshes and uplands, therefore the absolute abundance of food must be much greater in marshes that support much larger and denser nesting colonies than are found in uplands (cf. Table 2). Since clutch size and the number fledged per successful nest is nearly the same in both habitats, while nesting density differs considerably, it would appear that breeding populations may be adjusting their density to suit local conditions

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of food availability (cf. Brenner 1966). The occurrence of some starvation in all colonies suggests that no breeding populations were nesting at a density far below the maximum level possible for the available food. On the other hand, it is possible that in a sample of nests from any breeding population, regardless of the relative abundance of food, there will be some starvation due to individual differences in food getting ability of females. In any case, the relationship between breeding density and food is not simple because complex patterns of social behavior are often the proximate regulators of density and the ultimate factors are difficult to determine (Willson and Orians 1963). Obvious differences in the phenology of vegetation used as nest support are also correlated with differences in nesting density. However, the absolute abundance of food is likely another ultimate factor in the determination of nesting density as regulated by territory size.

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SUMMARY

Growth rates of Redwing nestlings in marsh and upland habitats are similar in that they result in the same mean weight at fledging. They are different in that, until 8 days of age, upland nestlings are consistently larger.

The percentage of nests with some nestlings starving, and the percentage of nestlings that die from starvation are similar in both habitats. The mean number fledged per successful nest is also similar between habitats.

It is suggested that the relative abundance of food is approximately the same for nestlings in either marshes or uplands, but that a higher absolute abundance of food in marshes makes large, dense nesting colonies possible. The relationship between nesting density and food supply is not simple because obvious differences in the phenology of vegetation used as nest support are also correlated with colony size and density.

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LITERATURE CITED

Allen, A.A. 1914. The red-winged blackbird: a study in the ecology of a cat-tail marsh. Proc. Linn. Soc. N.Y. 24-25: 43-128.

Beecher, W.J. 1942. Nesting birds and the vegetation substrate. Chicago Ornith. Soc. 69 p.

Beer, J.R., and D. Tibbitts. 1950. Nesting behavior of the red-wing blackbird. Flicker 22: 61-77.

Bird, R.D., and L.B. Smith. 1964. The food habits of the red-winged blackbird, Agelaius phoeniceus, in Manitoba. Can. Field Naturalist 78: 179-186.

Brenner, F.J. 1964. Growth, fat deposition, and development of endothermy in nestling red-winged blackbirds. J. Sci. Labs. Denison Univ. 46: 81-89.

_____. 1966. The influence of drought on reproduction in a breeding population of Redwinged Blackbirds. Amer. Midl. Naturalist 76: 201-210.

_____. 1967. Seasonal correlations of reserve energy of the red-winged blackbird. Bird-Banding 38: 195-211.

Case, N.A., and O.H. Hewitt. 1963. Nesting and productivity of the red-winged blackbird in relation to habitat. Living Bird 2: 7-20.

Dyer, M.I. 1967. An analysis of blackbird flock feeding behavior. Can. Jour. Zool. 45: 765-772.

_____. 1968. Respiratory metabolism studies on red-winged blackbird nestlings. Can. Jour. Zool. 46: 223-233.

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Giltz, M.L., and T.M. Stockdale. 1960. The redwinged blackbird story. Ohio Agr. Exper. Sta. Special Circular 95, 18 p.

Haigh, C.R. 1968. Sexual dimorphism, sex ratios and polygyny in the Red-winged Blackbird. Ph.D. Dissertation. Univ. of Washington 116 p.

Hintz, J.V., and M.I. Dyer. 1970. Daily rhythm and seasonal change in the summer diet of adult Redwinged Blackbirds. J. Wild. Man. 34: 789-799.

Holcomb, L.C., and G. Twiest. 1970. Growth rates and sex ratios of Redwinged Blackbird nestlings. Wilson Bull. 82: 294-303.

Kalma, D.L. 1970. Some aspects of the breeding ecology and annual cycle of three populations of the Rufous-Collared Sparrow (Zonotrichia capensis) in western Panama. Ph.D. Dissertation, Yale University. 218 p.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford. 343 p.

_____. 1968. Ecological adaptations for breeding in birds. Methuen and Co., London. 409 p.

Meanly, B. 1962. Feeding behavior of the Red-winged Blackbird in the Dismal Swamp region of Virginia. Wilson Bull. 74: 91-93.

Miller, R.S. 1968. Conditions of competition between Redwings and Yellowheaded Blackbirds. J. Anim. Ecol. 37: 43-61.

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Neff, J.A., and B. Meanley. 1957. Blackbirds and the Arkansas rice crop. Univ. Ark. Agr. Exp. Sta. Bull. 584. 89 p.

Orians, G.H. 1961a. Social stimulation within blackbird colonies. Condor 63: 330-337.

_____. 1961b. The ecology of blackbird (Agelaius) social systems. Ecol. Monogr. 31: 285-312.

_____. 1966. Food of nestling Yellow-headed Blackbirds, Cariboo Parklands, British Columbia. Condor 68: 321-337.

_____. 1969. On the evolution of mating systems in birds and mammals. Amer. Naturalist 103: 589-603.

Orians, G.H., and H.S. Horn. 1969. Overlap in food and foraging of four species of blackbirds in the potholes of central Washington. Ecology 50: 930-938.

Parker, G.H. 1968. On the development of temperature regulation in Red-Winged Blackbird (Agelaius phoeniceus) nestlings from two habitats. M.S. Thesis. Univ. Guelph. 34 p.

Ricklefs, R.E. 1968. Patterns of growth in birds. Ibis 110: 419-451.

Robertson, R.J. in prep. a. Optimal niche space of the Redwinged Blackbird. I. Nesting success in marsh and upland habitat.

_____. in prep. b. Optimal niche space of the Redwinged Blackbird. II. Spatial and temporal patterns of nesting activity and success.

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Royama, T. 1966. Factors governing feeding rate, food requirement, and brood size of nestling great tits, Parus major. Ibis 108: 313-347.

Smith, M. 1943. Size of breeding populations in relation to egglaying and reproductive success in the Eastern Red-wing (Agelaius phoeniceus). Ecology 24: 183-207.

Snelling, J.C. 1968. Overlap in feeding habits of red-winged blackbirds and common grackles nesting in a cattail marsh. Auk 85: 560-585.

Stone, C. P. 1969. Phenetic variation of breeding Red-winged Blackbirds in Ohio. Ohio Coop. Wild. Res. Unit. Quart. Rept. Oct-Dec 1969. p. 15-22.

Voigts, D.K. 1970. Comparative food habits of two Iowa marsh icterids. M.S. Thesis. Iowa State University. 53 p.

Weins, J.A. 1965. Behavioral interactions of redwinged blackbirds and common grackles on a common breeding ground. Auk 82: 356-374.

Willson, M.F. 1966. Breeding ecology of the yellow-headed blackbird. Ecol. Monogr. 36: 52-77.

Willson, M.F., and G.H. Orians. 1963. Comparative ecology of red-winged and yellow-headed blackbirds during the breeding season. Proc. XVI Int. Congr. Zool. 3: 342-346.

Young, H. 1963. Age specific mortality in the eggs and nestlings of blackbirds. Auk 80: 145-155.

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