

THE BREEDING DISTRIBUTION, POPULATION DYNAMICS,
AND HABITAT AVAILABILITY AND SUITABILITY OF AN
UPPER MIDWEST LOGGERHEAD SHRIKE POPULATION.

by

BONNIE LOUISE BROOKS

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"Listen to advice and accept instruction, and
in the end you will be wise"

Proverbs 19:20

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PREFACE

This thesis is composed of 3 separate papers each of which addresses a different aspect of Loggerhead Shrike natural history. The first manuscript was published in The Loon 58:151-154, and the other 2 manuscripts will be submitted for publication separately. The manuscripts to be submitted for publication will differ somewhat from the style presented herein to meet the requirements of the journals for which they are intended.

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THE BREEDING DISTRIBUTION OF THE LOGGERHEAD SHRIKE IN MINNESOTA:

A PRELIMINARY REPORT

Bonnie L. Brooks
Stanley A. Temple
Department of Wildlife Ecology
University of Wisconsin-Madison

INTRODUCTION

The Loggerhead Shrike (Lanius ludovicianus migrans), once a common breeding bird of Minnesota's prairies, has become the subject of concern among state ornithologists and birdwatchers. The entire midwestern population of Loggerhead Shrikes has declined over the last several decades (Morrison 1981, Robbins et al. 1986). Minnesota's population is no exception. A review of state records of observations indicates that the once abundant "butcherbird" is becoming less common throughout its breeding range in the southern 2/3 of Minnesota. As a result, the Loggerhead Shrike was placed on the state's threatened species list in 1984.

In 1986 we undertook a statewide shrike survey. Our objectives were to locate as many breeding pairs of shrikes as possible, to identify areas with relatively high nesting densities in the state, to describe characteristics of breeding habitat, to monitor reproductive success, and to identify causes of nest failures. This paper primarily addresses the first two of these objectives. These preliminary results are based on the first year of a two-year study.

METHODS

We located breeding shrikes in several ways. The most productive approach was to investigate reports of sightings by members of the Minnesota Ornithologists' Union, The Nature Conservancy, and the Department of Natural Resources during the nesting period (April-July). We recruited the help of additional volunteer observers through newspaper and magazine articles. Nest reports and sighting records from previous years also led us to possible nest locations. In addition to these reports, seven field assistants helped us search areas that either were known to contain shrikes in the past or were judged to have potential shrike habitat. From 29 April to 10 June 1986 we searched for nesting shrikes in ten counties (Figure 1) by driving slowly along township roads and looking for shrikes perched in conspicuous places. The township roads in most of these counties followed section lines, allowing us to scan virtually every square mile of suitable habitat. In open areas we could see shrikes at distances up to 1/4-mile from the road. We made a thorough search of hedgerows and potential nest trees wherever a bird was observed or reported.

Toward the end of the nesting period (10 June to 20 August 1986) when most young had fledged and family groups were particularly conspicuous, we systematically surveyed the six counties, as illustrated in Figure 1, in which we had found the highest number of nests. Within these counties we searched for shrikes in as many townships as possible, averaging eight townships per county. Along each township road, we stopped every

1/2 mile with the stops located 1/4 mile from each intersection of north-south and east-west roads. At each stop, we classified the habitat within a 1/4-mile radius of the stop as either suitable for shrikes (i.e., grassland containing potential nest sites and perch sites) or unsuitable. If the habitat was judged to be suitable, the observer searched for shrikes continuously with binoculars for 8 minutes. We had previously determined in 71 trials that 8 minutes of searching in known nesting territories gives a 90% probability of observing a shrike, if one was present within 1/4 mile of the observer.

RESULTS

We located 29 nesting pairs of shrikes during the 1986 nesting season, and these pairs made 34 nest attempts during the season. Reports of an additional three nesting pairs and six individual birds were received after the nesting season. Reports from birdwatchers and naturalists proved very helpful. Their reports led us to 18 (56%) of the 32 nesting pairs. The 32 nesting pairs were distributed among 12 counties (Table 1). Clay County had the northernmost nest, and Fillmore County had the southern-most nest. Sherburne County had the highest number of nesting pairs (8) and nesting attempts (9). Morrison County had the highest local density of nests in any one area: three nesting pairs occurred in a 70-acre area.

Three pairs re-nested after their clutch or brood had been destroyed by predators or a spring storm. Two other pairs were double-brooded, hatching a second clutch after already fledging their first brood. Figure 2 illustrates the distribution of known nesting pairs, of reports by observers, and of additional family groups or territories discovered during the late-season road surveys.

DISCUSSION

Although Loggerhead Shrikes are still fairly widespread in the southern 2/3 of Minnesota (Figure 2), the number of birds found in this region is low. The discovery of 32 nesting pairs in 12 counties in 1986 seems encouraging (only 41 nests had been reported for the same areas during the previous 10 years), but this large number of nests probably reflected the intensity of our search effort rather than an increase in the breeding population over previous years when fewer nesting pairs were reported annually.

Based on recent reports published in The Loon (Table 1), the statewide distribution of breeding shrikes has not changed dramatically. Benton, Clay, Dakota, Morrison, and Sherburne Counties had relatively high numbers of nesting shrikes in the past, and they still did in 1986. These counties contained 51% of all known nesting pairs between 1975 and 1985. In 1986 they contained a 63% of the known nesting pairs. Goodhue County, which had no records of nesting shrikes in the last ten years, contributed substantially to the total number of nests in 1986.

Our work was supported by The Minnesota Chapter of The Nature Conservancy, the Minnesota Department of Natural Resources, and The Graduate School of the University of Wisconsin-Madison. We thank Bob Janssen, editor of The Loon, for helping us contact the members of the Minnesota Ornithologists' Union who aided us in finding shrikes and nests. We look forward to working with M.O.U members again in 1987.

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Figure 1. Minnesota counties in which we searched for shrike nests and carried out road counts in 1986.

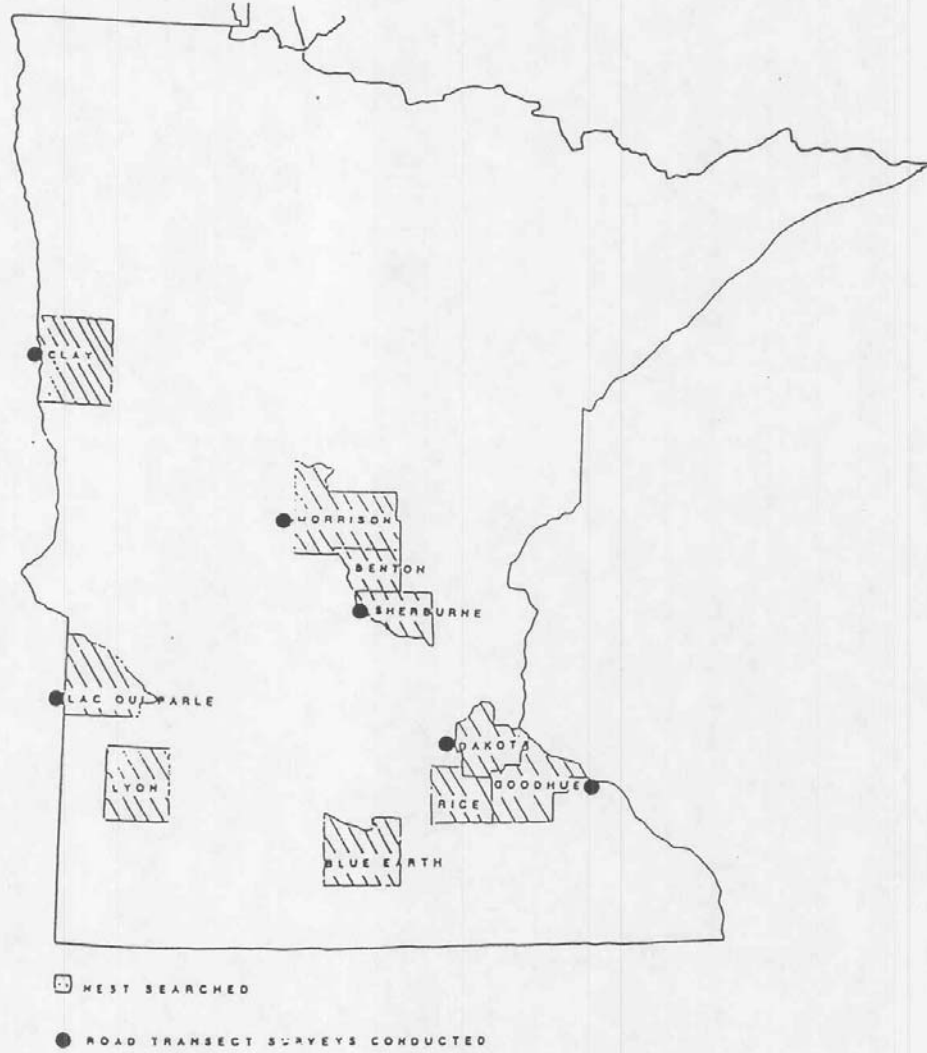
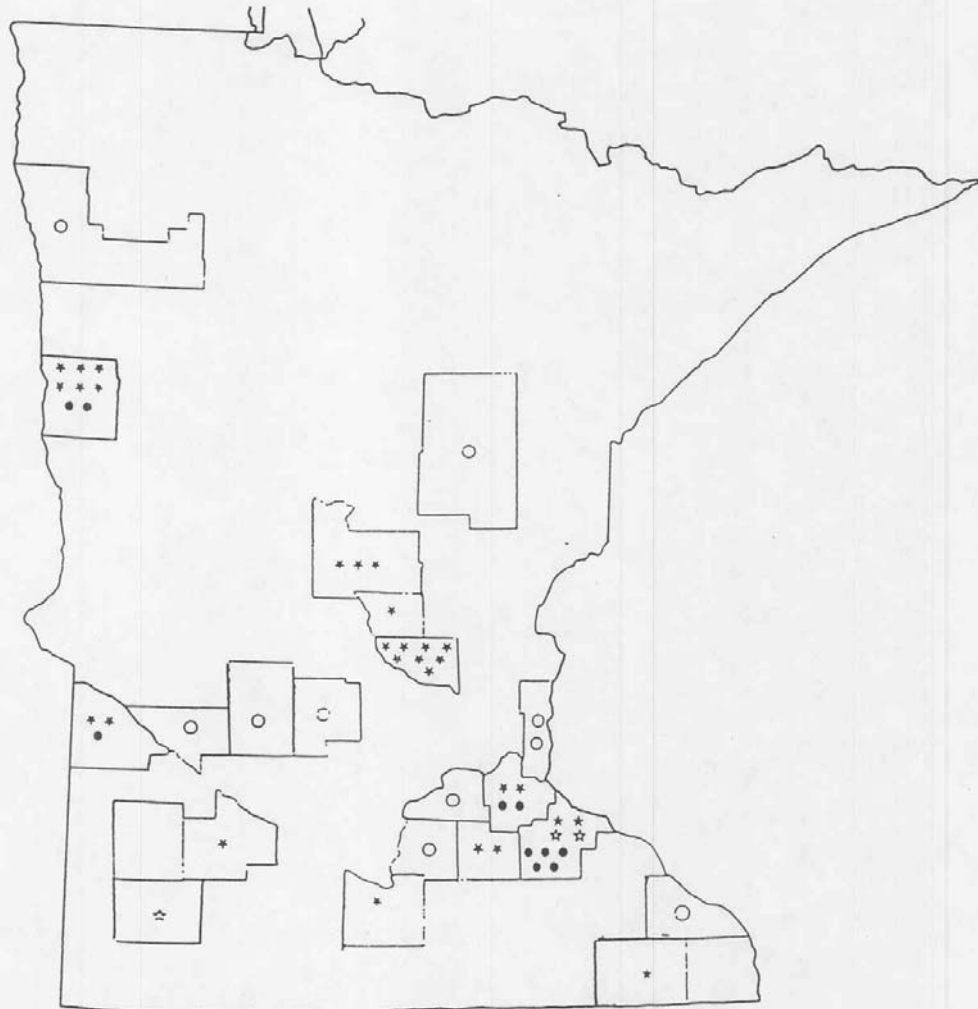


Figure 2. Known distribution of breeding Loggerhead Shrikes in Minnesota, 1986.



* CONFIRMED NEST SITE
 ☆ REPORTED NEST SITE
 ● NEW SHRIKE(S) FOUND DOING TRANSECTS
 ○ REPORTED OBSERVATION UNRELATED TO NEST SITE

Table 1. A summary of Loggerhead Shrike nest records in 12 Minnesota counties, 1975-85 and 1986.

County	Number(and percentage) of nests, 1975-85 ^a	Number(and percentage) of nests, 1986
Benton	4(17%)	1(3%)
Blue Earth	2(8%)	1(3%)
Clay	4(17%)	6(19%)
Dakota	4(17%)	2(6%)
Fillmore	0(0%)	1(3%)
Goodhue	0(0%)	4(13%)
Lac Qui Parle	1(4%)	2(6%)
Morrison	5(21%)	3(9%)
Murray	0(0%)	1(3%)
Redwood	0(0%)	1(3%)
Rice	0(0%)	2(6%)
Sherburne	4(17%)	8(25%)

^a Based on 41 nest reports from The Loon

DYNAMICS OF AN ENDANGERED LOGGERHEAD SHRIKE
POPULATION IN THE UPPER MIDWEST

Bonnie L. Brooks
Stanley A. Temple
Department of Wildlife Ecology
University of Wisconsin-Madison
Madison, WI 53706

ABSTRACT

Reproductive, and demographic data were collected on 48 breeding pairs of Loggerhead Shrikes (Lanius ludovicianus) in Minnesota during 1986 and 1987 in an attempt to identify possible causes of a noted decline in midwestern shrike populations. These data, combined with data taken from other passerine studies, were used to construct a stochastic model of the population dynamics of a hypothetical Loggerhead Shrike population based on the following variables: productivity per pair, annual adult survival rate, and annual juvenile survival rate. Our model predicted a 20% mean annual rate of decline for the population, which closely resembles and observed 29% decline in breeding pairs from 1986 to 1987. Reproductive success was high; therefore, we conclude that a decline in the upper midwestern shrike population is probably due to factors on their nonbreeding range.

INTRODUCTION

Loggerhead Shrike populations are declining throughout the species' range in midwestern, New England and mid-Atlantic states (Bull 1974, Burnside 1985, Bystrak and Robbins 1977, Clark 1970, Erdman 1970, Graber et al. 1973, Hess 1980, Kridelbaugh 1981, Mayfield 1949, 1950, Milburn 1981, Morrison 1981, Petersen 1965, Temple and Temple 1976, Wilson 1979). As a result, the Loggerhead Shrike has been included on the National Audubon Society's "Bluebird" of birds thought to be declining ever since the list first came into existence in 1972 (Tate 1986), and it is currently considered endangered or threatened in most New England and midwestern states. The Loggerhead Shrike is one of the few species showing significant declines in all continental regions of the Breeding Bird Surveys (Robbins et al. 1986).

Recent studies have addressed the possibility that inadequate reproduction is responsible for the decline (Gawlik 1988, Kridelbaugh 1983, Luukkonen 1987, Porter et al. 1975, Strong 1972). In all cases, these studies concluded that reproductive success was normal and, hence, not contributing to population declines. Other studies have focused on the possibility of pesticide poisoning (Anderson and Duzan 1978, Busbee 1977, Morrison 1979, Rudd et al. 1981). These experiments have shown that organochlorines can reduce the thickness of shrike eggshells and retard behavioral development of young (Anderson and Duzan 1978, Busbee 1977), but Anderson and Duzan (1978) concluded that a slight 2.57% decrease in the eggshell

thickness index from 1895 to 1972, was not hindering reproduction. Furthermore, widescale use of organochlorines was curtailed in the early 1970's, yet Loggerhead Shrike numbers have continued to decline.

Loss of habitat on the breeding range has also been considered as a possible cause of the decline (Brooks and Temple 1989, Gawlik 1988, Luukkonen 1987, Kridelbaugh 1983). However, most studies conclude that availability of breeding habitat is not limiting Loggerhead Shrikes.

In this paper we examine the dynamics of a Loggerhead Shrike population in the upper midwest. We use demographic parameters obtained from our field studies and others in a stochastic simulation model that projects trends in population size. We compare the results of our simulations with trends detected by the Breeding Bird Survey and other estimators of population trends, and we discuss some possible causes for the continued decline of midwestern shrike populations.

STUDY AREA AND METHODS

The breeding range of the Loggerhead Shrike in Minnesota is restricted primarily to the southern 2/3 of the state (Brooks and Temple 1986). Our field work took place in 11 counties in southern Minnesota during the nesting seasons of 1986, 1987, and

1988. These counties include Benton, Blue Earth, Clay, Dakota, Fillmore, Goodhue, Lac Qui Parle, Morrison, Redwood, Rice and Sherburne (Figure 1). The dominant vegetative cover types in these 11 counties are agricultural fields and pastures, with small prairie fragments scattered around the landscape.

From 27 April through 20 August, 1986, we searched for breeding Loggerhead Shrikes in townships where they had been reported over the previous 10 years. We also investigated reports of shrikes from cooperating observers who had been solicited through the Minnesota Ornithological Union and the Minnesota Department of Natural Resources. We searched for birds by driving slowly along county and township roads, stopping to scan areas of particularly good habitat (i.e., Brooks and Temple 1989). From 21 April through 15 June 1987, and from 14 April through 16 May, 1988, we searched for Loggerhead Shrikes in previously occupied breeding territories and adjacent areas. We found nests by observing the behavior of adults or by thoroughly searching all possible nest trees in the area.

In 1986, we established 20-mile-long road transects in each of five counties that had relatively high densities of shrikes (Clay, Sherburne, Morrison, Lac Qui Parle, and Goodhue). Once a week from 15 June through 15 July in 1986 and 1987, we searched for shrikes along these census routes. Observers stopped every 1/2 mile and scanned a 1/4-mile-radius circle with binoculars for 5 minutes.

In 1986 and 1987 we monitored 61 nest sites at three- to five-day intervals until the young left the nest or the nest failed. Data were collected on clutch size, hatching success (percent of eggs that hatch), fledging success (percent of young that fledge) and nest fate (number of nests that fledged ≥ 1 young). We calculated daily nest survival rates using the "Mayfield method" (Mayfield 1961). Nest success was calculated by raising the daily nest survival rate to the 35th power (i.e., the average length of a nesting cycle). In cases where an entire near-fledging-age brood disappeared simultaneously and fledglings were not observed near the nest site on subsequent visits, we concluded that the nest had failed. Each nestling was banded with a U.S Fish and Wildlife Service aluminum legband prior to fledging.

Each year we trapped adult shrikes during the breeding season using modified versions of a "Bal-Chatrri" trap (Burger and Mueller 1959) or a "Potter" trap (Blake 1951). Lab mice and Zebra Finches (Taeniopygia guttata) were used as lures in the traps. We concentrated trapping efforts in areas where we had banded birds in previous years. Trapping efforts were greater in 1987 and 1988 than in 1986.

We constructed a stochastic model of the dynamics of a hypothetical Loggerhead Shrike population based on the following variables: productivity per pair, annual adult survival rate, and annual juvenile survival rate. In our model, productivity was a normally distributed stochastic function with a mean value taken

from our data. We assumed that all adult birds breed, as we found no evidence of non-breeders in our population. Annual adult survival was a normally distributed stochastic function. We used territory re-occupancy rates from our study to estimate the annual adult survival rate, the assumptions being that males return to their previous breeding territory if they survive the winter, that male survival rate equals female survival rate, and that there is always an even sex ratio. There are no estimates of juvenile survival rates for Loggerhead Shrikes. Therefore, in our model, first-year survival rate was assumed to be a fraction of the adult survival rate for that year. We used the mean ratio of juvenile-to-adult survival calculated from Woolfenden and Fitzpatrick's (1986) data on Scrub Jays (Aphelocoma coerulescens), a similar sized passerine, to estimate the mean value of this fraction. We multiplied that fraction, which is a normally distributed stochastic function, by our estimate of adult survival to estimate juvenile survival rate each year. Because there are no long-term studies of year-to-year variations in shrike population parameters, we used results of Woolfenden and Fitzpatrick's (1986) long-term study of Scrub Jays to estimate the coefficients of variation of our model parameters.

Our model begins with a population of breeding shrikes-and then predicts the population's size in subsequent years using the following equation: $N_t = N_{t-1}(S_a) + N_{t-1}(P/2)(S_j)$, where N_t = size of the breeding population in year t , S_a = annual survival rate of adults, S_j - annual survival rate of juveniles, and P - number of young raised per breeding pair. During each annual cycle, a value for productivity and annual survival rate of adult

birds is stochastically determined by randomly selecting a value from a normally distributed pool of values with a mean based on our field data and a coefficient of variation derived from the literature. A value for juvenile survival rate is stochastically determined by randomly selecting a value for the ratio of juvenile-to adult survival, whose mean and coefficient of variation are taken from the literature, and multiplying it by the adult survival rate for that year. We ran our model 100 times and each time observed the change in population size over 50 years.

RESULTS

We collected nesting data on 48 breeding pairs of Loggerhead Shrikes in Minnesota during 1986 and 1987. The pairs were scattered throughout 11 counties and occurred at low densities. In 1986, 29 pairs of shrikes made 34 nest attempts, and in 1987, 19 pairs made 27 nest attempts. Most of the second nest attempts resulted after a failed first nest attempt. Five (10%) of the 48 pairs attempted to raise second broods; four of them were successful. In 1986, 24 breeding pairs were found along five 20-mile survey routes. In 1987, 17 breeding pairs were found along these same survey routes; the surveyed population had experienced a 29% decline in one year.

Productivity data

The mean clutch size was 5.65 (SD = 1.17, N = 46), ranging from a minimum of three eggs to a maximum of seven eggs. The modal clutch size was six. On average, 4.18 eggs hatched per nest

(SD = 2.33, N = 51), 3.02 young fledged per nesting attempt (SD = 2.07, N = 60), and 3.73 young fledged per pair (SD = 1.82, N = 48). There were no significant differences between years in clutch size, number of eggs hatched, number of young fledged per nest, or number of young fledged per pair ($P > 0.10$ in all cases, students t-test). See Table 1 for a summary of nesting parameters.

Of 48 pairs of shrikes, 40 (83%) successfully fledged at least one young. However, because of re-nesting attempts, only 74% of all nest attempts successfully fledged at least one young. Hatching success was higher in 1986 (81%) than in 1987 (71%) ($\chi^2 = 3.006$, $0.10 > P > 0.05$). However, fledging success was lower in 1986 (66%) than in 1987 (77%) ($\chi^2 = 2.940$, $0.10 > P > 0.05$). On average, 55% of eggs laid resulted in independent young. Using Mayfield's estimate of reproductive success based on exposure days, we calculated a reproductive success of 62%. Reproductive success is summarized in Table 1.

Survival data

We found 37 occupied territories in 1986; 22 in 1987; and 16 in 1988. In 1987, 15 (41%) of the 37 breeding territories used the previous year were reoccupied; in 1988, 13 (59%) of the 22 breeding territories used in 1987 were reoccupied. When both seasons' data were combined, the average re-occupancy rate was 47%.

We trapped and banded 27 adult Loggerhead Shrikes. Of the five territories in which we had banded adults in 1986, one was

reoccupied in 1987. In 1988, eight of 10 territories occupied by banded birds in 1987 were reoccupied. Seven of the banded adults from 1987 were males, and three (43%) of these banded males returned to reoccupy their previous year's territories. We neither trapped nor observed in subsequent years any of the 196 shrikes we banded as nestlings in 1986 and 1987.

Population modeling

Table 2 summarizes the model parameters and their corresponding coefficients of variation. Based on 100 simulations, the model predicted a 20% (range: 14-30%) mean annual rate of decline for the hypothetical Loggerhead Shrike population. This rate of decline leads to a halving of the population's size every 3.5 years.

To determine which of the demographic parameters had the greatest influence on the rate of change in population size, we tested the sensitivity of the model to changes in each of its components. We sequentially multiplied each model parameter's mean by 105%, while holding the other two variables constant, and ran the model 100 times. The population's rate of change decreased by 15% (i.e., from 20% to 17%) in response to a 5% increase in each of the model's parameters. Thus, each of the parameters exerted the same amount of influence on the rate of change in population size.

DISCUSSION

Shrike Demography

Reproductive performance of Minnesota shrikes was similar to that found in other shrike populations in the United States (i.e.; Haas 1988, Gawlik 1988, Luukkonen 1987, Kridelbaugh 1982, Siegel 1980, Anderson and Duzan 1978, Porter et al. 1975, Graber et al. 1973). Reported values of nesting success range from 43% in Alabama (Siegel 1980) to 80% in Illinois (Graber et al. 1973). The lowest value, 43%, is well below the second lowest value of 62% (Luukkonen 1987), suggesting that values greater than 60% are more typical of Loggerhead Shrike nesting success. Ricklefs (1973) notes that nest success of temperate zone passerines with open nests averages 47%, suggesting that Loggerhead Shrikes have relatively high reproductive success for a passerine.

The number of young produced per female in Minnesota (3.73) closely resembles values from other recent shrike studies. Loggerhead Shrikes in South Carolina produced 3.0 fledglings per nesting attempt (Gawlik 1988); in North Dakota, 4.0 fledglings were produced per nesting attempt (Haas 1988); in Colorado, Porter et al. (1975) observed 3.57 fledglings per nesting attempt; and in Wisconsin, Erdman (1970) found 3.77 fledglings per nesting attempt. Data from our study and others suggest that Loggerhead Shrikes are reproducing at near-optimal levels for an open-nesting passerine species in the temperate zone.

Because there have been no long-term studies of marked shrike populations, we lack precise estimates of observed survival rates. Our estimates of survival rates must, therefore, be inferred from less than ideal data. Our best estimates are based on territory re-occupancy rates for males. Using territory

re-occupancy rate to estimate annual adult survival, requires an important assumption: that those males that did not return to their previous year's territories are dead. Although we cannot strictly test this assumption, our re-occupancy rate (47%) did closely resemble our adult male band-return rate (43%), an indication that the assumption is valid. Kridelbaugh (1983) reported that 47% of banded male shrikes returned to their territories of the previous year and that 54% of the previous year's territories were reoccupied. Likewise, Blumton (pers. comm.) reported a 50% return rate of banded adult shrikes in Virginia. Ricklefs (1973) notes that adult survivorship is generally low among small land birds (40-60 percent in most temperate passerines). Our estimate of adult survival is, therefore, not at all unusual for a temperate zone passerine.

There are few data that reveal the relationship between adult and juvenile survival rates in passerines. We calculated juvenile survival to be, on average, 41% of the adult survival rate, based on data from Woolfenden and Fitzpatrick's (1986) study of Scrub Jays. Ricklefs (1973) states that, in general, juvenile survival rates of passerines are typically one quarter of the adult survival rate. The European Blackbird, a similar sized, migratory passerine, with fecundity rates similar to Loggerhead Shrikes, had the highest reported ratio of juvenile-to-adult survival: the mean annual juvenile survival rate was 65% of the adult survival rate (Snow 1966). Our estimate of juvenile-to-adult survival ratio is typical of values for other passerines.

The annual survival rates of adult and juvenile Loggerhead Shrikes in the upper midwest, despite being within the range typical of passerines, are too low with respect to annual productivity. Henney (1971, Table 1) provides a deterministic model which estimates the productivity per pair required to maintain a stable population, given survival rates for adult and juvenile age-classes. If our population is surviving at average rates of 47% and 19% for adults and juveniles, respectively, then approximately 5.5 young must be produced per pair. No shrike population is known to produce this many young, which would require almost 100% nest success or consistently successful double brooding.

Because our Minnesota shrike population is achieving good reproductive success, and habitat conditions on the breeding range seem more than adequate to accommodate the present population (Brooks and Temple 1989), it seems likely that survival of birds while they are on the summer breeding range is also good. We found no evidence of adult mortality during the breeding season, and survival of post-fledging birds to the age of dispersal seemed to be high, although we did not quantify it. Overwinter survival on the non-breeding range is, therefore, a likely point in the shrike's annual cycle to look for evidence of problems. In a six-year study of a declining population of Red-backed Shrikes (Lanius collurio) in Britain, Ash (1970) suggested that reductions in annual survival rates were

responsible for that population's decline, rather than a reduction in the production of young.

Causes of low overwinter survival

Although the exact location of our Minnesota population's wintering quarters is yet unknown, Burnside (1987) found that banded shrikes from northern mid-continental populations have been recovered during the winter in Texas, Arkansas, Oklahoma, Mississippi, Louisiana, Kansas, and Missouri.

Burnside and Shepherd (1985), in their study of a shrike population in Arkansas, suggested that recent land-use changes have eliminated prime shrike habitat in Arkansas. Kridelbaugh (1981) attributed the decline of the Loggerhead Shrike in Missouri to the conversion of pastureland and hayfields to row crops. The extensive conversion of pastureland and old fields to cereal-crop production has resulted in the elimination of large areas of grassland habitat throughout the gulf coast and adjacent regions. The rice acreage, in Arkansas alone, increased from 162,000 acres in the 1930's to 434,000 acres in 1955 (Neff and Meanley 1957). Most of this agricultural expansion has been at the expense of grassland habitats. Since then, the amount of land devoted to rice production in Arkansas has again increased three-fold (1950-1985). Further evidence of the continuing loss of suitable wintering habitat is a 13% increase in cropland acreage in the southern states of Arkansas, Mississippi, Louisiana, and Texas from 1969 to 1982. Concurrently there was a

17% decline in the amount of pasture and rangeland in these states. During those 13 years, Louisiana experienced the most dramatic increase in crop production (36%) as well as the most pronounced decrease in acreage of pasture and rangeland (62%), while Mississippi, Arkansas and Texas experienced 22%, 18% and 88 increases in cropland, respectively (USDA 1950, 1975, 1986).

There is good evidence indicating that these habitat changes have impacted populations of birds that winter in the region. The best documented population responses have been dramatic increases in species that feed on grain, notably members of the family Icteridae (Stepney 1975). Because these wintering blackbirds feed primarily on cultivated grains, their populations have steadily increased over the same 50-year period that shrike populations sharing the same wintering areas have steadily decreased. For example, compare the shrike population trends in Temple and Temple (1976) with the cowbird population trends in Brittingham and Temple (1983).

The impact of this massive loss of wintering habitat for migrating shrikes from northern breeding areas is made even more threatening by the presence of resident shrike populations throughout these southern states (Miller 1931). Southern populations of shrikes are non-migratory and defend winter territories (Gawlik 1988, A. Blumton, pers. comm.). Habitat alterations in the gulf coast region and adjacent states have apparently reduced the habitat available for resident shrikes;

their populations have declined (Robbins et al. 1986, Burnside 1985), although not as severely as more northerly populations. If resident shrike populations are being limited by habitat availability, migrant shrikes wintering in the same area are almost certainly being forced to occupy marginal habitats that are not being held by territorial residents. Both resident southern shrikes and migrants from further north have apparently suffered from a loss of habitat that reduces overwinter survival to inadequately low levels.

Population declines

The possibility that a local or regional shrike population could decline and become extirpated within a few decades, is an alarming prospect, but Anderson and Duzan (1978) provide evidence of one such extirpation of a local population of Loggerhead Shrikes in central Illinois. Similarly, the European Red-backed Shrike is undergoing a population decline and it is believed to be at risk of being extirpated in Great Britain in the next several decades; Bibby (1973) calculated an annual rate of decline of 6.1% and 9.6% for the decades 1950-59 and 1961-70, respectively. The results of the Breeding Bird Survey indicate that the entire upper midwestern shrike population (including the states of Minnesota, Iowa, Illinois, Wisconsin, Michigan, and Indiana) has been declining at a rate of 6% per year from 1966-1987. (Robbins et al. 1986, S. Droege, pers. comm.). Our

data suggest even more severe declines in local populations within the midwestern United States. Between 1986 and 1987, our population in southern Minnesota declined by 29%, based on the rate at which we detected shrikes along established survey routes. Our simulation model predicted a 20% decline using the demographic information taken from our study, which very closely resembles the demographic estimates of other recent shrike studies, and from other passerine studies, all of which helped us focus on overwinter survival as a crucial parameter that seems to be the proximate cause of population declines.

All available evidence shows that Loggerhead Shrike populations in the upper midwest are declining at alarming rates. These rates of decline have endangered shrike populations and could lead to their extirpation within a few decades. Research attention should now focus on the wintering areas of midwestern shrikes and how habitat management there could reduce the population's rate of decline. It seems unlikely that conservation efforts on midwestern breeding areas will succeed in slowing or reversing the declines in these shrike populations if they are being limited by factors on their non-breeding range.

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Figure 1. Eleven counties in Minnesota where breeding pairs of Loggerhead Shrikes were studied.

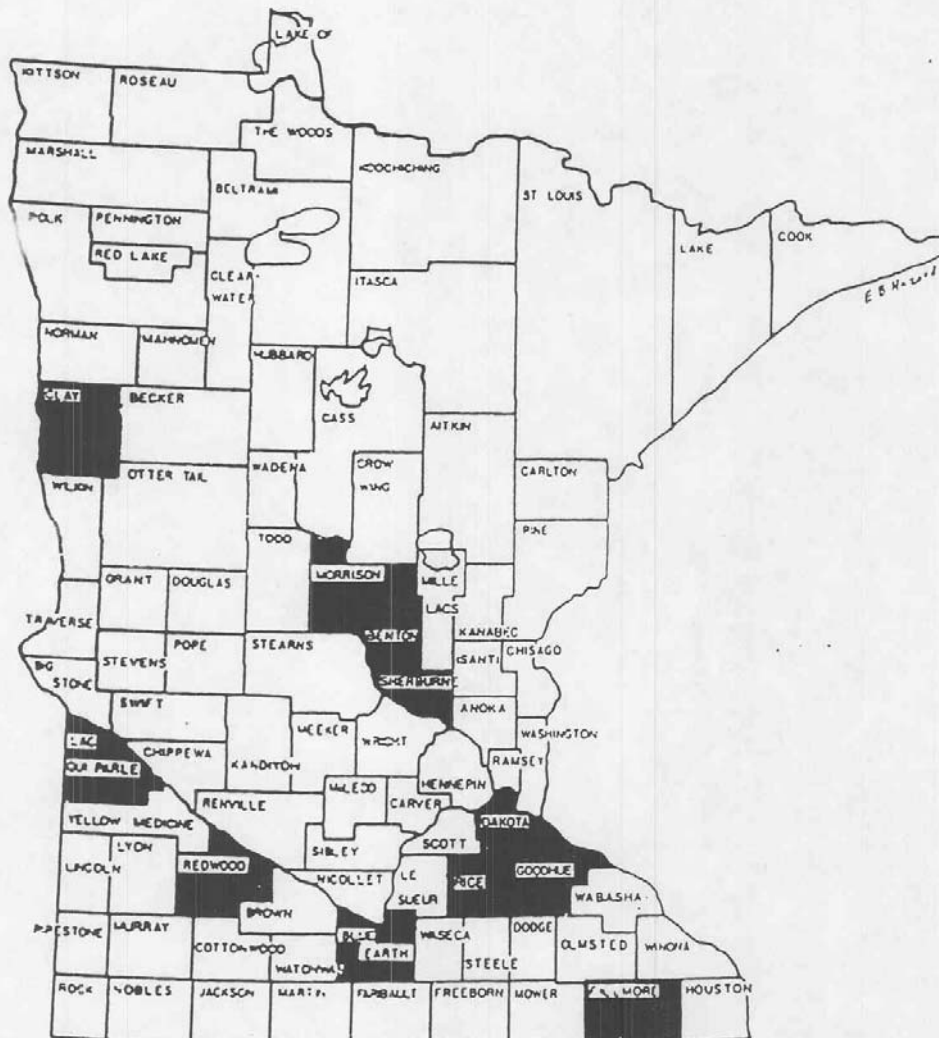


Table 1. Summary of Minnesota Loggerhead Shrike nesting data, 1986-87.

Parameter	Mean \pm SD or Percentage (N)		
	1986	1987	Both years
Clutch size	5.58 \pm 1.38 (24)	5.73 \pm 0.94 (22)	5.65 \pm 1.17 (46)
Nestlings per nest	4.54 \pm 2.20 (26)	3.80 \pm 2.45 (25)	4.18 \pm 2.33 (51)
Fledglings per nest	3.12 \pm 2.17 (33)	2.89 \pm 2.10 (27)	3.02 \pm 2.17 (60)
Fledglings per pair	3.48 \pm 1.91 (29)	4.11 \pm 1.74 (19)	3.73 \pm 1.82 (48)
Hatching success	81% (24)	71% (22)	76% (46)
Fledging success	66% (26)	77% (25)	72% (51)
Percent nests that fledged > 1 young	74% (34)	70% (27)	73% (61)
Percent pairs that fledged > 1 young	83% (29)	84% (19)	83% (48)
Mayfield estimate of nest success	66% (24)	56% (23)	62% (47)

Table 2. Model parameters and their means and coefficients of variation.

Model Parameter	Mean Value	Coefficient of Variation
Productivity per pair	3.73	29%*
Annual adult survival	0.47	11%*
Ratio of juvenile-to adult survival	0.41*	22%*
Annual juvenile survival	0.19	36%*

* Taken from Woolfenden and Fitzpatrick (1986).

HABITAT AVAILABILITY AND SUITABILITY FOR LOGGERHEAD SHRIKES
IN THE UPPER MIDWEST

Bonnie L. Brooks
Stanley A. Temple
Department of Wildlife Ecology
University of Wisconsin-Madison

ABSTRACT

A decline of the Loggerhead Shrike (Lanius ludovicianus) in the eastern United States has evoked much concern over the status of the species and the need for conservation activities. Several explanations for the decline have been proposed, including: poor reproduction, shortage of suitable breeding habitat, and high overwinter mortality. This paper describes a system for assessing the suitability and availability of Loggerhead Shrike breeding habitat in the upper Midwest. Using information from previous studies—to supplement our own data, we have constructed a habitat evaluation model using procedures analogous to the U.S. Fish and Wildlife Service's Habitat Suitability Index (HSI) models. Our model is based on habitat features, such as the percent grassland cover, availability of perch sites, and availability of nest sites. It also incorporates measures of the fitness of shrikes occupying various habitats. We were unable to find convincing evidence that the abundance of Loggerhead Shrikes is limited primarily by availability of breeding habitat.

INTRODUCTION

Recent declines in Loggerhead Shrike (Lanius ludovicianus) populations in the eastern United States (Bystrak and Robbins 1977, Graber et al. 1973, Kridelbaugh 1981, Morrison 1981, Robbins et al. 1986) might be caused by reductions in the availability of suitable breeding habitat. Loss of breeding habitat has been addressed as a possible cause of the decline (Gawlik 1988, Luukkonen 1987, Kridelbaugh 1983, and D. Degeus, pers. comm.), and characteristics of the breeding habitat have been described in Colorado (Porter et al. 1975), Alabama (Siegel 1980), Missouri (Kridelbaugh 1983), Virginia (Luukkonen 1987), and South Carolina (Gawlik 1988).

None of these studies, however, provide guidelines for assessing the suitability and availability of shrike breeding habitat in the upper Midwest. Moreover, the suitability and availability of breeding habitat in the upper Midwest, an area where shrikes have declined severely, have never been assessed. The objectives of this paper are to describe a system for assessing the suitability of Loggerhead Shrike breeding habitat in the upper Midwest and to evaluate the suitability and availability of breeding habitat in Minnesota.

Using information from previous shrike studies to supplement our own data, we evaluated shrike habitat using procedures analogous to the U.S. Fish and Wildlife Service's Habitat Suitability Index (HSI) models (USFWS 1981). An HSI model provides a numerical assessment of the capacity of a given area to support a particular wildlife species. Our HSI model was used

to evaluate habitat for breeding pairs of shrikes during the nesting season in Minnesota.

STUDY AREA AND METHODS

From 22 April-20 August, 1986, and from 14 April-10 August, 1987, we studied shrike breeding habitat in nine counties in the southern 2/3 of Minnesota: Benton, Clay, Dakota, Goodhue, Lac Qui Parle, Morrison, Redwood, Rice, and Sherburne (Figure 1). These counties were part of the state's extensive tall-grass prairie and savannah ecosystems during pre-settlement times. Agriculture has replaced tall grass prairie almost in its entirety, leaving less than 1% of the original area as prairie (Wendt 1984). Today, the dominant vegetative cover types in the nine counties are agricultural fields and pasturelands.

Our study areas were centered on 48 Loggerhead Shrike nest sites. We recorded nesting tree species, type of tree complex (i.e., isolated tree, hedgerow, or copse), and nest height for each nest area. We constructed cover maps of a 25-ha circular plot (1/6-mi radius) and a 50-ha circular plot (1/4- mi radius) centered on each nest site. A 25-ha circular plot encompassed the territory and most of the home range used by nesting pairs; a 50-ha circular plot encompassed nearly all of the areas likely to be used by nesting pairs during a breeding season (Ash 1970, Luukkonen 1987). The following habitat features were measured within each 25-ha and 50-ha plot: number of potential nesting

sites (isolated trees, copses, and one-tree-wide hedgerows), number of discrete perch sites and linear length of continuous perch sites (high wires, hedgerows, and forest edges), distance from the nest site to the nearest building, and total area of each habitat type. We measured 8 habitat types: row crop, non-row crop, pasture, grassland (prairies, cedar glades and lawns), woodlot, wetland (standing water, marshes, and riparian), residential, and miscellaneous ground cover (non-herbaceous cover, such as buildings, paved lots, gravel pits, and coal mounds). Habitat features that could not be measured on aerial photographs (e.g., length of high wires) were recorded in the field. The number of potential nest sites was estimated by measuring the length of one-tree-wide hedgerows and dividing by 5 m (the average distance between trees in a hedgerow), plus the number of isolated trees, and the number of copses < 40 m in circumference.

We randomly located 15 points in shrike-occupied-townships and adjacent townships, and mapped 25-ha and 50-ha circular plots centered on each point. We excluded randomly selected plots that overlapped or were adjacent to an occupied shrike territory. Therefore, all random plots were known to be unoccupied by breeding shrikes. These unoccupied random plots were mapped according to the procedures described above for the occupied plots. We used Wilcoxon's rank test to test the hypothesis that

there was no difference in the mean value of each of the habitat variables between the occupied and unoccupied plots.

We measured the distance from all occupied nest sites and potential nest sites to their respective nearest buildings in the 50-ha circular plots. We used a chi-square goodness-of-fit test to test the hypothesis that shrikes do not nest nearer to homes than would be expected given the distribution of all available nest sites. A nest was considered "near" if it was < 220 m from a building, based on a bimodal histogram of all potential nest sites. The Mann-Whitney test was used to determine if there was a difference in nesting success between nests that were near to buildings and those that were far from buildings.

From 12 May to 8 August, 1986, we weighed nestlings in 17 shrike nests. Beginning 5 days after the first egg hatched, we weighed individually marked nestlings to the nearest 0.1 g once every three days until the oldest nestling was 14 days old. The slope of the linear segment of the growth curve (between the ages of 6 and 11 days) was used to estimate the average growth rate of each nest. We continued to monitor each nest until the young successfully fledged, or the nest failed. We looked for correlations between various habitat parameters and growth rates, average weights at 8 days of age, hatching success (percent of eggs that hatched), fledging success (percent of nestlings that fledged), or nesting success (percent of eggs that resulted in fledged young).

We developed suitability indices for each of four variables that represented important breeding-habitat requirements of the Loggerhead Shrike: percentage of a plot with herbaceous ground cover (V_1), percentage of the area that is potential foraging habitat (V_2), percentage of the area that is useable foraging habitat (i.e., that is within potential striking distance of elevated hunting perches) (V_3), and number of potential nesting sites in a plot (V_4).

Table 1 summarizes the variables used to construct habitat suitability indices. Data used to construct suitability indices were taken from our 25-ha plots and include some combination of two or more parameters measured in our study areas. The percent coverage of herbaceous ground cover is defined as the percentage of the 25-ha plot that is "open" (i.e., covered by non-woody vegetation); woodlands, wetlands, and miscellaneous ground cover are not considered herbaceous ground cover. Percent coverage of potential foraging habitat is defined as the percentage of the 25-ha plot that is covered by grassland (prairies, cedar glades, or lawn), pasture, or hayfield. The number of potential nest sites is defined as the sum of all isolated trees, copses < 40 m in circumference, and the length of one-tree-wide hedgerows divided by 5 m. A tree was considered suitable for nesting if its height was between 1.5 and 12.0 m, and the lowest tree branch was less than 3 m from the ground.

The percentage of a 25-ha plot that was useable foraging habitat is defined as the total area within 18 m of each discrete elevated hunting perch (i.e., trees, snags, poles, etc.) plus the area within 18 m of all continuous linear perches (i.e., hedgerows and high-wires). Eighteen meters was the mean distance plus two standard deviations at which perched shrikes attacked prey, based on data from Morrison (1980). Shrikes normally forage from perches 4-7 m above the ground (Morrison 1980); therefore, barbed wire fences and other non-elevated perch sites were not included in this variable.

A suitability index (SI), rated on a scale from 0-1, is assigned to the value for each habitat variable; this yields 4 suitability indices (SI1, SI2, SI3, and SI4) for each 25-ha plot. The geometric mean of the four suitability indices for a 25-ha plot is the overall habitat suitability index (HSI) for the area (i.e., the capacity of the area to support a single pair of shrikes):

$$HSI = (SI_1 \times SI_2 \times SI_3 \times SI_4)^{1/4} .$$

The values of HSI can range from 1.0 (highly suitable) to 0 (completely unsuitable).

We surveyed five 20-mile road transects once a week in five counties from 30 June to 31 July 1987. We made a 5minute stop every 1/2 mile along the transect and scanned a 1/4-mi-radius semicircle (25-ha) on both sides of the road with binoculars in search of shrikes; the presence or absence of shrikes was

recorded. Each 25-ha semicircle was classified as either suitable or unsuitable habitat based on the 4 variables used in our HSI model. A 25-ha semicircle was considered suitable (i.e., it had an HIS value > 0.5) if it had at least 75% herbaceous ground cover at least 50% potential foraging habitat, at least 5% useable foraging habitat, and at least 7 suitable nesting sites.

RESULTS

Nest Site Characteristics

Loggerhead Shrikes nested in 13 different tree species. The most frequently used trees were those that had a very shrubby or bushy growth form: 44% were located in eastern red cedar trees (Juniperus virginiana), 21% were in deciduous trees bearing thorns or spines (Prunus americana, Grataegus sp., Elaeagnus angustifolia), 12% were located in spruce trees (Picea pungens and P. glauca), and the remaining 23 were located in one of 7 other tree species.

Sixty-one percent of nests were in isolated trees, the most common of which were eastern red cedars in a cedar glade. Thirty-two percent of the nests were located in either a hedgerow or windbreak, all of which were only one-tree-wide. Seven percent of nests were in a copse. Nest heights ranged from 1.0-5.5 m. The average nest height was 2.3 m (N = 57, SD = 1.0). Although we did not measure nesting tree height, we estimated that nesting trees ranged from 1.7-9.2 m in height.

Shrike nests occurred most frequently in or amid agricultural fields; 37% of the nests were located in or immediately adjacent to a row or non-row crop field. Forty-five percent of the nests were located in grassland habitat, and 18% of the nests were in pastures.

When we compared habitat parameters associated with occupied nest sites and unoccupied random sites differences were detected (Table 2). There was a difference ($\underline{P}<0.10$) in the mean percent coverage of grassland in both the 25-ha and 50-ha plots; occupied sites had a higher percentage of grassland than random unoccupied sites. There were no differences in the mean percent coverages of any other habitat types. However, the combined coverage of pasture and grassland was greater ($\underline{P}<0.10$) in occupied sites for both the 25-ha and 50-ha plots. The mean length of hedgerows was greater in the occupied sites than in the unoccupied sites, but the difference was significant ($\underline{P}<0.10$) only in the 50-ha plots. The total number of potential nesting sites was significantly higher ($\underline{P}<0.10$) in the 50-ha occupied plots than in the 50-ha un-occupied plots.

Shrikes did not nest nearer to buildings than would be expected by chance ($\underline{X}^2=0.228$, $df=1$, $\underline{P}>0.30$). There was no difference in nest success between nests that either were near to or far from buildings (Mann-Whitney $U=187$, $\underline{P}=0.22$). The mean distance to the nearest building for successful nests was 271 m, while that for unsuccessful nests was 316 m, suggesting that nests near buildings were not prone to lower nesting success.

Nestling growth rate was positively correlated with percent coverage of grassland and percent coverage of potential foraging

habitat (Table 3). Nestling weight at 8 days of age was positively correlated with percent coverage of pasture, percent coverage of grassland, percent coverage of potential foraging habitat, and the percent of the area that was useable foraging habitat (Table 3). Nesting success was positively correlated with percent coverage of grassland (Table 3). Fledging success was positively correlated with the percent of herbaceous ground cover and with the percent coverage of grassland (Table 3).

Habitat Suitability Indices

A habitat suitability index is typically based on the relationship between habitat parameters and population parameters, usually population density (USFWS 1981). Shrike densities in our study areas were too low to measure numerical responses to habitat parameters. As an alternative, we used the relationship between various habitat parameters and measures of reproductive performance such as fledging success, nesting success, or nestling growth. On the basis of linear correlations between reproductive parameters and habitat parameters, and also based on the frequency distribution of certain parameters, we were able to associate suitability indices with each of the four variables used in our habitat suitability model.

The percent coverage of herbaceous ground cover reflects the importance of open habitat types to Loggerhead Shrikes (Miller 1931, Bent 1950). The distribution of this variable (Figure 2) clearly indicates that the more "open" the habitat is, the better suited it is for shrike occupancy; all of our occupied sites had greater than 50% herbaceous ground cover. The

suitability index curve for this variable is derived directly from the frequency distribution of the variable; 50\$ is the lower limit of suitability for this variable, and values equal to or greater than 958 are assigned an "optimal" suitability index value of 1.0 (Figure 3).

Our data indicate that occupied sites had greater coverage of potential foraging habitats than unoccupied sites, suggesting that suitability increased as potential foraging habitat increased.

We used the relationship between percent coverage of potential foraging habitat and nestling growth rate to construct a suitability index curve for this habitat variable (Figure 4). Fourteen percent was the lowest observed value for this variable in our study, so the curve drops off to a suitability index value of zero where the percent coverage of potential foraging habitat is less than 15%. We used the relationship between weight of 8-day-old nestlings and the percentage of the area that was useable foraging habitat to construct a suitability index curve for this variable (Figure 5). The lowest observed value on our occupied sites for this variable was 2%.

We constructed a suitability index curve for the number of potential nesting sites based on a subjective evaluation of the data (Figure 6). There were at least 7 potential nesting sites within a 1/4-mi radius of the center of every occupied 25-ha plot, suggesting that at least this many potential nesting sites are required for an area to be suitable. The suitability index drops to zero for values less than 7. The suitability index value increases as the number of nesting sites increase beyond 7. We

arbitrarily assigned an optimal rating (SI = 1.0) for all values greater than 50.

Habitat Use and Availability

The presence or absence of shrikes was recorded at 312 road transect sites. Based on our HSI model, 139 (45%) of the sites were classified as suitable and 173 (55%) were classified as unsuitable. Shrikes were present in 33 of the 312 road transect sites. A Chi-square contingency, analysis indicated that shrikes occurred more frequently in suitable habitat than in unsuitable habitat, based on the proportional number of occurrences of each habitat category ($X^2=3.80$, $df=1$, $P<0.05$). Of the 139 suitable sites, 20 were occupied by shrikes and 119 were unoccupied, indicating that shrikes are probably well below carrying capacity in Minnesota.

DISCUSSION

These results indicate that shrikes use primarily open, agricultural areas interspersed with grassland habitat for their breeding territories in the upper Midwest. Loggerhead Shrikes were described by Miller (1930) as a bird chiefly of farming country, especially abundant in the prairie region. Similarly, Bent (1950) stated that shrikes are birds of open country. More recently, Gawlik (1988), Luukkonen (1987), Kridelbaugh (1982), Siegel (1980), and Porter, et al. (1975) have reported on the importance of open habitat types, specifically improved pastures, grasslands and hayfields, within shrike breeding areas.

Applicability of HSI Model

Although our HSI model is simple, it incorporates the major requirements of Loggerhead Shrike breeding habitat. The importance of open habitat, foraging areas, elevated perch sites, and nesting sites, has been identified and confirmed independently by many others (Miller 1930, Bent 1950, Porter et al. 1975, Craig 1978, Bildstein and Grubb 1980, Morrison 1980, Siegel 1980, Kridelbaugh 1982, Bohall-Wood 1987, Luukkonen 1987, Gawlik 1988). Likewise, Durango (1955) described essential habitat for the Red-backed Shrike (*Lanius collurio*) in Europe to be open ground covered with grass, dense bushes and thickets, and suitable look-out points from which the shrike can hunt. Therefore, our choice of habitat variables is consistent with earlier descriptions of shrike habitat requirements.

Our decision to use 25-ha plots for determining whether a given area had the capacity to support a breeding pair of shrikes was based on three criteria: the distance from the nest that shrikes typically travel to hunt, Loggerhead Shrike territory size, and the convenience with which road transect surveys could be conducted on such sized plots. Ash (1970) noted that much of the food for Red-backed Shrike chicks in Great Britain was collected close to the nest, whereas the males would wander 300 yds away to hunt for themselves. We observed shrikes hunting up to 1/4 mi away from their nest sites during the nesting season. Loggerhead Shrike home range size and territory size have not been measured often. Kridelbaugh (1982) found Loggerhead Shrike

territory size in Missouri averaged 4.6 ha, and the largest territory size was 12 ha. Other studies of territory size in the genus and reported sizes ranging from 1.6-10.5 ha (summary taken from Kridelbaugh 1982). We found that Loggerhead Shrikes are easily visible up to 1/4 mi away in open country when the observer is using 7X binoculars (Brooks and Temple 1986), making it convenient to conduct surveys at 1/2-mi intervals. Scanning a 1/4-mi radius semicircle is equivalent to surveying 25 ha of habitat. Thus, 25 ha is not only a reasonably sized area for an observer to survey in a few minutes, but it is also a large enough area to encompass a pair's defended territory, as well as most of its potential home range.

Habitat Availability in Minnesota

Our data indicate that there is a substantial area of suitable but unoccupied breeding habitat in Minnesota, strongly suggesting that availability of breeding habitat is not limiting the Minnesota shrike population. This conclusion agrees with the results of other recent shrike studies conducted elsewhere in the U.S. (Gawlik 1988, Luukkonen 1987, Kridelbaugh 1983, and D. Degeus, pers. comm. ,). Shrike breeding habitat in Minnesota is similar in vegetative composition to shrike breeding habitat found throughout the range of the species in the Midwest, so our HSI model could be used to provide guidelines for assessing habitat suitability and availability in other areas of the Midwest.

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Figure 1. Nine counties in Minnesota where Loggerhead Shrike breeding habitat data were gathered.

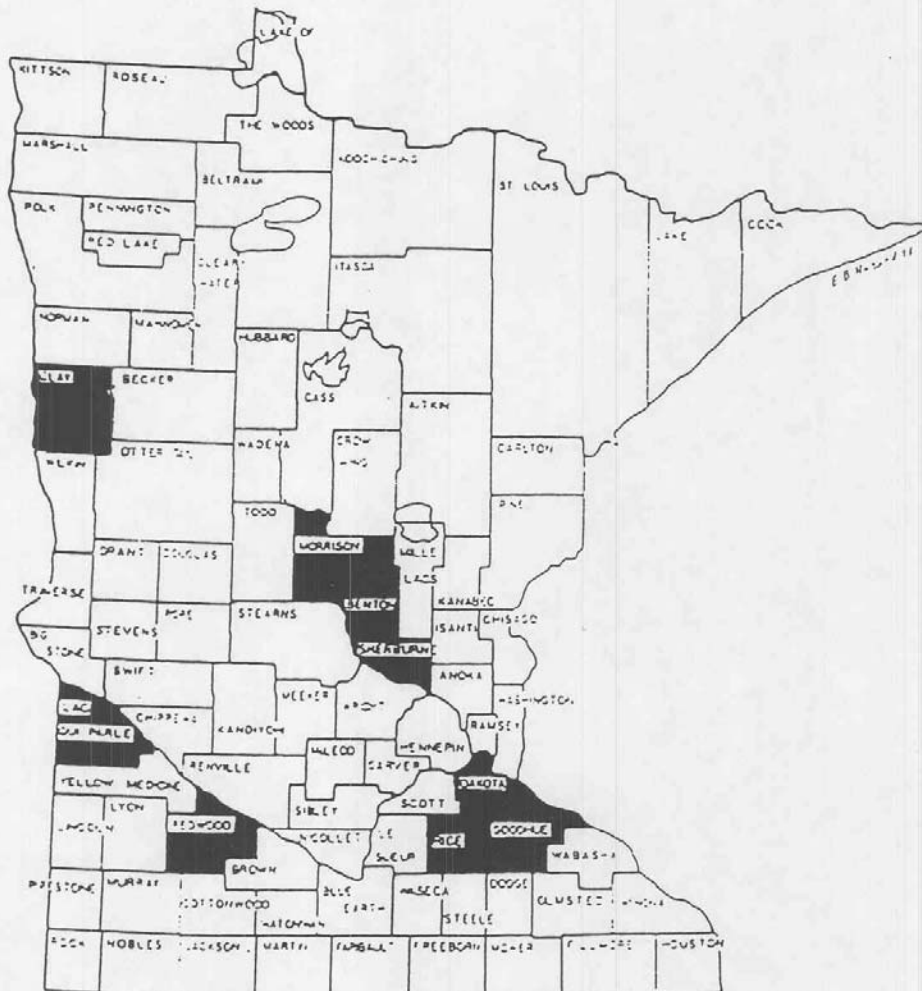


Figure 2. Histogram of the percent coverage of herbaceous ground cover found in the 25 ha surrounding 42 Loggerhead Shrike nest sites.

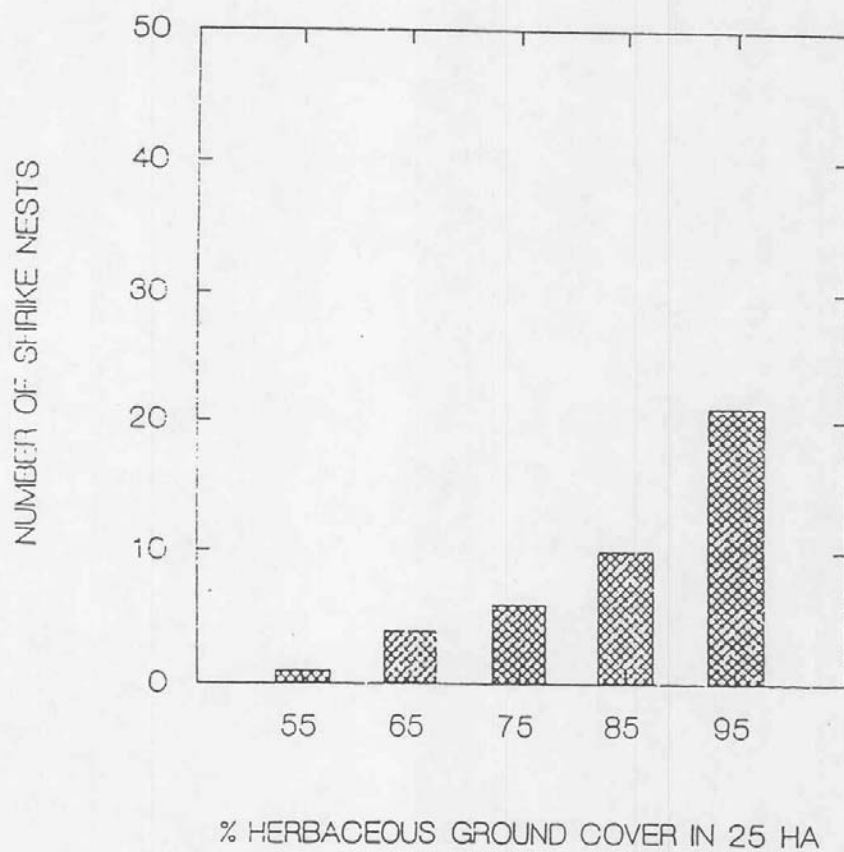


Figure 3. Suitability Index (SI_1) curve for the percent coverage of herbaceous ground cover in a 25-ha plot (V_1).

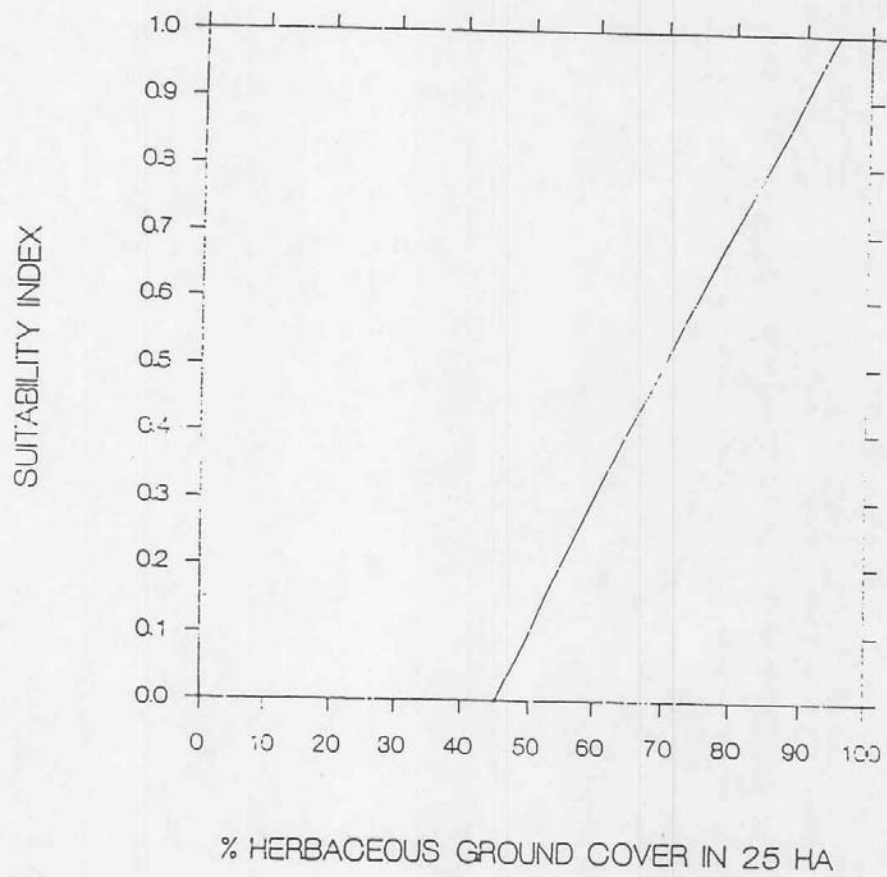


Figure 4. Suitability Index (SI_2) curve for the percent coverage of potential foraging habitat in a 25-ha plot (V_2).

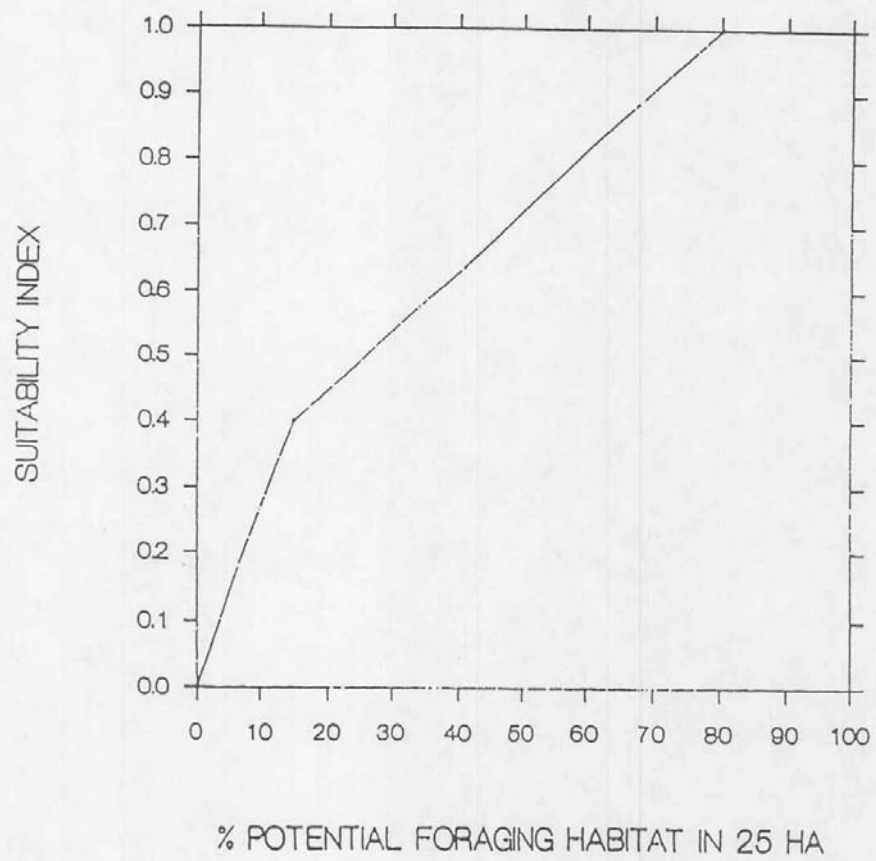


Figure 5. Suitability Index (SI_3) curve for the percent coverage of useable foraging habitat in a 25-ha plot (V_3).

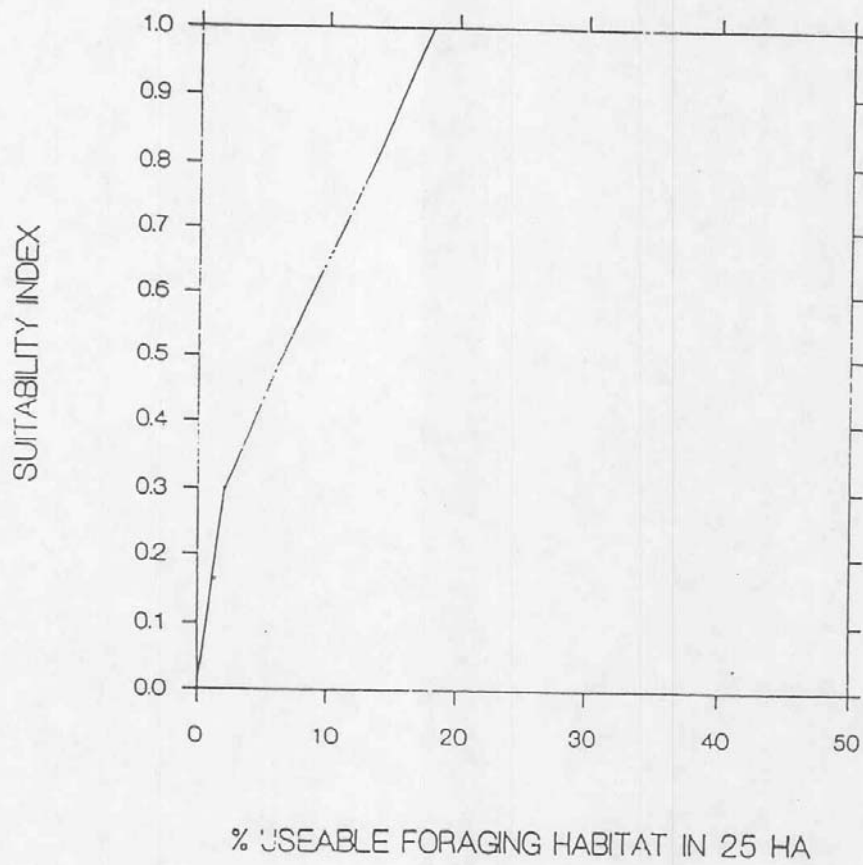


Figure 6. Suitability Index (SI_4) curve for the number of potential nesting sites within a 1/4-mile radius from the center of a 25-ha plot (V_4).

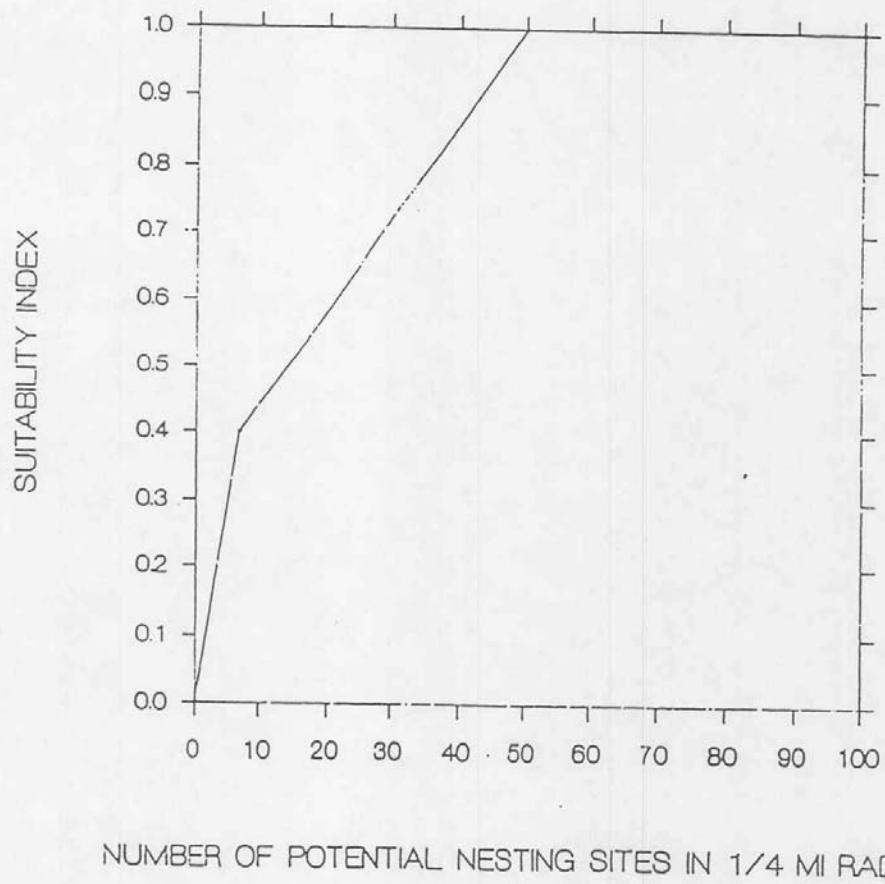


Table 1. Description of habitat variables used in habitat assessment of 25-ha plots in Minnesota.

Model variable	Description
V ₁	The percentage of the area that is covered with upland herbaceous vegetation (i.e., nonwoody vegetation).
V ₂	The percentage of the area that is covered with potential foraging habitat (i.e., pasture, upland prairie, grassland, and hayfield).
V ₄	<p>The percentage of the area that is covered by useable foraging habitat (i.e., potential foraging habitat that is within 18 m of an elevated hunting perch) as expressed by the following formula:</p> $V_4 = 18(U+H+F) + E(3.14)(18)^2 + \sum_{i=1}^k [3.14(C_i / ((2)3.14) + 18)^2 - (C_i^2 / 4(3.14))]$ <p>where U = the length of high wires, H = the length of hedgerows (U and H are multiplied by 2, if foraging habitat is on both sides of the high wire or hedgerow), F = the length of the forest edge, E = number of discrete elevated perch sites (trees, snags, poles) C = the circumference of the ith copse > 40 m in circumference.</p>
V ₃	<p>The number of potential nesting trees within 1/4 mi radius from the center of the plot as expressed by the following formula:</p> $V_3 = T + C + H/5$ <p>where T = the number of 1.5 to 12.0 m tall, isolated trees with lowest branches less than 3 m from the ground; C = the number of isolated copses with trees having characteristics described in T (above) and a circumference of less than 40 m; H = the total length (in meters) of one-tree-wide hedgerows with trees having characteristics described in T (above).</p>

Table 2. Comparisons of selected habitat parameters between occupied and unoccupied sites.

Habitat parameter	Mean value for:		Significance of difference ¹
	Occupied sites(n=42)	Unoccupied sites(n=15)	
% grassland in 50 ha	19.6	11.7	T=2.26, P=0.02
% grassland in 25 ha	24.3	14.3	T=1.89, P=0.06
% pasture in 50 ha	12.6	11.3	T=1.30, P=0.19
% pasture in 25 ha	12.8	13.1	T=1.15, P=0.25
% pasture + grassland in 50 ha	32.2	22.9	T=1.99, P=0.05
% pasture + grassland in 25 ha	37.1	27.4	T=1.68, P=0.09
% nonrow crop in 50 ha	15.6	24.0	T=-1.57, P=0.12
% nonrow crop in 25 ha	15.3	24.5	T=-1.12, P=0.26
% row crop in 50 ha	29.6	34.7	T=-0.77, P=0.44
% row crop in 25 ha	29.5	30.3	T=-0.17, P=0.86
Number of nesting sites in 50 ha	71.2	35.8	T=3.19, P=0.002
Number of nesting sites in 25 ha	51.1	35.7	T=1.45, P=0.14
Length of hedgerows in 50 ha (m)	198.0	51.6	T=2.45, P=0.02
Length of hedgerows in 25 ha (m)	145.6	90.5	T=0.74, P=0.46

¹ Wilcoxon's two sample rank test

Table 3. A matrix of correlation coefficients (r) between habitat parameters in 25-ha nest plots and measures of reproductive performance.

Habitat parameter	Nestling growth rate ¹	Weight at age 8 days ¹	Nesting success ²	Fledging success ²
% herbaceous ground cover	0.032	0.016	0.003	0.045
% grassland	0.252	0.032	0.320 ³	0.354 ³
% pasture	0.048	0.290	0.091	0.086
% potential foraging habitat	0.313	0.003	0.049	0.010
% useable foraging habitat	0.045	0.290	0.021	0.045

¹ n=17

² n=42

³ P<0.05