SPATIAL STRUCTURE AND FRAGMENTATION EFFECTS OF GRASSHOPPER SPARROWS IN MENDON PONDS, NEW YORK

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by
Karla Lynn Balent
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Karla Balent

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Christopher J. Nault — 25 July 2000
Major Advisor — Date

[signature] — 25 July 2000
Committee Member — Date

[signature] — 11 July 2000
Committee Member — Date

Christopher J. Nault
Chairman, Graduate Committee

Larry K. Klein — 8/8/00
Chairman, Dept. of Biological Sciences

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Abstract

Grasshopper Sparrows *(Ammodramus savannarum)* in Mendon, New York, were studied from 1997 to 1999, as part of a long-term study incorporating data from 1995 to 2000. This population of Grasshopper Sparrows represents a dynamic metapopulation responding to pressures associated with a decrease in the area of suitable breeding habitat patches, and an increase in habitat fragmentation. Ten fields occupied by Grasshopper Sparrows in the Mendon Ponds area ranged from 1.7 ha to 13.2 ha. From 1997 to 1999, Grasshopper Sparrows were mist-netted and banded, nests were monitored and vegetation analysis was conducted using the fixed-quadrat and Robel pole methods. Both fields with and without Grasshopper Sparrows were studied. A significant difference was found in the % bare ground between fields with and without Grasshopper Sparrows, with the lower value being found in fields with Grasshopper Sparrows. Robel pole measurements of fields with and without Grasshopper Sparrows showed the sparrows preferred fields with shorter, less dense vegetation. Large fields (>8 ha) showed a higher proportion of pairing and nesting success than did small (< 8 ha) fields. The overall proportion of successful nests in large fields averaged 66%, while the small fields' proportion of nest success only averaged 44%.

Five fields suffered population extinction of Grasshopper Sparrows between 1995 and 1999, and two fields were colonized. Neither large nor small fields could be considered "source" fields-- fields in which births outnumber deaths and which provide individuals to colonize empty fields within the metapopulation; however, large fields were more likely to persist than were smaller fields and produced more young than small fields. Chances of extinction increased with a decrease in the average number of males present, and fields which did not suffer population extinctions were significantly larger than fields which did suffer population extinctions. Changes in land use, as when fields are developed into subdivisions, and the transformation of early successional grasslands into old fields or forests, also affect the persistence of Grasshopper Sparrows. As suitable grassland

becomes unsuitable through landuse change and succession, Grasshopper Sparrows abandon the fields. Results of this study suggest that the metapopulation of Grasshopper Sparrows in Mendon Ponds occupies highly fragmented, relatively small habitat patches, and must be replenished by individuals from other populations via long-distance migration.

Introduction

Nationwide, 34 species of breeding birds are restricted to grasslands (Ehrlich et al. 1988, Knopf 1996, Vickery et al. 1999). Obligate species are defined as those exclusively adapted to and entirely dependent on grasslands (Vickery et al. 1999). New York's grasslands provide nesting habitat for 11 of these 34 species, six of which are listed as threatened or of special concern at the state level (NYSDEC 1997). However, many of these species are suffering declines due to the massive loss of grassland and prairie habitat (Samson and Knopf 1994, Herkert et al. 1996). Grassland habitat across the United States has declined by as much as 99% since European settlement (Samson and Knopf 1994, Vickery et al. 1999). In New England and New York, grasslands have declined by 60% since the 1930's (Vickery et al. 1994). Additionally, in the past 50 years, conversion of pastures and hayfields into row crops, and shortened cutting rotations of hay, have reduced the suitability of some habitat for grassland birds (Vickery et al. 1999). As a result, bird populations associated with these grasslands have also declined. The USFWS Breeding Bird Survey (Sauer et al. 1999) showed that of all the groups of birds it monitors, grassland birds nationwide have the most consistent declines. Overall, fewer than 30% of the species designated as grassland birds showed any population increase (Sauer et al. 1999). In the USFWS Region 5, which includes New York, Savannah Sparrow *(Passerculus sandwichensis)*, Henslow's Sparrow *(Ammodramus henslowii)*, Eastern Meadowlark *(Sturnella magna)*, and Bobolink *(Dolichonyx oryzivorus)* suffered declines of 1.2%/yr, 11.0%/yr, 2.5%/yr, and 3.8%/yr respectively, from 1980 to 1998 (Sauer et al. 1999).

As available habitat declines and populations of species living there decline with it, the chances of local extinction increase. The fragmentation of large, unbroken tracts of hospitable habitat leads to a decrease in patch size and an increase in isolation from source populations. These effects are detrimental to maintaining thriving populations of species which rely on large or close patches of breeding habitat (Dunning et al. 1995, Breininger

1999, Roberts and Norment 1999). Small populations of individuals are naturally more susceptible to extinction than large ones, although some small populations may persist for years (see Simberloff 1994). Once populations fall to critically low levels, stochastic processes and human interference can push them to extinction (Shaffer 1981). The decline and breakup of North America's grasslands into fragments is one of these human interferences.

Studies on the effects of fragmentation on population persistence are numerous. One potential negative effect of fragmentation is its effect on dispersal ability (Burkey 1989, Peacock and Smith 1997, Tweksbury et al. 1998, Breininger 1999). In fragmented environments, local populations may be separated from one another by areas of unsuitable habitat. A species' ability to disperse across inhospitable habitat to hospitable habitat will determine its persistence in a fragmented environment. A population consisting of many local populations connected through dispersal has been defined as a metapopulation (Levins 1970). Many researchers have used metapopulation theory and its mechanisms in an attempt to analyze and explain fragmentation's effects on spatially distinct but interacting populations across a landscape (Nee and May 1992, Simberloff 1994, Wiens 1994, Wiens 1996, Hanski 1996, Hanski 1999). Briefly, this theory focuses on the dynamics of divided populations linked through migration and requires the population in question to meet four conditions: local breeding populations must occur in discrete habitats; no one population is so large that its expected lifetime is long relative to the others in the metapopulation; the dynamics of the local populations are asynchronous, and habitat patches are not so isolated that they cannot be recolonized (Wiens 1996).

Metapopulation theory has been applied to species as diverse as pika *(Ochotona princeps)* (Peacock and Smith 1997), Glanville Fritillary butterflies *(Melitaea cinxia)* (Hanski and Thomas 1994), Checkerspot butterflies *(Euphydryas editha bayensis)* (Gotelli 1995), carabid beetles *(Pterostichus versicolor)* (den Boer 1981) and stream fishes (Gotelli

1995). These species are good candidates for such studies as they all disperse at some point in their lives to surrounding patches of habitat, but since they do not migrate long distances, the population and its associated processes are restricted to a relatively discrete space within the landscape. Few metapopulation studies have broadened the spatial focus to include species which migrate long distances, such as migratory birds.

Ultimately, to understand fragmentation's effects on local populations, one must account for the ability of individuals from the population in question to disperse and find empty patches, which may result from extinction or newly created habitat. Patch quality plays a major role in the presence or absence of a species. Pulliam (1996) defines patch quality in terms of reproductive success and survival of individuals occupying the patches. Patch quality can vary from year to year, depending upon whether the patch is a "source," in which births or immigration exceed deaths or emigration; or a "sink" in which deaths or emigration exceed births or immigration. Understanding how each patch is distributed across the landscape, how the size of each patch influences species presence and persistence, how the population in each patch interacts with other local populations and how patch quality affects reproductive success and survivorship will provide needed data for metapopulation and other models used to predict fragmentation's effects on species in general.

Given declining and ever increasing fragmented grassland habitat in western New York, the need to determine how, if at all, fragmentation affects grassland bird species is increasingly important. Total grassland area has an effect on bird species which rely on this habitat for breeding. In Maine, higher grassland bird species richness occurs in large (>64 ha) patches (Vickery et al. 1994). Norment et. al (1999) found that fields of ≤5 ha of contiguous habitat in western New York contained fewer species than typically were found in larger areas, but they also showed that vegetation characteristics of fields influenced the presence or absence of species. Many grassland species have been shown to be area-sensitive. Abundance of Henslow's Sparrow (Herkert 1994, Winter and Faaborg 1999), Savannah Sparrow, Eastern Meadowlark (Herkert 1994), and Greater Prairie Chicken *(Tympanuchus cupido)* (Winter and Faaborg 1999) all increase with habitat area.

The Grasshopper Sparrow *(Ammodramus savannarum)* is another area-sensitive, obligate grassland bird. In the United States, it breeds from western Montana, eastern Colorado, Wyoming and Montana east to the Atlantic, south to central Texas, southern Arizona, northern Mississippi, Alabama, and Georgia, and north to extreme southern Maine and the Canadian border (Vickery 1996). Grasshopper Sparrows migrate south to the southern U.S., Mexico, Cuba and the Caribbean in mid-August to late September (except for the non-migratory subspecies *A.s. floridana* ,which breeds in central Florida) and return to their breeding grounds in mid-May to June (Vickery 1996). On their breeding grounds, Grasshopper Sparrows prefer moderately open grasslands and prairies with patchy bare ground, and they avoid grasslands with extensive shrub cover (Vickery 1996).

Grasshopper Sparrows declined in the eastern Breeding Bird Survey region (US Fish and Wildlife Service Region 5) by 3.3%/yr from 1980 to 1998 (Sauer et al. 1999). In New York state, Grasshopper Sparrow numbers declined by 8.2%/yr from 1980 to 1998 (Sauer et al. 1999) and it is listed by New York State as a species of special concern (NYSDEC 1997). Heavy loss and fragmentation of its breeding habitat may be responsible for this decline. Decreasing patch size limits the number of Grasshopper Sparrows a patch can hold. Individual territory sizes of grassland birds are generally small, and Grasshopper Sparrows defend territories ranging from (on average) 0.8 ha to 1.8 ha (Delany et al. 1994, Vickery 1996). A successful population of sparrows may be able to survive in a collection of small patches, but the number of breeding birds in each patch can be only as large as the patch will allow. Smaller patches mean fewer breeding birds, fewer breeding birds means smaller overall populations, and smaller populations suffer from a greater risk of extinction.

Closer examination of how fragmentation affects Grasshopper Sparrow populations in western New York can provide clues as to how fragmentation affects other grassland species. Specifically, the focus of my study was to look at the breeding biology, density, return rates, movement between and among patches, and site fidelity of a Grasshopper Sparrow population. Additionally, I measured the vegetation characteristics of each field, and monitored the local extinctions and colonizations of each field. My objectives were to determine: 1. how fragmentation affected return rates and breeding biology of a population of Grasshopper Sparrows, and 2. how these responses, coupled with patch quality, may affect continued persistence of the population.

Methods

This study began in 1997 and continued through 1999, although some data on Grasshopper Sparrows were collected by C. Norment in 1995, 1996 and 2000. The study was conducted in the Mendon Ponds County Park area in Mendon, New York. The study area included the county park, and habitat within a 10 km radius around the park. The landscape consisted of grassland habitat patches interspersed among deciduous forest patches, agricultural fields and suburban developments.

In 1995 bird surveys found Grasshopper Sparrows present in two fields within Mendon Ponds County Park (C. Norment, pers. comm.). In 1996 additional fields in the Mendon Ponds Park area were surveyed for Grasshopper Sparrows (Keenan 1996). Aerial photos of the Mendon Ponds area were obtained from the Agricultural Stabilization and Conservation Service (scale 1:20,000). Fields in Mendon Ponds Park known to contain Grasshopper Sparrows were identified on the photos, then used as references to identify fields outside the park containing comparable vegetative characteristics, and thus potential habitat for Grasshopper Sparrows.

Each potential field was surveyed from the road. All fields were classified as either containing Grasshopper Sparrows, having no Grasshopper Sparrows but having suitable habitat, or having habitat unsuitable for Grasshopper Sparrows (i.e. agricultural fields, etc.). Attempts were made to gain access to all fields through landowner consent, but not all landowners granted access. Fields in which access was denied were surveyed for Grasshopper Sparrows from the road. Potential fields which contained no Grasshopper Sparrows were surveyed for three subsequent breeding seasons to determine if any immigration of Grasshopper Sparrows had occurred.

Intensive field work within these fields began in mid-May to mid-July 1997 and continued in mid-May to mid-July, 1998 and 1999. Depending on the status of Grasshopper Sparrows in the field, surveys for Grasshopper Sparrows, mist-netting, nest searching, or vegetation analysis were carried out.

Whenever possible, Grasshopper Sparrows were captured in mist nets and banded to facilitate identification of individual birds. Mist-netting took place in the morning hours when birds were most active. Singing males were lured into the net with playback, or were flushed from perches into the net. Brooding females were flushed off the nest into the net. Each bird was measured and marked with a USFWS numbered aluminum band and a unique combination of colored plastic bands. Bill, tarsus, and unflattened wing length was measured on each individual. Bill length was measured from the anterior of the nares to the bill tip, and tarsus length was measured by placing calipers from the intertarsal joint to the distal end of the last leg scale (Pyle1997).

Each banded male's territory was then marked with orange flagging inscribed with the bird's band colors, date banded, and pairing status, if known. This provided for quick identification of the resident males when walking through any plot and allowed for an efficient means of counting the number of males/field. All territories with an unbanded male were marked with white flagging inscribed with the male's pairing status, if known. A male was considered paired if a female was seen consistently within his territory, he was seen carrying food, or if he consistently sang his sustained (secondary) song in addition to his primary song. The primary song is delivered from a fixed perch, and consists of short, staccato notes followed by a long, dry stridulation (Vickery 1996). It is thought to be associated with territorial displays (Vickery 1996, pers. obs.). The secondary song is more musical and is delivered from a fixed perch or in flight (Vickery 1996). This song is thought to be connected to mate attraction and maintaining pair bond and is not sung by unpaired males (Vickery 1996, pers. obs.). My flagging system allowed me to keep track of each male's territory, and any movements made out of those territories. It also represented, at a glance, the territorial layout of the plot, and enabled us to focus our banding efforts in the areas marked with white flagging. Return rates were determined by searching for previously banded birds throughout the breeding season.

Intensive fieldwork during the 1997 to 1999 field seasons allowed me to determine the number of male and female Grasshopper Sparrows, and their pairing status, in all occupied fields. In 1996 and 2000, less intensive work involving only counts of singing males only allowed determination of the number of territorial males.

Nest searches were conducted by walking through plots and either flushing females from the nest, following perched females to the nest, or spotting an adult carrying food. Once nests were found, their location was marked on a flag at least 5 m away. Egg length, breadth and mass were measured. Egg volume was measured using Hoyt's (1979) equation:

$$\text{Volume} = (0.51)(LB^2)$$

where L is egg length and B is egg breadth (maximum diameter). If the nests held chicks, the chicks were measured and banded when they were approximately five days old. Active nests were visited at least every other day until they fledged young, were abandoned or depredated. Because we were unable to find any nest before eggs were laid, an incubation period of 11 days and a nestling period of nine days was used for calculations of nest and fledgling success (Vickery 1996). When second nests with eggs were found, the hatching date was noted, based on the 11 day incubation period, the number of days which had passed between a first nest's fledge or depredation date to the date a second clutch was laid could be determined.

Daily nest survival (Mayfield 1975) and total probability of nest success (Winter and Faaborg 1999) were calculated for all nests found. The total probability of nest success is defined as the probability a nest successfully surviving both incubation and nestling periods and fledging at least one young (Winter and Faaborg 1999). Hatchability, defined as the number of eggs hatched divided by the number of eggs present on hatching day, was calculated for the three-year period. Overall proportion of successful nests was also calculated. The Mayfield method calculates daily and overall probabilities of nest survival for nests found during the incubation or nestling stage. This provides a more conservative estimate of nesting success than does simply determining the proportion of successful nests among all known nests (Mayfield 1975). Values for daily nest survival for eggs and chicks, the total probability of nest success and the proportion of successful nests are indicators of how well the population is doing to replace itself with future generations.

To determine the effects of field size on population dynamics, I separated the fields in large and small categories. Fields 8 ha and larger were considered large fields and fields less than 8 ha were considered small fields. Using these categories, I calculated each group's source-sink status. A source population is one in which births exceed deaths and emigration exceeds immigration. A sink population is one in which deaths exceed births and immigration exceeds emigration (Pulliam 1996). I used the equation in Fauth (2000) for the finite rate of increase:

$$\lambda = P_A + P_j \beta$$

where P_A is adult survival rate from one breeding season the next, P_j is the juvenile survival rate from fledging to the following breeding season, and β is the mean number of juveniles produced in a breeding season by successful and unsuccessful adult females (Fauth 2000). I estimated P_A, β and P_j from my own data, with the assumption that any marked bird not returning to the study area had died. Thus, $\lambda > 1$ indicates a source population, or a population which is capable of replacing itself without immigration from other areas, while a $\lambda < 1$ indicates a sink population, or a population that must be maintained through immigration of individuals from other areas.

Each year, vegetation characteristics were measured in all fields with Grasshopper Sparrows, as were an equal number of fields designated as potential habitat for Grasshopper Sparrows but containing none. Attempts were made to measure the same fields without Grasshopper Sparrows each year; however, some fields were converted to agriculture in mid-study, and had to be replaced with alternate fields.

In 1997 and 1998, the "fixed quadrat method" was used to quantify vegetation characteristics of each field. Thirteen vegetation variables were measured in each of 25 randomly located quadrats within each plot. These variables were: vegetation height (cm), litter depth (mm), total ground cover (%), legume (%), *Solidago* sp (%), dead grass and forbs (%), live grass and forbs (%), shrubs (%), canopy cover (%), genus richness, and maximum shrub height (cm). The percents represent coverage classes for each variable (Bollinger 1995). Coverage classes were: (1) <5%; (2) 5 - 25%; (3) 26 - 50%; (4) 51 - 75%; (5) >75% (Bollinger 1995); midpoint values for each coverage class were used in subsequent statistical analyses. In 1998 and 1999, a Robel pole (Robel et al. 1970) was used to measure the height and density of the vegetation. Twenty-five points within each field were chosen randomly. At each point, one measurement was taken in each cardinal direction around the pole. These four measurements were then averaged to determine the average height and density of the vegetation at that particular point.

Quadrat data from 1997 and 1998 were tested using two sample t-tests to determine if there were significant within-year differences between any of the 13 vegetation characteristics in the occupied vs. unoccupied fields. Two sample t-tests were also used for within-year comparisons of Robel pole data for 1998 and 1999 for fields with and without Grasshopper Sparrows.

All variables were compared using two-tailed tests, as there was no *a priori* expectation these variables would differ in a particular direction. To generate a reasonable fit to normality, all percents were transformed using the arcsine transformation, and the subsequent data analysis was performed on the transformed data. Two-tailed tests were also used in interpreting the Robel pole data and between-year comparisons. All tests used a significance level of $\alpha = 0.05$; unless otherwise noted; $\bar{x} \pm$ SE are given throughout. Because of small sample sizes, multivariate statistical methods could not be used.

Chi-square tests were used to compare return rates in large and small fields, return rates of successful and unsuccessful birds, side vs. top opening nests and nest success, nest success among years, average proportion of successful nests in large vs. small fields, and nest success in fields in which the sub-population persisted or went extinct.

Results

In 1995 55 fields within an approximate area of 154 km were identified from aerial photos as potential Grasshopper Sparrow habitat (Keenan 1996), including fields in Mendon Ponds Park. In 1996 ground surveys of these 55 fields were conducted. Among these, 10 had been plowed for agriculture which meant that they no longer could support Grasshopper Sparrows; 15 were inaccessible for a road survey or the landowner could not be identified or contacted; and the landowners of seven fields denied entry and road side surveys of these fields detected no Grasshopper Sparrows. This left 23 accessible fields containing Grasshopper Sparrows or as potential habitat for them. From 1997 to 1999, a detailed population study was conducted on these 23 fields. It is possible that fields inaccessible by roads and in which entry was denied may have contained Grasshopper Sparrows. However, these questionable fields were checked against the aerial maps, and none appeared to contain habitat suitable for Grasshopper Sparrows.

Of the 23 accessible fields, ten contained Grasshopper Sparrows during at least one breeding season from 1995 to 1999 (Table 1), seven did not contain Grasshopper Sparrows and were used only for vegetation analysis, and six fields within the study area contained potential Grasshopper Sparrow habitat, but none were found in these fields. The following analyses focus on the ten fields containing Grasshopper Sparrows and the seven unoccupied fields used for vegetation analysis.

The ten fields (F1 - F10) occupied by Grasshopper Sparrows ranged in size from 1.7 ha to 13.2 ha (Table 1). Distance between fields ranged from 15 m (the width of the hedgerow between F1 and F2) to 6.4 km. The average estimated population size in all ten fields during the 1996 to 2000 breeding seasons was 24 males and 16 females. The population of male Grasshopper Sparrows fluctuated somewhat over the five-year study (Fig. 1).

In 1996, eight fields within the study area contained breeding pairs of Grasshopper Sparrows. By 1999, the number of fields holding sparrows had dropped to five. Two of these five fields represented recent colonizations (see Figs. 2 to 5). These same five fields were occupied in 2000 (C. Norment, pers. comm.). Some fields which contained birds throughout the study also showed a decrease in the number of breeding pairs present. Fields 1 and 8 decreased from 14 and 11 birds (males and females combined) to six and five, respectively, from 1997 to 1999. Field 6, the largest of all the fields (13.2 ha), was the only field to contain a consistent number of Grasshopper Sparrows during each breeding season (Table 1). The number of birds in Field 4, colonized in 1997, increased from three Grasshopper Sparrows in 1997 to nine in 1999. Interestingly, no females were detected in Field 4 in 1997, but two and then four females were present in 1998 and 1999. Four males banded early in the breeding season (May) disappeared from their fields during that same breeding season, and these males did not turn up in any other field. The average number of males in fields which went extinct during the study (1.63 ± 0.39) was significantly less than ($t = 3.65$, $df = 4$, $p = 0.022$) the average number of males in fields where no extinction occurred (4.90 ± 0.81); in other words, chances of extinction increased with a decrease in the average number of males present. Additionally, fields which did not suffer population extinctions (8.55 ± 1.8) were significantly larger than fields which did (2.75 ± 0.53; $t = 3.06$, $df = 3$, $p = 0.055$).

In 1997, 1998, and 1999, a total of 12 female, 41 male, and 43 nestling Grasshopper Sparrows were banded. Data on wing cord, tarsus, bill length and mass are given in Table 2.

In 1998, six banded adult birds (five male, one female) returned to the Mendon Ponds area (return rate for both male and female = 36%, n = 22) (Table 3). Of these all except one returned to the same field and general territory in which they were banded the previous year. One adult male returned to a different field (F2 to F1; Fig. 2) than the one in which it was banded. However, this movement, averaged from the center of the first territory to the second, reflected a territory shift of only 100 m.

In 1999, six banded adult birds (four male, two female) returned to the same territories they held in the 1998 breeding season (return rate for both male and female = 27%, n = 17) (Table 3). Three of these birds (two male, one female) had been banded in 1997, making the 1999 return their third breeding season in the same territories. All four males set up territories in the same general areas as they held in the previous year; however, the female switched territories, making a move of about 80 m. Interestingly, the male with whom she mated in 1998 returned to their territory in 1999, and mated with another, unbanded female.

In 2000, four known adult birds (all male) returned to the same fields in which they were banded in 1999 (male return rate = 33%, n = 12) (Table 3) (C. Norment, pers. comm.).

Overall return rates (1997 - 1999) were 30% for males, 45% for females, and 32% for all adults (Table 3). Return rates for adult males and females in 1998 and 1999 could not be compared statistically because numbers were too low for females. Overall return rates (1998, 1999 and 2000 averages) per field are shown in Figure 2.

The return rates for first-year adults banded as juveniles was 4% in 1998 (n = 21). One first-year adult male returned to the same field in which he was banded as a nestling the previous spring. He also set up a territory which overlapped the one in which he was born. No nestlings banded in 1998 (n = 17) returned as first-year adults in 1999.

Although there was no significant difference between return rates in large and small fields ($X^2 = 0.643$, df = 1, p = 0.42), the two largest fields of 13.2 ha and 8.69 ha had the majority of overall returning adults in 1998 and 1999 (14 of 16), and only birds from fields >4 ha returned the following breeding season (Fig. 2). Nesting success did not affect return Grasshopper Sparrow return rates: 8 of 16 birds which successfully fledged young the previous breeding season returned the following year as opposed to 3 of 8 which were unsuccessful ($X^2 = 0.336$, df = 1, p = 0.56).

During my study, I found and monitored 42 nests. Nests were built in shallow depressions on the ground. The rims were woven out of surrounding grasses and forbs, and the cups were lined with fine grass. Internal cup width averaged 4.9 ± 0.46 cm (n = 15) and cup depth averaged 5.8 ± 0.16 cm (n = 15). Nest openings were either located facing upward (53%), leaving the nestlings exposed from above, or there was a side-like entrance, delineated by a rim of overhanging grasses, which hid the nestlings from above (47%). The proportion of known side-opening nests surviving to fledgling (80%, n = 15) was significantly greater than the proportion of known top-opening nests (29%, n = 17)(X^2 = 8.19, df = 1, p = 0.004).

Thirty nests were found during the incubation stage and 12 nests were found during the nestling stage. In 1997 nine of 17 (53%) known nests were successful in fledging at least one young, in 1998 ten of 15 (66%) known nests were successful, and in 1999 four of 10 (40%) known nests were successful; however, nest success was not significantly different among years (X^2 = 1.76, df = 2, p = 0.41).

There was evidence of double brooding in the Mendon Ponds area Grasshopper Sparrows. Four pairs successfully fledged young and attempted another clutch. Of these, two nests were abandoned due to flooding and two successfully fledged the second clutch. Five other pairs lost a nest due to depredation and attempted another clutch. Of these nests, three were depredated and two successfully fledged the second nest. These pairs were not considered double brooded because the first nest was unsuccessful. One pair which lost its first two nests renested a third time and successfully fledged young. Overall, there were ten nests attempted after the first nest fledged or failed. These nests were built an average of 30.6 ± 4.70 m (n = 10) from the first nest. Based on the 11-day incubation period, an average of 5.8 ± 1.98 days (n = 5) passed between the first nest's fledging or depredation date and the day the first egg was laid in the subsequent nest.

Average clutch size per nest was 4.6 ± 0.12 eggs (range 3 - 6, n = 28); egg mass, length, width and volume are given in Table 4. Clutch size between first and second nests did not increase or decrease with any pattern. Of the known clutch size of first and second nests (n = 9), clutch size decreased by one egg in four cases, increased by one egg in one case, and remained the same in four cases.

For the three-year period from 1997 to 1999 hatchability was 93%. The overall proportion of successful nests was 55% (n = 42). Proportion of successful nests fluctuated from year to year, with 1999 having the lowest success and 1998 having the highest success

(Table 5). Total Mayfield probability of nest survival was 24% (range 0.08 - 0.43). The largest fields (F1, F4, F6) had the highest overall proportion of successful nests. These fields also accounted for the majority of nests found per year; for daily nest survival, mortality/nest day, and survival/nest day, see Table 5.

The difference in overall proportion of successful nests in large vs. small fields approached statistical significance ($X^2 = 3.183$, df = 1, p = 0.07) with 66% of nests successful in fields > 8 ha and 44% of nests successful in fields < 8 ha. The proportion of successful and unsuccessful nests did not differ statistically between fields where Grasshopper Sparrows persisted or went extinct ($X^2 = 3.554$, df = 1, p = 0.60). The average number of fledglings/female for large fields was 2.3, and the average number of fledglings/female for small fields was 1.3.

In determining the source-sink status for small and large fields, I used the estimated juvenile return rate of 0.04 from my own data for P_j, and used the estimated adult return rate (P_A; Figure 2) and the average number of fledglings/female (β) for large (0.36 and 2.3, respectively) and small (0.18 and 1.3, respectively) fields. The finite rate of increase for large fields was $\lambda = 0.46$, and the finite rate of increase for small fields was $\lambda = 0.23$.

Vegetation analysis yielded varying results. Two-sample t-tests of quadrat data for percent ground cover between fields with and without Grasshopper Sparrows approached a significant difference in 1997 and showed a significant difference 1998 (Tables 6 and 7); percent shrub cover approached a significant difference in 1998 (Table 7). Values for *Solidago* sp., and dead forb approached significance in 1997 (p = 0.15, and 0.14, respectively) with the lower values occurring in fields with Grasshopper Sparrows (Table 6).

Two-sample t-tests using Robel pole data showed a significant difference between fields with and without birds (1998: t = 2.98, df = 10, p = 0.01; 1999: t = 4.70, df = 2, p = 0.04). During both years, Robel scores indicated that vegetation was lower and less dense in fields with Grasshopper Sparrows (1998: $\bar{x}$ = 2.48 ± 0.72 dm; 1999: $\bar{x}$ = 1.70 ± 0.32 dm) than in fields without Grasshopper Sparrows (1998: $\bar{x}$ = 4.01±1.1 dm; 1999: $\bar{x}$ = 3.45 ± 0.60 dm).

Discussion

Local extinctions and colonizations occurred during this study, as did decreases in the number of breeding pairs in fields which maintained subpopulations throughout the study. Five local populations (F2, F3, F5, F7, F9) of Grasshopper Sparrows went extinct between 1995 and 1999 (Figs. 2 to 5) while two fields (F4, F10) were colonized during the study (Figs. 2 to 5). Of the three fields that consistently held Grasshopper Sparrows (F1, F6, F8), only F6 held a relatively constant number of breeding pairs during the study period, while the number of pairs in F1 and F8 declined (Table 1). The extinction of local populations in some fields, colonization of others, and the general decline of breeding pairs could be due to a number of factors: a decrease in vegetation quality, decline of Grasshopper Sparrows in the region or population fluctuations due to between-year differences in Grasshopper Sparrow survival rates.

Because all fields were relatively small (< 13.2 ha, Table 1), I believe that I accurately counted the number of males in each field. Male Grasshopper Sparrows consistently use the same perches within their territories for display purposes (Vickery 1996; pers. obs.), and in this study the majority of males in each field were banded. These two factors made it easy to monitor each male throughout the season and increased the chances of detecting a newcomer mid-season. The number of females was easily determined through direct sighting or through the male's song repertoire. While there was always the danger of underestimating the number of birds in a habitat patch, the estimates for 1997 - 1999 reflect a thorough, consistent banding and monitoring effort across years.

The Grasshopper Sparrows in the Mendon Ponds area are relatively site-specific, as is the case for other eastern Grasshopper Sparrows populations (Wells 1997, Vickery 1996). Banded males and females that returned almost always returned to the same field they bred in the previous year and, in some cases, returned to the same territory. Overall return rates of 35% (1998) and 27% (1999) were equal to or lower than those found in previous studies of Grasshopper Sparrows in the Northeast [50% in Connecticut (n = 10) and 35% in Maine (n = 42), Vickery 1996]. Only one Grasshopper Sparrow returned to a different field, and this movement was a small territory shift of approximately 100 m.

Herkert (1994) found the Grasshopper Sparrow in Illinois to be an area-sensitive species, needing 30 unfragmented ha to meet its estimated individual requirements (area at which a species probability of occurrence equals 50% of its maximum occurrence). In Maine, Vickery et al. (1994) found individual area requirements to reach 50% around 100 ha. On a scale and latitude more closely related to the Mendon Ponds area Grasshopper Sparrows, Smith (1997) found that Grasshopper Sparrows in central New York occurred in an average pasture size of 43.4 ha. The smallest pasture size Smith (1997) found supporting Grasshopper Sparrows was 16.2 ha. Herkert (1991) found 10 ha to be the minimum field size for the species in Illinois while Smith and Smith (1992) found 10 ha to be the minimum in the Finger Lakes region of New York. One Ohio study found Grasshopper Sparrows using fields averaging 16 ha, and another Ohio study found Grasshopper Sparrows occupying fields averaging 11 ha (range 1 to 21 ha) (review in Swanson 1996).

Conversely, Winter and Faaborg (1999) found the Grasshopper Sparrow in Missouri to only be a moderately area-sensitive species. Their study revealed that when a species is not area-sensitive or moderately area sensitive, other demographic data, such as nesting success, should be investigated as a possible factor in the presence or absence of a species in a given field (Winter and Faaborg 1999).

The Grasshopper Sparrows in the Mendon Ponds area do not have the option of choosing a breeding site larger than 14 ha because larger fields simply do not exist. Field 6, despite being about one-third larger and supporting more breeding pairs than the next largest field of 8.7 ha (F1), did not produce considerably more fledglings over the three-year period than Field 1 (F1: 38 vs. F6: 37, Table 1). Additionally, Field 6 had a lower proportion of successful nests than did Field 1 over the three year period (F1: 0.78 vs. F6: 0.56, Fig. 2).

The smallest field to produce fledglings was Field 8 (4.32 ha; Fig. 2). Fields smaller than this did support breeding pairs, but either nests were depredated or no evidence of nesting was found. Winter and Faaborg (1999) found that fragment size did not influence density of Grasshopper Sparrows in grassland fragments in southwestern Missouri, but that the sparrow's density was dependent on vegetative characteristics. In my study, fields which suffered extinctions tended to have fewer Grasshopper Sparrows than those fields in which Grasshopper Sparrows persisted. However, density alone is not a good indicator of habitat quality, which also should be evaluated in terms of reproductive success (Van Horne 1983, Vickery et al. 1992, Roberts and Norment 1999). For Grasshopper Sparrows at Mendon Ponds, birds breeding in large fields tended to produce more successful nests than those in small fields, with the proportion of successful nests in large vs. small fields approaching statistical significance. In fields where the subpopulation did not go extinct, there were more nests overall (n = 39 vs. 3) and a higher number of successful nests (n = 24 vs. 3), than in fields where extinctions occurred.

Small fields (<8.0 ha) may support some breeding pairs of Grasshopper Sparrows, but pressures associated with increased edge effects (namely, predation) may be too overwhelming for Grasshopper Sparrows to overcome (Johnson and Temple 1990). Subpopulations in small fields in this study were significantly more likely to go extinct than subpopulations in large fields and in each year of the study average field size for fields which were colonized or in which the subpopulation persisted was higher than those fields in which the subpopulation went extinct (Figure 6). Thus, results of my study indicate that larger (> 8 ha) fields are more suitable for Grasshopper Sparrows than are smaller fields: Populations in fields with a larger number of birds, more returning birds and a higher proportion of successful nests are more likely to persist than those small, less densely populated and less productive fields.

The finite rates of increase for small and large fields indicate that the Mendon Ponds population of Grasshopper Sparrows is maintained through immigration each year. Although the large fields' lambda value of 0.45 is two times greater than the 0.21 lambda value for the small fields, both large and small fields in the Mendon Ponds area fall below the value of $\lambda = 1.0$. Thus, the small, scattered patches of Grasshopper Sparrow habitat in the Mendon Ponds area represent a population sink, with low adult and juvenile return rates and low nest success unable to maintain the population. Therefore, the population of Grasshopper Sparrows must be maintained by immigration of birds from other areas via long-distance migration.

Fragmentation has been shown to affect the breeding biology or occurrence of other grassland birds. Powell and Collier (1998) showed that Belding's Savannah Sparrows *(Passerculus sandwichensis beldingi)* in California had greater reproductive success in larger habitat patches than in smaller, isolated patches. Johnson and Temple (1990) found nest predation increased for five species of grassland nesting birds in small (16 - 32 ha) fragments. In grassland fragments <100 ha in Illinois, Herkert (1994) found area requirements to limit Grasshopper Sparrow distributions. Although 79% of transects in small fragments were found to be vegetatively suitable for Grasshopper Sparrows, they only occupied 36% of these fragments.

In addition to field size, vegetation characteristics strongly affect Grasshopper Sparrow presence within a field (Whitmore 1981, Delany and Linda 1994, review in

Swanson 1996, Vickery 1996). Whitmore (1981) found the effective and mean vegetation height of occupied fields was significantly lower than that of unoccupied fields. Swanson (1996) summarized a number of studies and found that throughout their range, Grasshopper Sparrows have higher nesting densities in fields with low, sparse vegetation, and they avoid tall, dense cover. Delany and Linda (1994) found significant differences in grass cover, shrub cover, bare ground, and vegetation height in fields with Grasshopper Sparrows vs. fields abandoned by Grasshopper Sparrows; as grass cover increased, and shrub cover, bare ground and vegetation height decreased, Grasshopper Sparrows moved out of the fields.

This study found the percent of bare ground in fields with and without Grasshopper Sparrows approached significance in 1997 and was significant in 1998, with more bare ground evident in fields with sparrows. The percent of shrub cover in fields with and without Grasshopper Sparrows approached significance in 1998, with less shurb cover evident in fields with Grasshopper Sparrows. Comparisons made using the Robel pole showed a significant difference between fields with and without Grasshopper Sparrows, with Grasshopper Sparrows present in fields with lower, less dense vegetation and absent in fields with higher, more dense vegetation.

The breeding biology of Mendon Ponds Grasshopper Sparrows is generally similar to that of other Grasshopper Sparrow populations. The sparrows in this study laid an average of 4.6 eggs per nest, which is within the reported range of values of 4 to 5 (Vickery 1996). Mean length and breadth of the Mendon Ponds Grasshopper Sparrow eggs (18.6 x 14.5, n = 93, Table 4) are also comparable to reported lengths and breadths (18.6 x 14.4, n = 50; Vickery 1996). Egg mass averaged 2.05 g (Table 4), but no other published reports include any information on mass of eggs for comparison. The overall proportion of successful nests was 55% (Table 5), which is comparable to the nesting success of Grasshopper Sparrows in Maine (40 - 50%; Vickery 1996) and Nebraska (52%; Vickery

1996). The total Mayfield probability of nest success was 24% (Table 5), which is comparable to Winter and Faaborg's (1999) probability of 22% for Grasshopper Sparrows in southwestern Missouri. Nests were built on the ground in clumps of vegetation. Vickery (1996) reported that Grasshopper Sparrow nests typically have a side entrance, with an overhanging dome of grass. However, of the 32 nest openings noted in this study, 15 were top opening, with no overhanging dome. Nest cup diameter averaged 4.9 cm, which is smaller than reported diameters of 6-8.5 cm in Pennsylvania and 7.5-8.8 cm in Florida (Vickery 1996). Nest depth averaged 5.8 cm in this study, which is deeper than reported nest depths in Pennsylvania of only 3-4 cm (Vickery 1996).

There was no evidence of brood parasitism by cowbirds in any Grasshopper Sparrow nest. This observation is consistent with other Grasshopper Sparrow studies, which found low or no incidences of parasitism (Vickery 1996), and consistent with the lack of brood parasitism in other grassland birds in western New York (Norment et al. 1999).

Newly fledged Grasshopper Sparrows disperse from the vicinity of the nest (Vickery 1996). Some parental care is provided to these fledged young for approximately four to 19 days after dispersal (Vickery 1996). Fledged nestlings were rarely seen during this study; however, when they were encountered it was by flushing them from the ground within the natal territory. These encounters only happened within a few days after fledging; beyond that time no evidence of juvenile Grasshopper Sparrows was detected.

The Grasshopper Sparrows in the Mendon Ponds area appear to represent a dynamic metapopulation (see criteria in Introduction) influenced by habitat factors such as field size, habitat fragmentation, continued habitat suitability based on vegetative structure, nesting success, and the availability of colonists. Breeding occurs in discreet habitat patches as evidenced by the fields scattered throughout the study area. Additionally, there was relatively little movement among these fields. Only one bird switched fields and this switch only occurred upon his return from migration, not during the breeding season. During the breeding season, there was no exchange of individuals among fields. Extinction in fields occured during this study, indicating chances of extinction are high within this metapopulation. While arrival times, general breeding biology and departure times were similar for Grasshopper Sparrows in all fields in the Mendon Ponds area, subpopulations were spatially discrete in that some fields went extinct or were colonized while others remained stable. Some fields were more productive than others. Finally, two suitable habitat patches (F4, F10) in the Mendon Ponds area were colonized. Although F4 was only 15 m from the nearest occupied field, F10 was 1.4 km from the nearest occupied field, which suggests isolation at the scale studied in this population did not affect colonization.

What is interesting to note, however, is that colonization was not achieved by the direct dispersal of individuals from an existing subpopulation. Field 4 was only 15 m from Field 1, and Field 10 was only 1.4 km from Field 6, yet no banded birds were found in these fields. There was very little movement of marked birds among the fields (1 switch of 69 known birds), despite some patches being separated only by a two-lane road. Thus colonization of the two habitat patches was due to the dispersal of birds from other breeding areas, via wintering grounds in the southern United States and beyond, a distance of at least 1900 km.

Hanski (1999) discussed several bird populations that satisfy the criteria for designation as a metapopulation. These metapopulations are all non-migratory species such as the Northern Spotted Owl *(Strix occidentalis cauina)* (Hanski 1999), Bachman's Sparrow *(Aimophila aestivalis)* (Dunning 1995, Hanski 1999), and Florida Scrub-Jay *(Aphelocoma coerulescens)* (Breininger 1999). Each of these populations exhibit one common life history trait not shared by Mendon Ponds Grasshopper Sparrows-- the former do not spend their breeding and non-breeding seasons in widely separated locations. The fact that colonization occurs after long-distance migration is a unique aspect of the current study, in relation to other published studies of metapopulation dynamics. But no matter how many colonizers may be available to migrate into the metapopulation at Mendon Ponds, if suitable habitat does not continue to be available, the metapopulation will become extinct.

Grasshopper Sparrows prefer moderately open grasslands with low shrub cover and open patches of ground. Several studies have shown that grassland birds, including the Grasshopper Sparrow, respond favorably to grasslands which are mowed to keep vegetation thinned and shrub cover to a minimum (Herkert et. al 1996, Swengel 1996, Norment et al. 1999). In the Northeast, fields which are left undisturbed will undergo succession, and the vegetative changes associated with this process are unsuitable as Grasshopper Sparrow habitat; namely, the grassland will become dominated by shrubs, then trees (Barbour et al. 1987). Thus it is imperative that the fields where the Mendon Ponds Grasshopper Sparrows currently reside be maintained to promote their continued persistence. Mowing and burning fields in the summer have been shown to kill shrubs, reduce shrub frequency and height, and increase cool-season grass frequency (Mitchell 2000). Prescribed management such as this would help maintain the vegetation structure and composition preferred by Grasshopper Sparrows. However, even if suitable habitat could be maintained in fields through mowing and burning, increasing field size wherever possible would help ensure the continued presence of birds. For example, removing the hedgerow separating Field 1 and Field 2, and continued vegetation management of both fields would increase field size to over 13 ha, and would probably increase the number of Grasshopper Sparrows in the habitat patch.

As land use and vegetation change through time, associated bird species will also change. For example, Litwin and Smith (1992) showed that in a large forest fragment in Ithaca, NY ten migrant species went extinct while species richness of non-migratory birds increased over a 31-year period as agriculture in surrounding areas decreased and the forests became increasingly older. Birds which normally chose open woods and early successional understories went locally extinct as ground, shrub and canopy cover increased.

Similar successional changes may be affecting the Mendon Ponds Grasshopper Sparrows both at the field and landscape level. Roberts (1996) reported that within 1 km of the Mendon Ponds Park area, forest cover increased from 28 ha in 1966 to 181 ha in 1990, a 546% change. This increase in forest cover means a proportional decrease in grasslands around Mendon Ponds. Additionally, of the open fields available, the majority are agricultural and the vegetation is such that they cannot support Grasshopper Sparrows, or they are undergoing suburban development, as occurred in Field 4, beginning in 1999. Succession, coupled with the small size of the fields and low breeding success, is the most likely reason Grasshopper Sparrows went extinct in five fields (F2, F3, F5, F7, F9).

The metapopulation of Grasshopper Sparrows in the Mendon Ponds area may decline as vegetation characteristics in the few fields left in the area change over the years and fields become less suitable due to lack of vegetation management and subsequent succession, or to suburban development. As habitat changes occur, return rates, density, and breeding success could decrease. More subpopulations will wink out of existence over time, with only a few larger, more suitable fields remaining as habitat for breeding Grasshopper Sparrows. If the metapopulation of Grasshopper Sparrows in the Mendon Ponds area of New York, and other small metapopulations across the country, are to persist, the fields in which they occur must be managed to promote proper habitat characteristics and not be further fragmented. Further, because even the largest fields of Grasshopper Sparrows in Mendon Ponds are not productive enough to act as sources for the metapopulation, colonizers must come from other populations. Therefore, the persistence of Grasshopper Sparrow in the eastern region of the U.S. must be maintained throughout its range to encourage the continued persistence of this species in fragmented habitats.

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Table 1. Estimated number of Grasshopper Sparrows present in 10 fields in the Mendon Ponds area. In 1995, only presence/absence was noted. In 1996, estimates were made using counts of singing males. From 1997 to 1999, estimates were determined using banding data and consistent surveys of territories in each field. Asterisks (*) under # Fledged represent evidence of fledglings through parents carrying food to unlocated nests.

	1995	1996	1997		#	1998		#	1999		#	% Successful
Area (ha)	**Present?**	**Est. # Pair**	**Male**	**Female**	**Fledged**	**Male**	**Female**	**Fledged**	**Male**	**Female**	**Fledged**	**Nests (n)**
Field 1 (8.7)	present	3	8	6	20	5	3	18	3	3	*	78 (11)
Field 2 (4.7)	present	1	2	0	no nests	0	0	n/a	0	0	n/a	no nests
Field 3 (3.0)	absent	1	4	2	0	0	0	n/a	0	0	n/a	0 (2)
Field 4 (8.0)	unknown	0	3	2	unknown	4	2	*	5	4	5*	75 (3)
Field 5 (1.8)	unknown	1	0	0	n/a	0	0	n/a	0	0	n/a	n/a
Field 6 (13)	unknown	6	7	7	13	7	6	19*	7	6	5*	57 (13)
Field 7 (2.4)	unknown	7	1	0	no nests	1	1	0	0	0	n/a	0
Field 8 (4.3)	unknown	3	6	5	1	5	1	5	3	2	5	40 (5)
Field 9 (1.9)	unknown	1	0	0	n/a	0	0	n/a	0	0	n/a	n/a
Field 10 (3.3)	unknown	0	0	0	n/a	0	0	n/a	1	1	1	100 (1)

Table 2. Grasshopper Sparrow body measurements from birds banded during the 1997 - 1999 study period. Values are $\bar{x} \pm$ SE, with *n* in parentheses.

	Females	Males	Nestlings
Wing cord(mm)	58.7 ± 0.29 (9)	61.7 ± 0.22 (35)	35.5 ± 1.42 (24)
Tarsus length (mm)	18.7 ± 0.27 (9)	19.2 ± 0.27 (36)	18.0 ± 0.52 (39)
Bill length (mm)	8.07 ± 0.12 (9)	7.93 ± 0.13 (34)	4.48 ± 0.80 (20)
Mass (g)	18.2 ± 0.21 (8)	17.6 ± 0.13 (32)	11.0 ± 0.30 (39)

Table 3. Return rates of male and female Grasshopper Sparrows. Number in parenthesis next to return rate is number of marked birds returned from previous year. Yearly overall return rates = males + females. Average return rate is the average of yearly rates. * indicates data from C. Norment (pers. comm.).

	Males		Females		Yearly
	Total Banded	Return Rate	Total Banded	Return Rate	Overall Return Rate
1997	15	n/a	2	n/a	
1998	17	0.33 (5)	5	0.50 (1)	0.36 (6)
1999	12	0.24 (4)	5	0.40 (2)	0.27 (6)
2000*	4	0.33 (4)			
Average Return Rate		0.30[a]		0.45[b]	0.32[b]

[a] average from 1998, 1999, and 2000 return rates
[b] average from 1998 and 1999 return rates

Table 4. Grasshopper Sparrow egg measurements for clutches found 1997 to 1999. Values are $\bar{x} \pm$ SE with $n = 93$ for all measurements.

Egg mass (g)	2.05 ± 0.03
Egg length (mm)	18.6 ± 0.11
Egg breadth (mm)	14.5 ± 0.08
Egg volume (mm^3)	2015 ± 304

Table 5. Mayfield method probabilities for mortality and survival of eggs and chicks over three years; n = # nests. Total probability of nest survival is the probability a nest successfully survived incubation and nestling periods, and fledged at least one young (Winter and Faaborg 1999).

	1997 (n = 17)		1998 (n = 15)		1999 (n = 10)		Overall (n = 42)	
	Eggs	Chicks	Eggs	Chicks	Eggs	Chicks	Eggs	Chicks
Mortality/nest day	0.19	0.074	0.05	0.03	0.09	0.07	0.09	0.05
Survival/nest day	0.81	0.93	0.95	0.97	0.91	0.93	0.91	0.95
Daily nest survival of incubating nest	0.11	n/a	0.56	n/a	0.35	n/a	0.35	n/a
Daily nest survival of nest with young	n/a	0.5	n/a	0.79	n/a	0.53	n/a	0.64
Proportion successful nests (n)	0.53 (17)		0.66 (15)		0.40 (10)		0.55 (42)	
Total probability of nest survival	0.08		0.47		0.18		0.24	

values were calculated from coverage class midpoints (%) (Bollinger 1995). Comparisons were made between fields with Grasshopper Sparrows and fields without Grasshopper Sparrows.

	Fields with sparrows		Fields w/out sparrows				
Variable	**Mean**	**SE**	**Mean**	**SE**	**df**	**t**	**P**
Veg. Height (cm)	67.22	6.08	77.56	7.6	11	1.06	0.31
Litter Depth (mm)	1.65	0.26	2.14	0.33	11	1.15	0.27
% Ground Cover	92.3	1.85	96.14	0.89	10	1.98	0.07
% Legume	9.49	1.84	7.42	2.15	11	0.81	0.44
% *Solidago*	6.55	1.59	14.36	4.72	8	1.61	0.15
% Dead Grass	3.4	0.55	3.13	0.41	11	0.36	0.72
% Dead Forb	4.13	0.45	3.84	0.72	11	1.6	0.14
% Live Grass	30.6	5.57	33.6	4.87	11	0.41	0.69
% Shrub	4.2	0.74	4.55	0.9	11	0.25	0.81
% Live Forb	36.4	5.15	35.93	5.16	11	0.03	0.98
Genus Richness	4.81	0.29	4.54	0.17	9	0.77	0.46
% Canopy Cover	67.83	3.18	67.42	4.74	10	0.02	0.98
Max. Shrub Hgt. (cm)	5.11	2.02	5.11	1.81	11	0.001	0.5

values were calculated from coverage class midpoints (%) (Bollinger 1995). Comparisons were made between fields with Grasshopper Sparrows and fields without Grasshopper Sparrows.

	Fields with sparrows		Fields w/out sparrows				
Variable	**Mean**	**SE**	**Mean**	**SE**	**df**	**t**	**P**
Veg. Height (cm)	52.33	2.85	64.05	6.61	5	1.56	0.18
Litter Depth (cm)	2.59	0.74	2.7	0.31	5	0.14	0.89
% Ground Cover	91.53	1.24	96.32	0.94	7	3.22	0.01
% Legume	4.06	0.68	5.32	1.17	6	0.86	0.42
% *Solidago*	8.56	1.19	7.61	1.68	6	0.55	0.6
% Dead Grass	2.6	0.1	2.7	0.12	7	0.03	0.55
% Dead Forb	3.48	0.41	3.08	0.45	7	0.7	0.51
% Live Grass	19.66	5.23	32.93	7.21	7	1.5	0.18
% Shrub	3.46	0.84	8.45	2.41	5	2.27	0.07
% Live Forb	25.4	5.92	20.31	5.64	7	0.6	0.57
Genus Richness	5.32	0.41	4.56	0.35	7	1.4	0.2
% Canopy Cover	49.32	6.91	65.61	5.35	7	1.83	0.11
Max. Shrub Hgt. (cm)	4.25	2.24	12.72	5.07	5	1.52	0.19

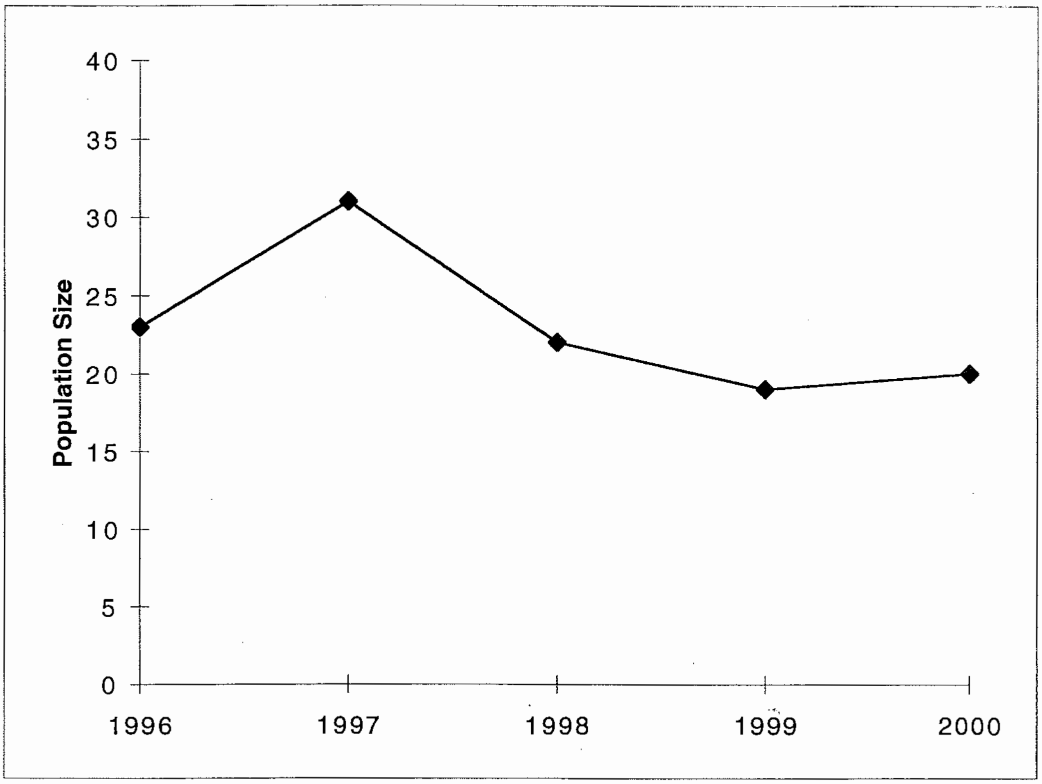

Figure 1. Estimated number of male Grasshopper Sparrows for the entire Mendon Ponds study area per year. 1996 and 2000 population size estimates based on number of singing males; 1997 - 1999 population size estimates based on number of singing and/or banded males.

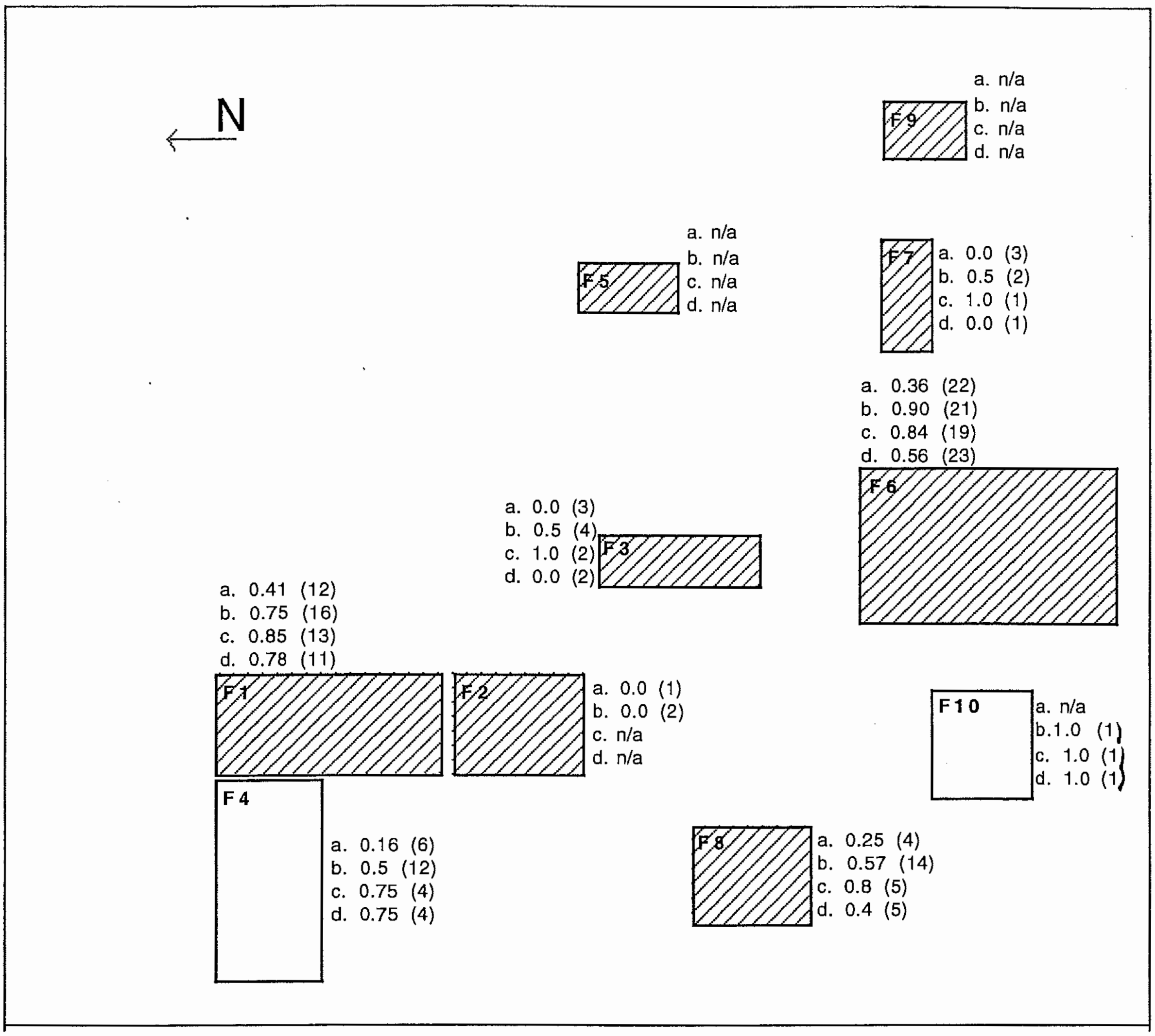

Figure 2. In 1996, eight of ten suitable fields contained Grasshopper Sparrows (cross-hatched fields). Field scale: 1 cm^2 = approx. 1 ha. Distance scale: 1 cm = approx. 1 km. See Table 1 for exact field sizes. Also shown for each field are overall (1997 to 1999) proportions of: a. return rate of banded adults; b. proportion of paired males; c. proportion of pairs nesting; d. proportion of successful nests. Sample size given in parenthesis.

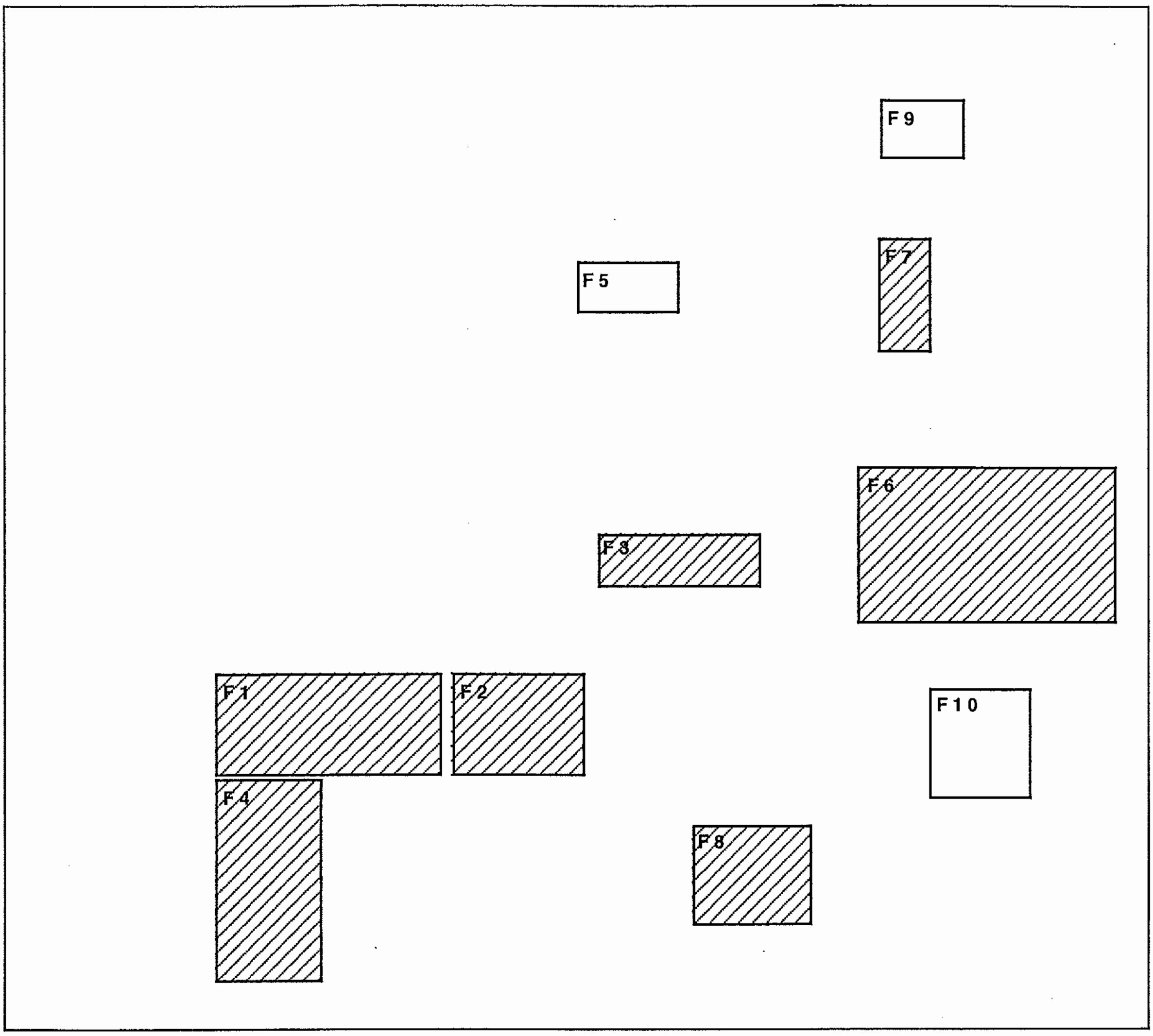

Figure 3. In 1997, Grasshopper Sparrow populations in Fields 9 and 5 suffer extinctions, and F4 is colonized by five sparrows. Field scale: 1 cm^2 = approx. 1 ha. Distance scale: 1 cm = approx. 1 km. See Table 1 for exact field sizes.

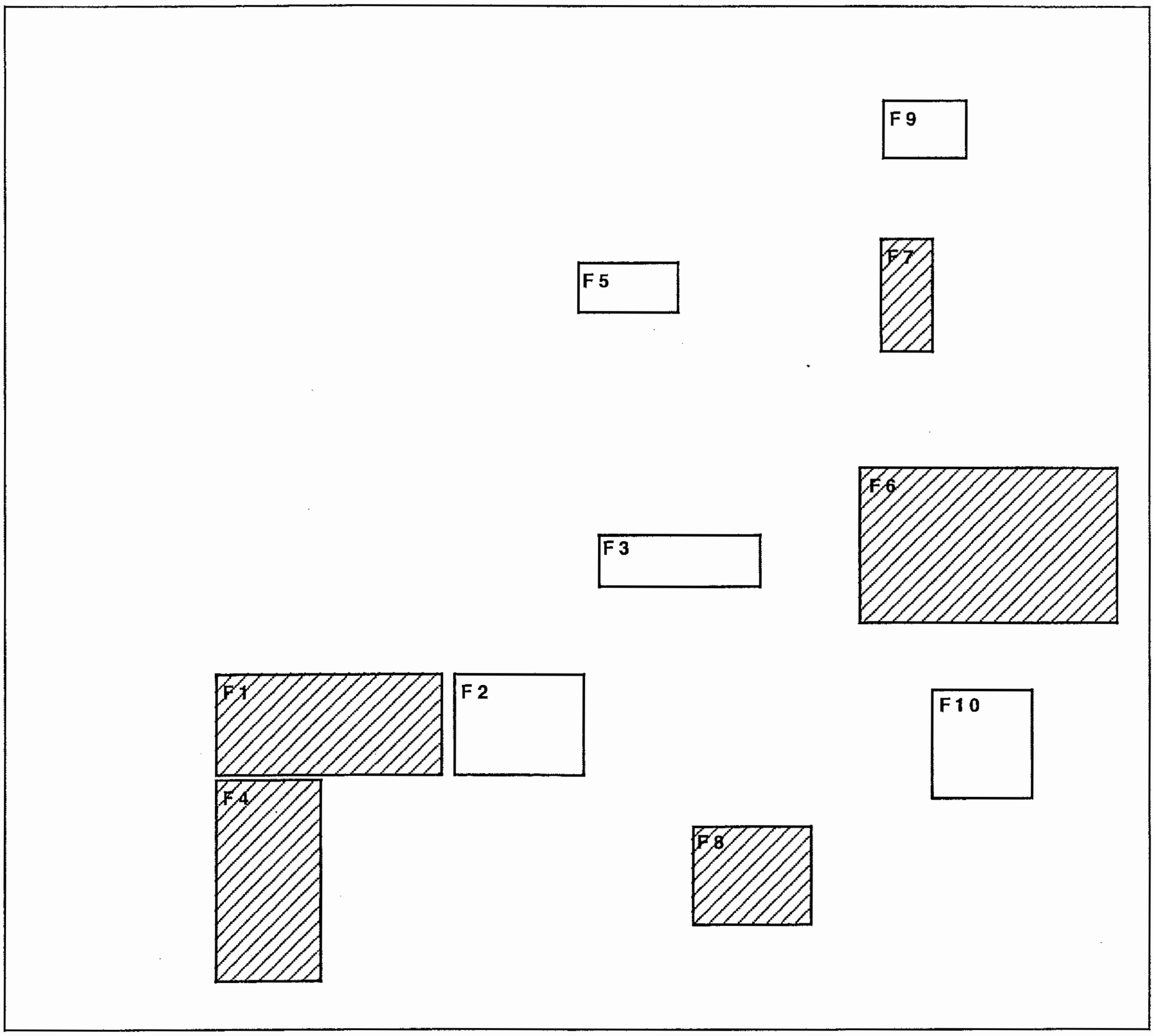

Figure 4. In 1998, Grasshopper Sparrow populations in Fields 2 and 3 go extinct. Field scale: 1 cm^2 = approx. 1 ha. Distance scale: 1 cm = approx. 1 km. See Table 1 for exact field sizes.

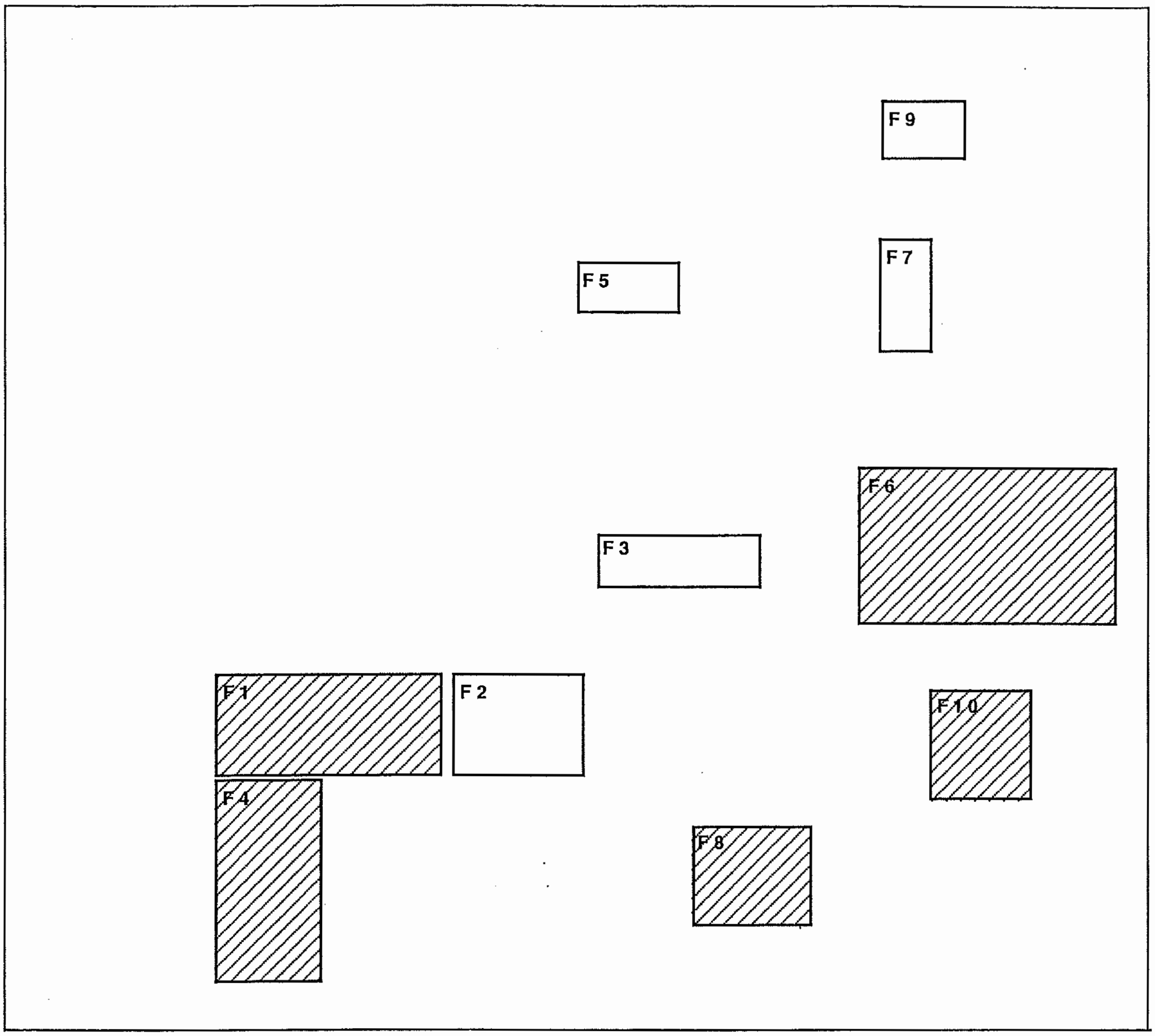

Figure 5. In 1999, the Grasshopper Sparrow population in Field 7 goes extinct and Field 10 is colonized by at least one pair of Grasshopper Sparrows. Field scale: 1 cm^2 = approx. 1 ha. Distance scale: 1 cm = approx. 1 km. See Table 1 for exact field sizes.

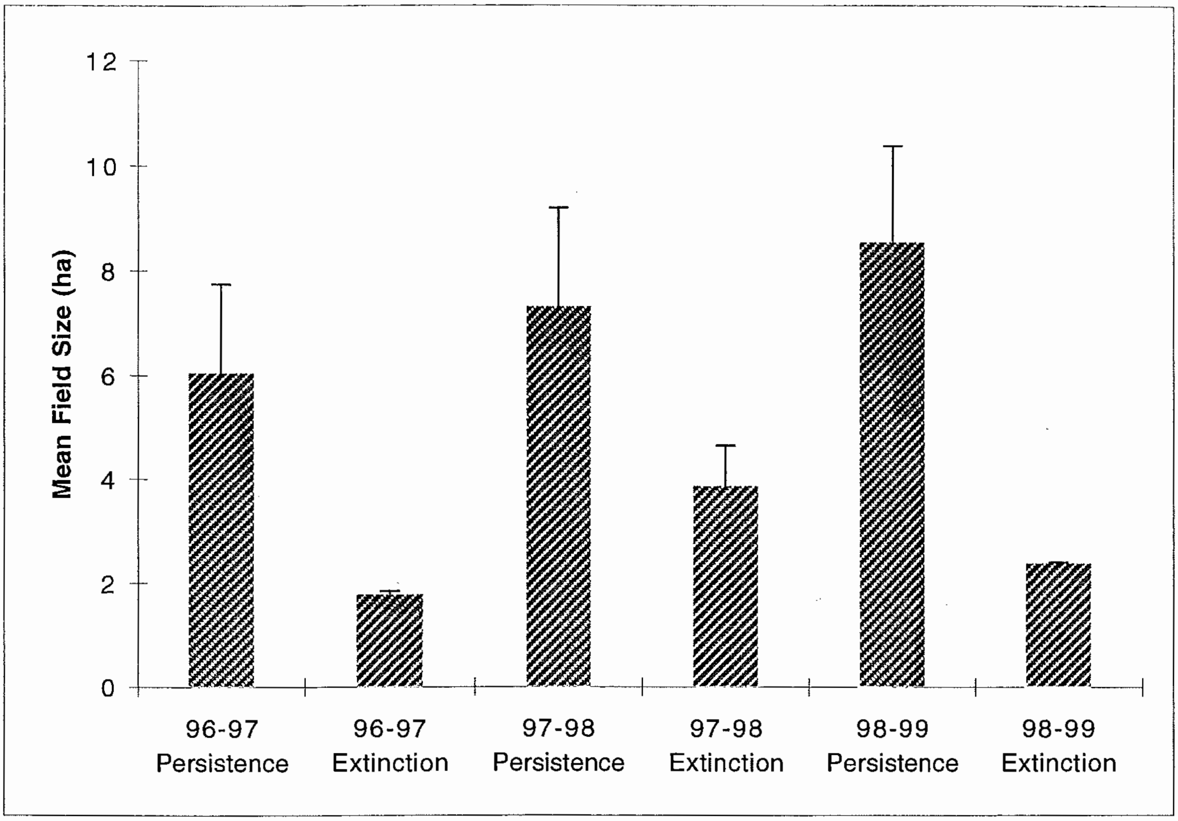

Figure 6. Comparison of field size for fields showing extinction or persistence from 1996 to 1999. Bars are mean field size with SE.