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**Resource availability, breeding site selection,
and reproductive success of red-winged blackbirds**

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Abstract Red-winged blackbirds are polygynous and show strong breeding site preferences, but it is unclear which environmental factors regulate their reproductive success and are ultimately responsible for shaping their patterns of habitat selection and their mating system. We evaluated the effect of variation in insect emergence rates on the reproductive success of male and female redwings nesting on replicate ponds. The number of male and female redwings that settled on a pond varied two- to three-fold among ponds, but was not related to insect emergence rates. Insect emergence rates had a positive effect on the number of nestlings successfully fledged by females, the number of nestlings fledged from male territories, and on the mass of nestlings at fledging. *Typha* stem density also varied widely among ponds, and was positively related to male and female settling density and mass of nestlings at fledging, but not to the number of nestlings fledged by females or males. We conclude that alternative breeding sites differ in their ability to support redwing reproduction, and that the availability of emerging odonates is an important environmental factor influencing the reproductive success of both male and female red-winged blackbirds.

Key words Aquatic insects · Habitat selection · Harem size · Marsh · Polygyny

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Introduction

Fretwell and Lucas (1970; Fretwell 1972) pioneered the development of a general theory of habitat selection. They pointed out that habitats may vary in their suitability, and that in order to understand habitat selection behavior, we should first consider environmental factors such as resource availability because they are the selective agents which have shaped behavior. Although Fretwell and Lucas developed their arguments in an effort to explain the spatial distributions of breeding passerine birds, relatively few of the subsequent studies of passerines have linked measurements of food availability with observations of breeding site selection and reproductive success. In this study we examine the relationships among food availability, breeding site selection, and the reproductive success of the red-winged blackbird (*Agelaius phoeniceus*).

The red-winged blackbird is a socially polygynous songbird that forms dense breeding colonies in marshes throughout much of the New World (Beletsky 1996). Redwings often forage in marshes on aquatic insects, particularly on emerging Odonata (Snelling 1968; Orians 1980; Patterson 1991). Orians (1969) suggested that the polygynous mating system of the red-winged blackbird evolved because marshes are patchy habitats with some areas holding more food than others, but few studies of redwing reproductive success have explicitly considered the food resources provided by marshes. Orians (1980; Beletsky and Orians 1996) observed that redwings nesting on two marshes with consistently large emergences of odonates fledged the same number of young from each nest as redwings nesting on two marshes with very few emerging odonates. Observational studies may be confounded though by the effects of female density: if reproductive success is density dependent and females select breeding sites in an ideal free manner, then breeding density, but not reproductive success, will reflect habitat suitability (Fretwell and Lucas 1970; Fretwell 1972). In an experimental study, Ritschel (1985)

increased food availability in one portion of a marsh after females had settled, and found no effect on the number of nestlings successfully fledged, but nestling growth rates were higher in the area with supplemental food. In sum, it has been hypothesized that food limitation plays an important role in shaping the habitat selection behavior and mating system of redwings, but there is little evidence to date that food availability within breeding territories affects redwing reproductive success (Searcy and Yasukawa 1989, 1995).

Although the role of food availability in determining redwing reproductive success is not well understood, a number of studies have attempted to link other features of the breeding environment to redwing reproductive success. Female reproductive success has been found to be correlated with water depth at the nest site, nest height, nest cover, vegetation type and density, proximity of nest to predators, and proximity to a prominent perch (e.g., Robertson 1972; Holm 1973; Weatherhead and Robertson 1977; Lenington 1980; Picman 1980; Ritschel 1985; Yasukawa et al. 1992). In particular, several studies have documented a relationship between natural variation in *Typha* density and the breeding density and performance of red-winged blackbirds (Weatherhead and Robertson 1977; Lenington 1980; Picman 1980). The specific results of these studies are somewhat inconsistent, but taken together they show that environmental factors other than food can influence redwing breeding site selection and reproductive success. The goal of this paper is to evaluate the influence of food resources on redwing breeding site selection and reproductive success.

Here we report the results of a study that tested the hypotheses that odonate emergence rates and *Typha* stem density are related to the settling patterns and reproductive success of red-winged blackbirds nesting on an array of ponds. Because our study ponds are virtually identical to each other except for variation in odonate emergence rates and *Typha* stem density, we can test our hypotheses without the complicating influence of variation in other environmental features. Further, by using entire ponds as our units of observation, we are able to evaluate the effects of environmental variation on redwing reproductive ecology at a scale similar to natural variation in environmental characteristics (e.g., Carpenter 1991). Our results show a strong positive relationship between odonate emergence rates and redwing reproductive success, but no relationship between odonate emergence rates and redwing breeding density, illustrating an apparent lack of concurrence between the environmental cues used in habitat selection and the environmental features regulating reproductive success.

Materials and methods

The experimental system

We studied a population of redwings breeding at the Experimental Ponds Facility of Michigan State University Kellogg Biological

Station (KBS) in southwestern Michigan (42°24'N, 85°24'W) in 1990. The Experimental Ponds Facility consists of 18 replicate ponds, each 29 m in diameter, 2 m in depth, and separated by 5 m. Each pond has a breeding population of redwings (observations of banded males show that male territories at this site do not include more than one pond), so we can relate the environmental characteristics of a pond to the average reproductive performance of birds breeding on that pond. Eight of the ponds attracted a total of 23 males and 72 females (mean male territory size = 402 m²); the remaining ten ponds contained sparse *Typha* stands and attracted few territorial males and no nesting attempts. Male red-winged blackbirds defend territories along the margins of the ponds, and females construct nests in the ring of *Typha latifolia* that encircles each pond (1.9–3.7 m in width).

We drained five of the eight ponds in early March, prior to the arrival of male redwings, in an effort to increase the among-pond variance in odonate emergence rates. A combination of drying and subfreezing temperatures killed many of the odonate larvae that overwinter in these ponds. After several days, the ponds were refilled to their original level, creating an array of ponds with substantial variation in the production of emergent odonates (see Results), but no differences in water level. Because we were interested in the effects of odonate emergence rates on redwing reproduction, and not the effects of pond draining per se, we chose to use odonate emergence rates as an independent variable in a regression analysis of food effects.

Monitoring

Redwing settling patterns were determined by mapping male territories and monitoring female nesting attempts. Territories of males, most of whom (19 of 23) were banded with colored leg bands, were delimited through observations of agonistic encounters and displays. Male reproductive success is calculated in this study as the performance of nests within a male's territory, although other studies have shown that 20–30% of the offspring in a territory are the products of extrapair copulations (Gibbs et al. 1990; Westneat 1993). We searched the ponds daily for nests, which were usually discovered while they were under construction. We estimated the number of females that settled on a pond from the number of nests initiated prior to mid-June. A few nests (less than ten) were initiated after mid-June, but tracking of banded females ($n = 26$) showed that each banded female initiated a single nest prior to mid-June, and that nest initiations after mid-June were second attempts by females who had suffered early nest failures. Therefore, we elected to exclude nests initiated after mid-June from the analyses, and assumed that each nest considered in the analyses corresponds with a single female.

We monitored nests by visiting them daily, and recorded whether nestlings died or successfully fledged from the nest. Nestlings were weighed to the nearest 0.1 g with a Pesola spring scale each day through 9 days of age (nestlings fledged at 10–12 days of age). We did not weigh nestlings on unseasonably cold or rainy days in order to avoid stressing them unduly.

The importance of starvation-related mortality was estimated using two methods. First, we assumed that if nestling mortality was preceded by a daily weight gain of less than 1 g that death was starvation related. Second, we calculated the proportion of total mortality associated with partial nest losses (cases in which some nestlings live while others in the same brood die between observations).

Redwings typically feed on odonates as the larvae climb from the water and onto a plant stem, shed their exuviae, and cling to the vegetation while their exoskeletons harden (Orians 1980). Therefore, we measured odonate availability by using floating emergence traps (Cook and Horn 1968). *Typha* stems were cut off 20 cm above the waterline, and a covered trap was placed over the cut stems. One trap (0.45 m²) was placed into each pond, and emerging odonates caught by the trap were censused daily and removed. We rotated each trap to a new randomly chosen location every 6 days, and operated the traps from 18 May through 16 June.

We measured the density of *Typha* stems during the peak period of nest construction in early May (most of the stems present in early May are growth from the previous year). We counted the number of stems at the waterline along six randomly selected 0.5-m-wide transects running from the inner to the outer edge of the *Typha* band that encircled each pond. The area censused depended on the length of each transect, and the mean stem density was calculated by dividing the counts by the area surveyed.

We monitored the foraging activity of male and female redwings at 19 nests containing nestlings. Thirty minutes of observation were devoted to each nest for a total of 9.5 h of observation. Observations were conducted between 8:00 and 12:00 a.m. during the last week of May. Because redwing foraging behavior is highly variable from day to day and from bird to bird, our data are too few for a strong test of odonate emergence effects on foraging behavior. Instead, we seek to describe the overall patterns of foraging site selection (on territory versus off territory) and male contribution to feeding in this population.

Data analysis

We focus our analyses of nestling performance on the number of birds successfully fledged from a nest and the mass of nestlings just prior to fledging. The mass of nestling passerines prior to fledging may affect their survivorship to adulthood (Magrath 1991; Davies 1992; Lindèn et al. 1992) and their probability of breeding (Richner 1989, 1992). We used nestling mass at 9 days of age as an index of fledging mass. The number of birds fledged from a nest depends on the number of eggs laid in the nest, and their survivorship to fledging. However, mean clutch size varied little among ponds, ranging from 3.42 eggs/nest to 3.75 eggs/nest, and was not related to odonate emergence rates or *Typha* stem density (least-squares regression, $n = 8$, $P > 0.20$). Therefore, most of the variation among ponds in the number of birds fledged from a nest is due to variation in egg and nestling survivorship, and the results are unchanged if egg and nestling survivorship is used as the dependent variable in the analyses.

We simultaneously evaluated the effects of two independent variables, odonate emergence rates and *Typha* stem density, on the dependent variables with multiple regression analyses. For each dependent variable considered (females/pond, males/pond, mean harem size, nestling survivorship, and fledging mass) we present the coefficient of multiple determination (R^2) and the P values associated with each partial regression coefficient. For those dependent variables significantly related to just one of the two independent variables (odonate emergence or *Typha* stem density), we illustrate the relationship with a bivariate plot and the associated least-squares regression line. The unit of observation for the analyses of odonate and *Typha* effects is ponds ($n = 8$).

We examined the effects of female density and harem size on female reproductive success by adding these independent variables separately to our regression model of female reproductive success, thereby holding the effects of odonate emergence and *Typha* constant. We also tested for male density-dependent reproductive success by adding male density to the regression model of male reproductive success. The unit of observation for the analyses of density dependence is individual birds ($n = 72$ females and $n = 23$ males).

Results

Odonate emergence and *Typha* stem density

Odonate emergence rates varied 44-fold among ponds, with pond means ranging from $0.07 \text{ insects} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ to $3.26 \text{ insects} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$. Emergence rates from undrained ponds averaged 2.05 ± 0.22 (1 SE) $\text{insects} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, and emergence rates from ponds drained and

refilled averaged $0.96 \pm 0.58 \text{ insects} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$. Most of the emerging odonates were the damselflies (Zygoptera) *Enallagma boreale* and *Ischnura verticalis*, along with a few dragonflies (Anisoptera: *Anax junius*).

Typha stem density also varied a great deal among ponds. The mean density of *Typha* stems within the ring encircling each pond ranged from $18.0 \text{ stems} \cdot \text{m}^{-2}$ to $65.8 \text{ stems} \cdot \text{m}^{-2}$. *Typha* stem density was not correlated with odonate emergence rates (Pearson $r = 0.43$, $P > 0.20$), so we include this independent variable as a covariate in our analyses.

Selection of breeding sites and feeding sites

Although the ponds were all of uniform size, the number of females initiating nests, the number of males establishing territories, and average harem sizes varied substantially from pond to pond (Fig. 1); the variation in mean harem size, however, was much less. Harem size varied less than male and female densities because the number of females and males settling on each pond was positively correlated (Pearson $r = 0.86$, $P = 0.01$).

Much of the variation in redwing settling density is predicted by *Typha* stem density. The number of females nesting per pond was a positive function of *Typha* stem density ($R^2 = 0.83$, $P = 0.002$, Fig. 2). The number of

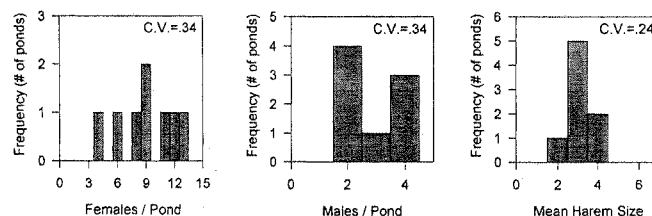


Fig. 1 Variation among ponds in the number of females per pond, the number of males per pond, and mean harem size. Frequency is the number of ponds with the observed value of the independent variable (C.V. coefficient of variation)

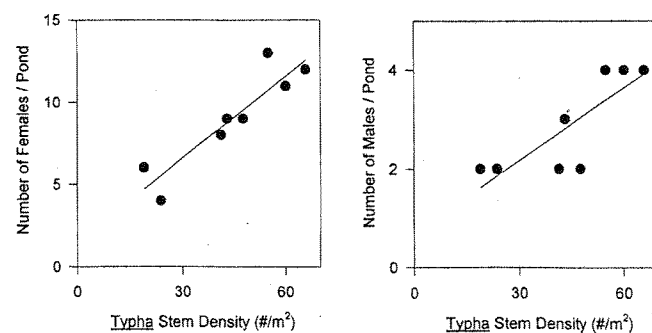


Fig. 2 Settling density of female and male redwings as a function of the mean density of *Typha* stems encircling a pond. Linear relationship fitted with least-squares regression. Females: $y = 0.17x + 1.56$, males: $y = 0.049x + 0.703$, where y is the number of birds per pond and x is the number of *Typha* stems per square meter within the vegetated band encircling each pond

males per pond was also a positive function of *Typha* stem density ($R^2 = 0.59$, $P = 0.03$, Fig. 2). Because females and males responded in a similar way to *Typha* density, harem size was constant across the *Typha* gradient ($P > 0.20$).

Odonate emergence rates were not related to bird settlement patterns. The number of males per pond, the number of females per pond, and mean harem size of a pond were independent of the abundance of emerging odonates ($P > 0.20$ for all three relationships).

Females feeding nestlings spent 40% of their time foraging among *Typha* stems near their nest, 48% of their time foraging off territory in adjacent alfalfa fields, and the remaining 12% of their time tending the nest. Males contributed less than 5% of all feeding visits to nests.

Reproductive success

Overall fledging production, averaged across ponds, was 1.78 chicks/nest (54% survivorship). Over half of the nestling mortality was starvation related, regardless of the method used to infer starvation. Using low daily weight gains as evidence for starvation, we estimated that 59% of nestling mortality was starvation related,

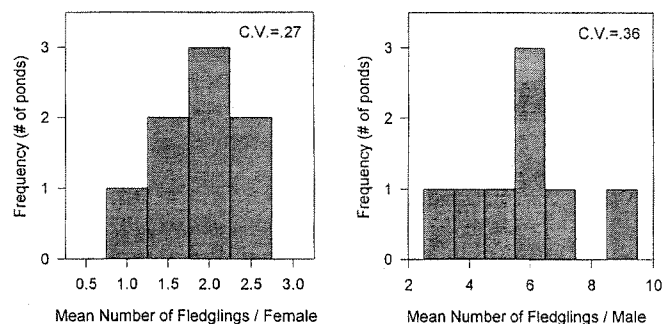


Fig. 3 Variation among ponds in the mean number of nestlings successfully fledged per female and the mean number of nestlings successfully fledged from each male territory

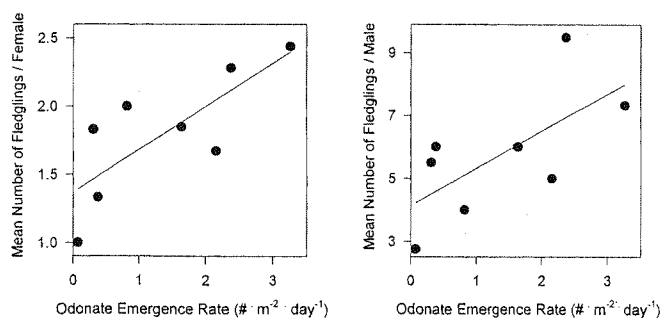


Fig. 4 Fledging production per female and per male as a function of odonate emergence rate. Females: $y = 0.35x + 1.37$, males: $y = 1.35x + 4.16$, where y is the mean number of fledglings per female or male for a pond, and x is the odonate emergence rate ($\text{number} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$)

but 92% of nestling mortality was associated with partial nest failures.

Like their breeding densities, the average reproductive success of female and male redwings varied a great deal among ponds (Fig. 3). Female reproductive success varied less among ponds than did male reproductive success (Fig. 3). The best pond, from the perspective of a female redwing, yielded on average 1.83-fold more fledglings per nest than did the worst pond, whereas the best pond from the perspective of a male redwing yielded on average 3.45-fold more fledglings per male than did the worst pond (Fig. 3).

Most importantly, much of the variance among ponds in both male and female reproductive success was related to odonate emergence rates from the ponds (Fig. 4). Odonate emergence had a positive effect on the mean number of nestlings successfully fledged by each female ($R^2 = 0.60$, $P = 0.05$, Fig. 4), as well as the mean number of nestlings successfully fledged from male territories ($R^2 = 0.53$, $P = 0.06$, Fig. 4). *Typha* stem density was not related to the number of nestlings successfully fledged by each female, nor was it related to the number of nestlings fledged from male territories ($P > 0.20$ for both tests). Both odonate emergence rates and *Typha* stem density were related to mass at fledging ($R^2 = 0.86$, Fig. 5). Odonate emergence rates had a positive effect on fledging mass ($P = 0.02$), as did *Typha* stem density ($P = 0.003$).

We found no evidence for density-dependent reproductive success by female or male redwings. Multiple regression analyses showed that after the effects of *Typha* stem density and odonate emergence rates were accounted for, there was no effect of harem size, or of female density, on the number of nestlings successfully fledged by a female ($P > 0.20$ for both tests). Male

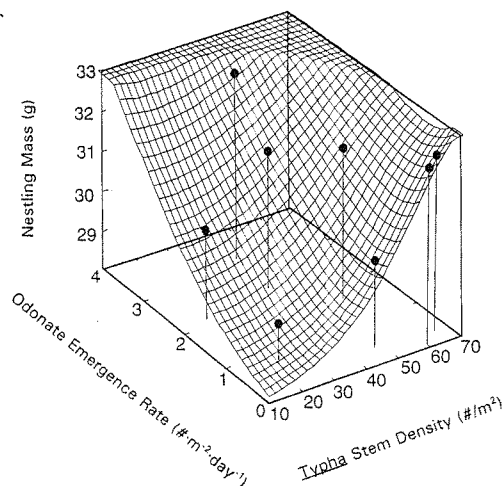


Fig. 5 Mass of redwing nestlings just prior to fledging as a function of odonate emergence rate and *Typha* stem density. $y = 0.053x_1 + 0.082x_2 + 26.7$, where y is the mean mass of nestlings at 9 days of age for a pond, x_1 is the odonate emergence rate for a pond ($\text{number} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$), and x_2 is the mean *Typha* stem density ($\text{number} \cdot \text{m}^{-2}$)

reproductive success was also independent of the number of males sharing a pond ($P > 0.20$).

Discussion

Our study demonstrates that the reproductive success of both male and female red-winged blackbirds breeding at the KBS Experimental Ponds Facility was related to the production of aquatic insects. These results offer insights into the evolution of the polygynous mating system of the red-winged blackbird. Searcy and Yasukawa (1995) recently reviewed the evidence supporting each of the many alternative models for the evolution of polygyny by red-winged blackbirds. They concluded that females consistently choose certain nesting sites (as opposed to male coercion or random settlement), and their choice appears to be influenced by environmental characteristics of nest sites. Polygyny results when two or more females choose a nest site within the same male territory [the "directed choice" model of Searcy and Yasukawa (1989)]. Searcy and Yasukawa (1995) also conclude that it is unclear which environmental characteristics of the marsh habitat are most critical to nest site selection and successful reproduction (see also Burger 1985). The data presented here confirm that some nesting sites are more suitable than others, and show that odonate production is an important factor in determining redwing reproductive success. Nests on ponds with high odonate emergence rates fledged more young at a higher mass than did nests on ponds with few emerging odonates. In addition, we detected no effects of nest density on female reproductive success, consistent with the no-cost, no-benefit models of polygyny (Searcy and Yasukawa 1989).

Red-winged blackbirds in this and other populations procure much of the food needed by their young from sites other than the breeding territory (Hurley and Robertson 1984; Whittingham and Robertson 1994; Searcy and Yasukawa 1995). This observation has been taken as evidence that resource levels within the breeding site are not important for reproductive success (Searcy and Yasukawa 1989, 1995). However, foraging away from the breeding site is likely to result in lower nestling provisioning rates because of time lost to travel (Charnov et al. 1976; Orians and Pearson 1979), as well as increased risk of nest predation (Robertson 1972). All else being equal, redwings should prefer to forage near their nest. Given an array of substitutable resources, foraging theory predicts that resource use will reflect resource preferences only if the supply of preferred resources is not limiting (Stephens and Krebs 1986). Thus, the large amount of time spent foraging off territory could be a result of the limited availability of preferred resources (food on territory) rather than a reflection of the relative importance of on- and off-territory resources.

Most models of habitat selection are based on the premise that natural selection should favor the selection of breeding sites that maximize reproductive success

(Pulliam 1989), but our results show that neither male nor female breeding density was related to aquatic insect production. Instead, males and females were more likely to settle on ponds with dense growths of *Typha*. One explanation for this discrepancy is that settling redwings may have imperfect knowledge of food availability (e.g., Abrahams 1986). Redwings typically establish territories and select breeding sites several weeks before odonates begin emerging from the marshes where they are breeding (A. Turner, unpublished data). Orians (1980) suggested that females choosing nesting sites may closely inspect the water, assessing the abundance of larval odonates, but our data do not support this idea. Other studies have suggested that redwings may use information acquired during previous breeding seasons when choosing breeding sites (Picman 1987; Beletsky and Orians 1987a, 1991, 1996). By manipulating insect abundance we unlinked current food availability from that of past years, possibly preventing returning adults from using their prior experiences to accurately predict food production.

Further support for the imperfect-knowledge explanation comes from the contrast with two previous studies that found a relationship between food availability and redwing settling patterns. Ewald and Rohwer (1982) and Wimberger (1988) manipulated food availability by adding supplemental food to redwing breeding areas, and both studies found larger harems in the areas with supplemental food. Their studies differ from ours in that they initiated food additions (sunflower seed, millet, and dog food) in late March and early April, before females had selected nesting sites, so females had ample opportunity to assess food availability in alternate breeding sites prior to settlement.

An additional factor that may contribute to the lack of concurrence between breeding density and resource availability is that territorial interactions among birds may prevent individuals from choosing sites based only on non-social environmental factors (Schoener 1968, 1983; Hixon 1987). Although both male territoriality and female-female aggression are well known in redwings (Nero 1956; Orians 1961; Beletsky and Orians 1987b; Eckert and Weatherhead 1987), most of the evidence suggests that females are not territorial (Searcy and Yasukawa 1995). Experimental removals of females from breeding sites have no effect on subsequent settlement of additional females (Searcy 1988; Searcy and Yasukawa 1995; but see Hurley and Robertson 1985 for an alternate view), and reduced female breeding density does not result in increased female reproductive success (Searcy 1988; Searcy and Yasukawa 1995). Thus, social interactions may prevent male densities from matching resource availability, but they probably are not responsible for the distribution of females among ponds.

Food supply is only one of the environmental factors that may influence redwing reproductive success, and the lack of concurrence between breeding density and food availability may reflect the importance of other types of resources. For example, male and female settlement in

our study was correlated with *Typha* stem density. Thick vegetation may provide redwings with nest construction sites, and it may deter nest predation (nest predation was a relatively unimportant source of nestling mortality in this population, but other studies of nesting red-winged blackbirds have documented high rates of nest predation, e.g., Beletsky 1996). If the availability of suitable vegetation limits reproduction more than food availability, then redwings should be relatively insensitive to variation in food availability when selecting breeding sites.

In conclusion, given the links shown here between features of the aquatic environment and redwing reproductive success, and the well-documented strong interactions among various biotic and abiotic components of aquatic communities (Hall et al. 1970; Carpenter et al. 1987; Power 1990; Mittelbach et al. 1995), the behavioral ecology and population dynamics of marsh nesting birds will likely be closely tied to characteristics of the aquatic environment such as nutrient loading and food web structure. For example, studies have shown that adding nutrients to ponds increases the emergence rates of insects on which birds feed, but adding fish decreases insect emergence rates (e.g., Hall et al. 1970). Marsh nesting birds, in turn, may be important vectors for nutrients (Frederick and Powell 1994; Manny et al. 1994), and may have substantial impacts on the populations of their aquatic prey (Peterson et al. 1989). However, factors such as nutrient loading and food web structure have largely been outside the scope of ornithological studies, and aquatic ecologists have been slow to acknowledge the potential role of birds in community and ecosystem dynamics. As with many questions, the ecology of birds that feed and nest in marshes will be best addressed by bridging the boundaries that have traditionally separated ornithology and aquatic ecology.

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