A TWO-YEAR STUDY OF BIRDS COLONIZING RESTORED GRASSLANDS ON THE EASTERN SHORE OF MARYLAND - WITH SPECIAL FOCUS ON THE GRASSHOPPER SPARROW (*Ammodramus savannarum*)

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I. EXECUTIVE SUMMARY

The purpose of this paper is to present the results of a two-year study on the avian response, with special focus on the Grasshopper Sparrow, to the restoration of 93 hectares (230 acres) of warm-season grasslands at the Chester River Field Research Center (CRFRC) in Chestertown, Maryland. Pre-Columbian native pine savannahs and prairies apparently existed on Maryland's Eastern Shore and were likely maintained by fires set by Native Americans. Conversion of these grasslands to early agricultural systems (hayfields and pastures) was compatible with grassland bird species. More recent conversion of these lands into intensive row-crop agriculture and loss of habitat associated with urbanization and succession of non-maintained grasslands into mixed-deciduous forest has led to drastic declines in Grasshopper Sparrow and other grassland bird populations.

Maryland's Conservation Reserve Program (CRP) and Conservation Reserve Enhancement Program (CREP) are federally funded efforts in Maryland with a primary goal to create and enhance habitat for wildlife. Although millions of dollars have been spent on these programs, little is known of the effect of the efforts on wildlife. Recent attention to management of declining grassland bird populations has focused on Midwest and New England populations but little has been published for Mid-Atlantic States. We provide data from ecological studies and offer insight into the management of Eastern Shore grasslands through field studies on the grassland restoration project at CRFRC.

Grasshopper Sparrows immediately invaded the CRFRC fields in the spring following the grassland establishment in March 1999. A total 362 Grasshopper Sparrows have been banded in the fields in 1999 and 2000. Analyses of reproductive success over the first two years in the fields indicate a positive annual growth rate. Grasshopper Sparrow nesting began in early to mid-May and continued until the beginning of August. Any large-scale management of the fields (mowing, burning, etc.) should not be conducted during this period due to high nest mortality. Prescribed fires during the dormant season is recommended to maintain the grasslands free of woody successional vegetation and remove standing dead vegetation and litter. Published literature suggests Grasshopper Sparrows respond favorably in the long-term to burning of fields but negatively in the short-term. It is important to maintain a heterogeneous landscape by a schedule of rotational burning of the fields. In this manner, suitable habitat can be maintained for multiple grassland bird species.

II. INTRODUCTION

The Need for Study of Maryland Grassland Birds

Grassland birds have recently received national conservation attention due to the alarming rates of population decrease in most species. Large conservation organizations including The Nature Conservancy's Wings of the Americas Program, National Wildlife Federation, Partners in Flight, Northern Prairie Wildlife Research Center, and the Massachusetts Audubon Society have published reports on the status of obligate grassland bird species, specifications of their habitat requirements, and recommendations for management. Many of these reports and advisories are readily accessible through the Internet. The most detailed and documented of the declines is in the Midwest prairie states (Howe 1994, Noss *et al*. 1995), but population decreases in most grassland species have occurred across entire breeding ranges including New England and Mid-Atlantic States. The grassland bird populations on the East Coast are equally if not more threatened due to the smaller population sizes and greater threats to habitat (Peterjohn and Sauer 1999). Recent studies of grassland birds in New York and Maine have addressed New England management priorities, but to date no such protocol has been established for grassland bird studies in Maryland and other Mid-Atlantic States.

Agency reports on grassland management and on their implications for bird populations have often emphasized interregional management recommendations, but there is considerable concern that similar management regimes may cause different and perhaps undesirable responses in different physiographic regions (Mitchell *et al*. 2000). Conservation technicians and wildlife managers will benefit from scientific studies designed to detect geographic variation in the ecology of target species and be able to incorporate the available information into management protocols. Conclusions drawn from research conducted on grassland bird species in New England and the Midwest may or may not be pertinent to Maryland populations. Here we report the results of studies on an experimental restoration of native prairie on the Eastern Shore of Maryland and the grassland birds that rapidly colonized the habitat, especially the Grasshopper Sparrow. Our intention is to fill a glaring gap in our knowledge of obligate grassland bird species, their habitat requirements, and appropriate basic ecological protocols for their management in the Mid-Atlantic States, especially the Atlantic Coastal region.

Conservation Status of Species and Threats

Grasshopper Sparrows have shown more consistent declines than any other grassland bird from 1966-1996 (Peterjohn and Sauer 1999). Annual rates of decline from 1966-1994 were 3.9% throughout North America, and 5.9% in the Eastern US (Vickery 1996, Sauer *et al*. 1999). We predict that, when compounded over years, these annual rates of decline are likely to result in threatened or endangered status. In Maryland from 1966 to 1989 the decade rate of decline was an alarming 80%; it has not recovered over the last decade (Holmes 1996). Although the Grasshopper Sparrow has not yet received federal protection status or specific protection status in Maryland, it has received special recognition along the East Coast in conservation activities (Table 1). All native passerines, of course, are protected against hunting under the Migratory Bird Act 1916.

The primary factors influencing Grasshopper Sparrow population declines in Maryland and throughout its range have been loss, degradation, and fragmentation of habitat (Holmes 1996, Vickery *et al*. 2000). Major causes of habitat loss include conversion of native grasslands to agricultural systems, and more recent conversion of hayfields and pastures into row-crop agriculture (Robbins *et al*. 1986, Warner 1992). Lands that are no longer suitable for modern agriculture production are not maintained as grasslands and are allowed to undergo ecological succession into mixed-deciduous forests. The only remnant grasslands that remain are excessively small blocks or fringe strips of habitat; these may not be suitable in ecological quality or large enough to support sustainable populations of Grasshopper Sparrows.

Natural History of Maryland's Eastern Shore

The history of grassland-dependent birds in the Eastern United States is uncertain. Prevailing views of pre-colonial times generally depict the Eastern US blanketed by mature hardwood forests. In this scenario, squirrels could walk from Delaware to Ohio on a continuous carpet of treetops. These forests persisted until Europeans arrived, cut the extensive woods, and opened the region for agriculture. Supposedly, grassland birds from the Midwest invaded the new habitat and thrived in the newly created pastures and hayfields.

More recent evidence has been found that pine savannah and prairie grasslands, mixtures of warm-season grasses and forbs, were native and stretched from Florida to New England. These savannah-grasslands were prevalent throughout the Delmarva Peninsula, through southern New Jersey and coastal New England (Kulikoff 1986, Patterson and Sassaman 1988, Tyndall 1992, Noss *et al*. 1995, Mehrhoff 1997). Evidence of this history is apparent in fire-selected plant species (Longleaf Pine (*Pinus palustris*), Little Bluestem (*Schizachyrium scoparium*) and Big Bluestem (*Andropogon gerardi*)) and corresponding animal populations associated with these habitats (several grassland butterflies and birds). Native Americans most likely managed these areas with fire, and the vegetation that thrived in these environs was largely fire-tolerant and fire-dependent (Patterson and Sassaman 1988, Tyndall 1992, Askins 1997). The East Coast grasslands were likely very similar floristically to the Midwest prairies (Askins 1997, Mehrhoff 1997), although some plant and animal species such as Sandplain Gerardia (*Agalinis acuta*), Eastern Henlsow's Sparrow (*Ammodramus henslowii susurrans*), and Heath Hen (*Tympanuchus cupido cupido*) adapted to the local grassland landscape and evolved distinctly from their relatives. Nevertheless, East Coast grasslands were smaller, scattered, and less contiguous than those in the Great Plains (Mehrhoff 1997).

When Europeans arrived, they quickly converted the prairie and savannah grasslands of the Eastern Shore of Maryland to cattle pastures and hayfields. Many grassland bird species were compatible with these farming practices and it is likely that the populations of grassland bird species increased markedly (Peterjohn and Sauer 1999). Eastward range extensions of obligate grassland birds in the 19^{th} century have been well documented for only a few grassland birds (Dickcissel – *Spiza americana* and Horned Lark – *Eremophila alpestris*) but there is no evidence of concurrent or later colonization of other common grassland birds including the Grasshopper Sparrow (Hurley and Franks 1976, Askins 1997). Other populations of birds, however, declined due to the disappearance of unaltered tracts of habitat. Breeding populations of some grassland birds were greatly reduced; the Eastern Henslow's Sparrow has been essentially extirpated regionally (Boone and Dowell 1996, Iliff *et al*. 1996), and the Heath Hen was last reported on Martha's Vineyard in 1932.

Not until recently has much attention been paid to these ancient Atlantic Coast grassland ecosystems - for the most part they are gone and therefore ignorable. They have succumbed to development, been converted into agriculture, or have undergone succession into hardwood forests and woody shrublands through absence of regular obligatory disturbance.

A cause for the recent focus on these habitats has been the drastic decline of the birds and plants that are obligate to the grasslands and presently persist only in hayfields and pastures. Howe (1994) and Noss (1995) state that only 1% of the tallgrass prairie of the Midwest remains. Researchers surmise that the prairies of the East Coast suffered equal losses (Tyndall 1992, Mehrhoff 1997), but no detailed records of historical grassland acreages have surfaced, so no quantitative estimates can be made. At present, the only contiguous blocks of native warm-season grasslands on the Eastern Shore of Maryland are in the Conservation Reserve Program (CRP) or Conservation Reserve Enhancement Program (CREP), and only a small percentage of these areas contain blocks of native bunch grasses of sufficient size to provide adequate habitat for the grassland-dependent bird species. Habitats used by grassland birds on the Eastern Shore currently are almost entirely non-native and non-natural, and most management practices are insufficient to maintain viable populations of grassland birds. Hayfields that could provide marginal habitat are regularly mowed earlier in the season than they were 50 years ago, and they are mowed multiple times, often before first broods of birds can fledge (Rodenhouse *et al.* 1995, Vickery 1996). Populations of Grasshopper Sparrows in Southern New England are mostly limited to regularly mowed airfields. Unless their habitats are managed properly, most of these populations of Grasshopper Sparrows will persist only through immigration from other populations and function as population sinks (have negative growth rates) rather than be population sources (with positive growth rates) (Gill 1978, Pulliam and Danielson 1991, Kershner and Bollinger 1996).

Grassland Restoration on Maryland's Eastern Shore

The Conservation Reserve Program (CRP) and Conservation Reserve Enhancement Program (CREP)

The Conservation Reserve Program (CRP) of the USDA was enacted as part of the 1985 Farm Bill and was established to remove marginal agriculture land from production to reduce soil erosion and chemical runoff into wetlands and aquatic ecosystems and to improve wildlife habitat. The program provides monetary incentives for farmers to participate by converting some of their lands to trees, grasses, or other stabilizing vegetation. CRP pays an annual rental for the land as well as provides funds for conversion (i.e. seed, seedlings, special planting equipment, etc.). Contracts are written for 10 or 15 years and administered through state and local government agencies. CRP has put a high priority on the restoration of warm-season grasslands.

The Maryland Conservation Reserve Enhancement Program (CREP) is a partnership between Maryland and the federal government, and is federally sponsored through the CRP. In 1997 Maryland launched CREP with provision of $195 million for conversion of marginal agriculture lands on or adjacent to wetlands or waterways to natural wildlife habitats. The program received a significant boost with Vice President Al Gore's 1997 announcement of CREP's mandate to protect and stabilize up to 40,469 hectares (100,000 acres) of land influencing the Chesapeake Bay and its tributaries (White House 1997). Within the federal contract, Maryland agreed to enlist the following target acreages: 28,328 hectares (70,000 acres) of riparian buffers, 4047 hectares (10,000 acres) of wetland restoration, and 8094 hectares (20,000 acres) of highly erodible land within 305 meters (1000 feet) of a body of water (USDA *et al.* 2001). Furthermore, the agreement states that Maryland is responsible for identifying the total acreage for enrollment by 31 December 2002.

CREP differs from the CRP primarily by supplementing a CRP enrollment with state funding. This additional state subsidy provides higher rental rates to farmers authorized to protect sensitive lands affecting the Chesapeake Bay watershed. Although it is apparent that the program aims to improve water quality, a stated primary goal of the program is to improve wildlife habitat (Conservation Reserve Enhancement Program 2001)**.**

Block and Strip Plantings

The overwhelming majority of effort from CRP and CREP in Maryland has been in riparian forest and forest/grassland strips and not in block grasslands. Current requirements state that a grassland strip 30.5-meter (100 ft.) wide at a *maximum* be installed as part of a riparian forest buffer (program CP22); in addition a *maximum* 36.5-meter (120 ft.) wide strip of cool or warm-season grass can act as a filter (program CP21). As of 2000 the total acreage enlisted in establishment of permanent native grasses (program CP2) on the Eastern Shore of Maryland was 777.6 hectares (1921.5 acres) or 5% of total enrollment. Acreage dedicated to filter strips (CP21) was 7076 hectares (17,484.5 acres) or 47% of total enrollment (Tables 2a and 2b). The effect of these strip grasslands on nutrient and sediment flow to riparian habitat has been documented well (Correll, 1999). The third way land can qualify for CREP is to have high topographic relief, be susceptible to erosion, and be within 305 meters (1000 ft.) of a body of water. Due to the low relief of the Eastern Shore and farmland, very little suitable habitat on the Eastern Shore will meet this qualification.

Although CRP and CREP were designed with a major goal of establishing wildlife habitat, analyses of the effect of block CRP grasslands on grassland birds in the Midwest have yielded mixed results. Some CRP fields are reported to have positive effects on grassland birds in the Midwest (Best *et al*. 1998, Herkert 1998), but other studies reported no effect, mixed effects, or negative growth in other CRP fields (Reynolds *et al*. 1994, McCoy *et al*. 1999). There is little scientific evidence that the filter/buffer strips established by both CRP and CREP have had any effect on Grasshopper Sparrows or most other grassland birds (Delisle *et al*. 1996 as reported in Vickery 1996, Herkert 1998). Grasshopper Sparrows have been shown to favor large grassland areas and do not responded to linear habitats (Johnson and Temple 1986a, Warner 1992, Herkert 1994a, Vickery *et al.* 1994, Smith 1997). Herkert (1994) suggested that 12.1 hectares (30 acres) is the minimum area needed to sustain a breeding population in Illinois, but Grasshopper Sparrows were more likely to be established in large fragments of 130 – 146 hectares (320 – 360 acres) in Minnesota (Johnson and Temple 1986a), and colonization reached 50% incidence of 90 grassland sites in Maine at about 100 ha (Vickery *et al*. 1994). Although CREP strip acreage may provide cover for some birds, it also may provide cover for edge-favoring predators such as foxes, raccoons, skunks and opossums. Abundance of Grasshopper Sparrow adults and nest success have been shown to increase with distance from the edge of the grassland habitat (Johnson and Temple 1986b, Bock *et al*. 1999).

There is little government-funded research on the effects of either the CRP or the CREP program in Maryland on wildlife despite the fact that $195,000,000 was dedicated by the federal government to Maryland CREP. Although the governing parties, Maryland Department of Natural Resources (DNR), the Department of Agriculture's Natural Resource Conservation Service (NRCS), and Maryland's Soil Conservation Service, are very enthusiastic about the hypothetical benefits of CREP on wildlife, there is little effort to fund and implement rigorous scientific research on its effects. Millions of dollars already have been spent on land conversions for the CRP program, but none has been allocated to the evaluation of the success of the restorations for wildlife and birds despite the fact that wildlife conservation is listed under both programs as a primary goal. In contrast, private funding has opened the doors for some evaluative studies of restored grasslands on wildlife and birds in Maryland.

CRFRC at Chino Farms

In the 1990's Dr. Henry F. Sears, owner and President of Chino Farms, Inc. near Chestertown, MD, and Farm Manager Mr. Evan Miles had enrolled substantial acres of the 2278 hectare (5630 acre) farm in CRP, CREP, and habitat enhancement programs. In 1999 Dr. Sears took several ambitious steps toward preserving the entire farm in Rural Legacy and Conservation Easement. One key element of the plan was the conversion of a contiguous 93-hectare (230-acre) block from corn and soybean row-crop production to a native, warm season grassland. On 23 June 2000 Governor Parris N. Glendening announced the appropriation of $5.5 million to protect 1264 hectares (3124 acres) of Chino Farms from development in Rural Legacy as a model of excellence in environmentally sensitive farming.

In March 1999, the 93-hectare (230-acres) block was planted with mixtures of nine species of native perennial bunch grasses (Table 3). The 93 hectares were divided into twelve fields of approximately 8.1 hectares (20 acres) each and separated by firebreaks planted in clover. Each field was planted in a mixture of three species of grass. Five treatments (mixtures) with two replicates were created in Fields 1-10 (Fields 11 and 12 were not included in the experimental design). The planting design is shown in Table 4. Called the Experimental Grassland Restoration Project (on-site roadside signs refer to it as Grassland Plantation), this is the largest block of contiguous warm-season grasslands presently on the Eastern Shore of Maryland.

In order to encourage scientific studies in this unique, restored Atlantic Coast native prairie project, Dr. Harry Sears invited DEG to direct ecological studies of the experimental grassland. Together they created the Chester River Field Research Center (CRFRC). The Chester River Field Research Center has as its mission: 1) the scientific study of the dynamic changes in ecology of grassland restoration on the Eastern Shore, 2) the evaluation of habitat restoration to "gardening" populations of obligate grassland birds and wildlife that are threatened, 3) the preparation of research and management protocols for the Grassland Restoration Project, and 4) the establishment of a training platform for future professional scientists in basic, applied, and conservation ecology.

CRFRC is a facility designed to be a practical laboratory for investigation of field ecology and conservation sciences. It provides an opportunity for conservation biologists that have interests in evaluating how agriculture interfaces with natural surroundings (environment), and how initiatives in habitat restoration affect wildlife populations. Proposed studies will assess the effectiveness, in terms of wildlife enhancement, of two governmental restoration programs already in place at Chino Farms. The consultant faculty will provide the investigators in training with instruction in field study design, protocol formation, data management, and practical field research techniques.

To date CRFRC has been exclusively funded through private donations. Chino Farms, Inc. and the Sears Foundation generously provided basic financial support for student research fellowships, facilities, and equipment. A spacious house was provided for conversion into a laboratory and dormitory, and the farm equipment and personnel (especially Farm Manager Mr. Evan Miles) of Chino Farms were available for large-scale management and consultation. Four fellowships were offered to support a team of student researchers in both summer 1999 and 2000. Quail Unlimited, Inc., Maryland Chapter, Mr. James Farmer, President generously provided another fellowship in 2000. Directed by DEG, these teams conducted the ecological studies of the vegetation, and birds and wildlife colonizing the new Grassland Restoration Project.

An additional and substantial benefit to establishing CRFRC at Chino Farms was the cooperation of Master Bird-Bander Mr. James Gruber who has been operating a long-term banding station on the farm property near the experimental fields. Mr. Gruber offered his considerable experience with avian studies and has trained the bird team in banding operations. Jim has greatly enhanced the ability to conduct scientific studies on the project fields.

III. GRASSHOPPER SPARROW STUDIES

Introduction

We conducted comprehensive ecological studies on the Experimental Grassland Restoration Project of CRFRC during May through August of both summer 1999 and 2000. Due to resource limitations and the apparent concentration of Grasshopper Sparrow territories in Fields 1-8, we limited our study to these contiguous restored grassland blocks and only occasionally explored Fields 9-12. Summer 2001 will be the third year of the critical establishment period for these grasslands. Our 1999 and 2000 studies focused on –

1) the population responses of bird species of special concern, including Grasshopper Sparrow, Dickcissel, Bobolink, and Bobwhite Quail, to the restored grasslands, with particular attention to a comparison of the breeding performance of Grasshopper Sparrows in the five different treatments of plantings,
2) the growth performance of the eight species of native Warm Season Grasses planted in March 1999 and the complex plant community of alien and native species already present under alternative management protocols for effective grassland establishment,

Here we report detailed results of the intensive studies on the Grasshopper Sparrow, one of the target bird species of the restored grassland project. Grasshopper Sparrows invaded the newly planted grasslands in Spring 1999 in such numbers that the opportunity to conduct detailed studies on their ecology and breeding behavior became immediately available.

Methods

High priority was placed on permanently marking all individuals in the breeding population of Grasshopper Sparrows so that aspects of their ecology, dynamic population demography, and breeding behavior could be studied. Knowing every individual is an indispensable advantage in population studies.

Capturing, Banding, and Measurements

Two groups of three four-meter mist nets and two groups of two four-meter nets were used in a mobile system that easily allowed us to move nets every few hours. Iron reinforcement bars (rebar) in one-meter sections were driven about 0.3 m into the soil and the nest poles (electrical metal conduit) were slid over the top. Ten mist nets were set up six days each week in an effort to band the entire population of Grasshopper Sparrows in the experimental Fields 1-8.

Uniquely numbered aluminum United States Fish & Wildlife Service (USFWS) bands of size 1C were placed on the bird’s left leg, lower (distal) position. In addition, a unique combination of color bands (Hughes Solid Color Celluloid) was placed on each captured Grasshopper Sparrow. Colors that proved effective for field identification of individuals were White (W), Yellow (Y), Orange (O), Red (R), Hot Pink (P), Light Pink = Flamingo (F), Light Green (G), Dark Blue (B), Light Blue = Turquoise (T), Purple = Mauve (M), and Black (K). Dark Green was not used because it was difficult to distinguish from Black (K) at a distance. Dark Blue (B) or Light Blue

(T) were placed above (proximal) to the USFWS band on the bird's left leg to designate males; Hot Pink (P) or Light Pink (F) was placed above the USFWS band on the left leg of females. Juveniles caught in mist nets were banded with only a federal aluminum band on the left leg. Nestlings from a common nest (siblings) were marked with a common colored band on their right leg to denote their nestship and an aluminum band on their right leg.

We used Student's T-Tests to compare morphometric differences between males and females.

Nest Ecology and Studies

Most Grasshopper Sparrow nests were discovered incidentally while conducting censuses, operating mist nets, and mapping territories in the fields. We occasionally flushed adult birds from nests during the course of our research activities, usually when we approached within five meters of a nest. Flushed adults often behaved with a broken-wing display as the bird ran and vocalized chip notes. In most cases the adults would persistently chip while researchers were in the immediate nest area. Early in 1999 we systematically searched the fields by walking in pairs 4-5 meters apart, but this method proved unproductive. On occasion we found nests by following adult birds carrying food to the nest until they dropped from a perch; we then rushed into the area to force a flush from the nest. Nevertheless, the nests were difficult to find and often required several minutes to find following the flush.

Once a flush was noted, the spot was marked with a hat or flag, and we would systematically search the area. After the nest was located, a strip of flagging was tied to a prominent piece of vegetation no closer than seven meters to the nest (most often 10 meters) and a nest record card was created with directions and a drawing to the nest from the flagging. We used a Garmin 12XL GPS receiver to note locations of both the flag and the nest.

We visited nests every other day to monitor the progress of development but not often enough to interfere with the parenting or to attract predators. Our routine was to approach the flags that marked nests from opposite direction of the nest and then visually locate the nest site from the flag before approaching. Nests were then checked for adult presence, number of eggs, chicks, and age of the chicks. If chicks or eggs were present (and weren't ready to be banded), researchers would leave the area quickly to minimize disturbance. If the nest was empty, it was assessed for signs of predation or fledging.

Nests were considered successful if at least one chick fledged. Fledging was determined by age and development of the chicks at the previous observation, and condition of the nest. Fecal sacs in and around the nest site were further evidence in support of fledging.

Once a nest was vacated, a vegetation analysis was conducted of the nest and the nest area. The composition of the nest itself was determined, including percent visibility from directly above, direction of entrance to the nest, and placement of the nest (including plant species integrated into or adjacent to the nest. The vegetation surrounding the nest was assessed within one meter and again within five meters of the nest site. The percent total live vegetation, bare ground, and duff were estimated and then live vegetation was described in detail by estimating cover of each plant species that comprised more than one percent of total cover.

In order to compare the vegetation around a nest to the plant community on the field as a whole, we conducted vegetation surveys by locating eight 1 m^2 square plots at random in each of the eight primary fields. The plants in the plots were identified and species richness determined. The percentages in three categories, namely live vegetation, bare ground, and duff (dead non-woody vegetation) were estimated to the nearest 1 %. Then the percent cover attributable to each species was estimated, summing to the value already determined for live vegetation as a whole. These surveys were conducted once every month in each of the eight fields over a two or three-day period. The results of these vegetation studies are reported in the Vegetation Report of Experimental Restored Grassland on the Eastern Shore of Maryland (Eilts *et al.* In preparation).

Analyses of nest choice site were conducted using a single-factor ANOVA. To check for microhabitat preferences/biases that the sparrows might use in selecting nest sites, we compared the vegetation around nest sites with the vegetation survey data for the entire field (taken early in the season on 8 June and 10 June 2000). This analysis was conducted for fields in which we found five or more nests.

Reproductive Success

Due to biased sampling of nests that stay active longer, nest success is calculated through exposure in nest-days (Mayfield 1975). Probability of nest success is determined by calculating a daily probability of survival (P):

$$P = \left(1 - \frac{F}{D}\right)$$

Where P is the daily survival probability, F is the number of failure events, and D is the total number of nest-days observed (Mayfield 1975).

Grasshopper Sparrows require 21 days from egg-laying to fledge so the probability of survival for a nest attempt is P raised to the 21st power (P^{21}). This model assumes equal chance of predation or failure over each day of incubation and chick development and is an unbiased estimator of nest success from such survey data sets.

Fecundity was measured as the total number of female chicks produced by an adult female in a season. This was constructed following the methodology of McCoy *et al.* (1999). The methods assume a 1:1 sex ratio among chicks, equal reproductive success and fecundity through the entire breeding season, and equal fecundity among all age classes. The methodology calculates fecundity per individual based on the estimation that each adult female had four opportunities to hatch a maximum of two broods. For example if a female's first nest fails, she will still have three more opportunities to fledge offspring successfully. Published accounts of Grasshopper Sparrows suggest that they can produce a maximum of two successful broods per season, and that attempts at a third brood later in the season lead to poor survival of offspring (Wiens 1969, Vickery 1996). Our observations at Chino Farms also agree that there is enough time for only two broods. A single very late nest attempt was observed in September 1999 and it is likely that some third brood attempts are made each year. We did not include these in our analyses.

Whether a population was a source of recruits for the region or a local reproductive sink was determined by estimating of the realized annual rate of population increase, R, where $R = N_{t+1} / N_t$. If a population was growing, R >1; for a stationary population R = 1; R <1 denoted a declining population. To estimate the fecundity (*m*) needed for a stable population the following equation was used:

$$N_{t+1} = N_t S_a + 0.5 S_a N_t m$$

Where S_a is the adult annual survivorship and $0.5S_a$ is the hatchling survivorship. Juvenile survivorship is estimated to be half that of an adult (Ricklefs 1973, McCoy *et al.* 1999).

Territory Studies

Territory studies were conducted using a flush and follow method (Wiens 1969). Each singing adult (male) Grasshopper Sparrow was identified by its unique color leg band combination. We flushed a target territorial male off its advertising perch and marked the location of the perch as a waypoint with a Garmin 12x GPS receiver. We would then walk to the point where the bird flew to and repeat the process. Male Grasshopper Sparrows tend to be very loyal to their territories and will generally not stray from it. As many as twenty perches were marked in each territory, but in most cases there were many repeats of perches. Ten perches were often suitable to get a satisfactory estimate of the area, but this was determined on a case by case basis depending on the locality of the perches. Territory waypoints were then downloaded into ArcView (ESRI 1992-1999) for analysis.

Territory waypoints were manually converted into polygons representing territories and the polygons were projected in ArcView as State Plane 1983 for Maryland. Territory size was then calculated using ArcView ReturnArea script.

IV. RESULTS AND DISCUSSION

Banding and Observations

A total of 362 Grasshopper Sparrows were banded in the restored grasslands in the two field seasons of 1999 and 2000. This total included 214 breeding adults (AHY) and 148 young of the year, including both juveniles (HY) and nestlings (L) (Table 5).

Physical Characteristics of Sex and Age

Adult males and females differed significantly with respect to wing length, tail length and lore length, but not in weight, bill length, bill width, and exposed culmen (Table 6). Males had diagnostically longer wings, longer tails, and longer yellow loral stripes. The sex of young birds was not distinguishable from external measurements, but young age was unambiguously recognized by juvenal plumage. The variance in weights of females is much greater than that of males. This large female variance was due to the various stages of egg formation and egg deposition of captured females; it was not always possible to identify in what stages a female was from external examination, but weights offered good clues. The variances in bill measurements (length, width, and culmen) in both males and females were sufficiently large to obscure any differences between the sexes. It is possible that measurement error, especially differences in technique between researchers, contributed to these large variances. Aging of adult Grasshopper Sparrows was difficult. Second-year birds (SY) sometimes retained a few juvenal feathers, especially the alula, but can be reliably distinguished from older (ASY) adults by external morphology only 5-25% of the time (Pyle 1997).

Returning Adults and Population Age-structure

A total of 23 adults (twenty males and three females) banded in 1999 returned to the CRFRC grasslands as breeders in 2000. The banded males were territorial and were recorded on the breeding ground at earlier dates than unmarked individuals. The return rate of males was 40% (a total of 50 adult males were banded in 1999). This gives a good, but minimum, estimate of the annual adult male survivorship because some of the 1999 males might have been alive but residing elsewhere or simply were not observed. This number compares favorably to return rates of 35% in Maine (Wells 1997), and the estimate of adult survival of 49% for ground nesting sparrows in general (Martin 1995), but is strikingly less than the 60% reported for the non-migratory subspecies in Florida (Delany *et al*. 1993 as reported in Vickery, 1996).

When estimating the population age-structure, one must make the following assumptions in an analysis of Grasshopper Sparrow population age-structure: a 1:1 male to female sex ratio, equal survivorship among males and females, breeding site fidelity among adult males, and that we have captured and banded all of the adult males in the population. If adults have a 40% chance of survival each year we could extrapolate a 1% chance of a one-year-old adult to live six years. Our estimates for Grasshopper Sparrows are consistent with the rate of survival data from Field Sparrows in Maryland (J. Gruber, pers. comm.) and other Grasshopper Sparrows (Delaney, M. F. and T. F. Dean, as reported in Vickery 1996).

Grasshopper Sparrow Reproductive Studies

Nest Site Choice

In 2000 Grasshopper Sparrows chose nest sites that averaged 34% bare ground, 36% duff, and 30% live vegetation in a one-meter radius circle around the nest (Table 7). Bare ground and duff ranged from 5% to 70% cover, and live vegetation ranged from 15% to 65% in the area five meters around the nest.

The literature reports that Grasshopper Sparrows favor a moderate amount of bare ground (Whitmore 1979, Bollinger 1995). We have evidence that nest sites were chosen with a bias toward sparse vegetation. In Field 7 where we found 10 nests, the nest sites (1-meter radius centered at nest) had less live vegetation than the field average ($p<0.05$) whereas differences in duff and bare ground were not significant. The live vegetation - bare ground - duff profiles in the circles with 5-meter radius around the nests were not significantly different in any category with the field as a whole. No significant differences were found in Field 6 nest sites (5 nests). One possible error in this evaluation would be that the birds chose the nest sites up to three weeks prior to our vegetation analysis. This result should be checked in future studies by surveying ground cover in late May when most birds are selecting nest sites.

No relation between the planting mixes of warm-season grasses and the nesting of Grasshopper Sparrows is yet emerging. In 2000, 29 of the 30 nests were found in all eight experimental blocks of different grasses that were under study (Table 8). Although the distributions of the nests were not found to be significantly associated with the grass mixtures after two years, we expect greater differences in the vegetative makeup of the fields as the grasses continue to mature and the rotation schedules of prescribed burns become routine.

Timing of Grasshopper Sparrow Nesting

In both 1999 and 2000 there appeared to be three periods of egg-laying over the spring and summer, perhaps associated with three nest attempts. The timing of oviposition was different between the two years (Figure 1). In 1999, we found peak periods of egg-laying in the end of May/beginning of June, a smaller one in the middle of June and then a third in the end of June/beginning of July. In 2000 we again found three periods of increased egg-laying, but they were in mid-May, in the end of May/beginning of June, and then to a lesser extent in the end of June. A few nests were made in early to mid-July.

The causes of the shifts in egg-laying periods between the two years merit some investigation. One possible explanation of the earlier start in 2000 is that returning male and female sparrows were able to establish territories and begin nesting at an earlier date. Although there was a breeding group of Grasshopper Sparrows on the adjacent airstrip prior to the installation of the Grassland Restoration Project, the number of individuals there was small and could not account for the numbers of breeding Grasshopper Sparrow on the fields in 1999 and 2000. Despite the fact that a high percentage of the first Grasshopper Sparrows to show up at the grasslands in May 2000 were returning banded adult males, we surmise that many of the breeding Grasshopper Sparrows in those inaugural years of the project were immigrants from more distant localities.

Our priorities at the onset of both the 1999 and 2000 seasons were to get the team of researchers trained and the adult population of Grasshopper Sparrows banded. We therefore did not investigate return dates and the establishment of territories as thoroughly as wished. As noted above we do have some evidence that AHY males with territories in 1999 at CRFRC returned earlier than SY birds or immigrants. Half of the 6 nests that began in the first week of breeding in 2000 belonged to returning males (Table 9). Although the sample size is small, this ratio 50% is larger than the actual makeup (20%) of the adult male population returning from 1999.

In 1999 the two main nesting peaks tentatively encouraged us to consider early July as an appropriate time to mow the fields; that brief window seemed to correspond to a lull between broods. That guess appears *not* to be a trend now. The shifts in timing and the pattern of nesting activities in 2000 recommend against mowing at any time between the start and conclusion of the breeding season. The graphs of actual active nests (observed) and of expected nesting activity shows a general trend of nest activity beginning in mid-May, peaking from the beginning of June for about three weeks and then declining until the end of July (Figure 2). A single nest with three eggs was located on 27 August 1999 and two of the eggs had hatched by 1 September. The two chicks in this extraordinarily late nest would have fledged on 10 September. This nest set a record for late egg date for Maryland, the previous Maryland record being 17 August (Iliff *et al.* 1996). Although the nest season lasts past the end of July, the number of nests certainly decreases, and danger of unwanted destruction by mowing protocols is concomitantly reduced by mid to late August.

The difference in peaks of breeding activity between 1999 and 2000 might be related to the unusual weather patterns experienced during both field seasons. Summer 1999 was one of the hottest and driest of the century and Summer 2000 was one of the coolest and wettest on record for the Eastern Shore of Maryland. One would have guessed that cooler weather would have shifted the brood rearing periods to a later time rather than earlier, but such was not the case. It was noted that there were fewer insects in the fields during the early summer.

Reproductive Success

It has been shown for other grassland birds that the preferred measure of habitat quality was reproductive success rather than abundance of adults (Hughes *et al*. 1999). A total of 42 Grasshopper Sparrow nests were found in the CRFRC experimental grasslands over the course of the two-year study (12 in 1999 and 30 in 2000). In 1999, nine active nests were found and observed for a total 59 nest-days. Of the nine active nests, five were determined to be successful and 4 were unsuccessful (four nest-killing events were observed). We calculated a daily probability of nest survival of 0.932. Probability of nest survival to fledging for any given nest attempt therefore was estimated to be $0.932^{21} = 0.228$, or a 22.8% chance of survival (see Methods).

In 2000, 30 Grasshopper Sparrow nests were observed a total of 308 nest-days (Table 10). Five predation and one farm equipment mortality events were observed. We calculated a daily probability of survival of 0.981 and a 66.8% chance of survival to fledging. By pooling the data for the two years, we observed 39 nests for a total 367 nest-days with 10 failures. This converts to a daily probability of nest survival of .973 and a probability of nest survival to fledging of 56.3%.

Estimates of fecundity are shown in Table 11. In 1999, the average number of eggs laid per nest was 3.8 (n=5 nests) and average number of chicks per successful nest was 3.8 (n=7 nests). In 2000, the average number of eggs laid per nest was 4.8 (n=21 nests) and average number of chicks per successful nest was 4.4 (n=22 nests). Pooled over both years the average number of eggs per nest was 4.6 (n=27 nests) and the average number of chicks per successful nest was 4.3 (n=29 nests). These estimates of nest production are consistent with those reported by Vickery (1996). We haven't yet determined how many offspring each pair fledges in the breeding season and whether there are significant differences among adult age groups.

Dispersal of Hatching-year Grasshopper Sparrows

A total of twelve Local (banded in the nest) and six HY (hatching year – post fledge birds in juvenal plumage) Grasshopper Sparrows were banded in 1999 but none were ever observed again. In 2000 84 Local and 46 HY birds were banded, but none of these HY birds were seen again in 2000. We hope that some of these 130 birds will be found in 2001 and give us insight into the survival, dispersal, and behavior of the first-year/nestling birds from the CRFRC grasslands. The lack of repeat observations for the total 148 HY birds has several possible explanations: 1) fledglings instantly dispersed from their natal patch and established home bases (pre-SY territories) in new but distant habitat patches (J. Sheppard, pers. comm.); 2) all fledglings fell prey to predators – the Grassland Restoration fields could be a reproductive sink; 3) fledgling behavior was such that they eluded mist nets and observation.

Despite our failure to relocate any of our marked HY birds, we observed and captured numerous unbanded HY birds in the project fields in August of both years. The origin of these unbanded HY birds is intriguing. Clearly, they were either fledged from undiscovered nests in our grasslands or they were immigrants from other localities. The abundance of the unmarked HY birds argues in favor of the dispersal hypothesis (1) and against the hypothetical predation explanation (2) as the cause of the disappearance of our marked young Grasshopper Sparrows. In addition we cannot identify any candidate predator(s) common enough to account for the losses of our marked birds and not the numerous unbanded individuals. Dispersal of Grasshopper Sparrow offspring is still an enigma (Vickery 1996) and there is no published literature that addresses their dispersal processes.

Estimation of Per Capita Annual Population Growth Rate

With an annual adult survivorship of 0.40 (assuming our return rate of adult males is a good measure of annual survival rates of both males and females) and a predicted juvenile survivorship of half of the adult survivorship (Ricklefs 1973, McCoy *et al*. 1999) a stable, unchanging population size (R = 1) would require 3.0 female chicks fledged to each adult female.

$$N_{t+1} = N_t(0.40) + 0.5(0.40)N_t m$$

If $R = \frac{N_t}{N_{t+1}} = 1$ then $m = 3$.

Our results show that in 1999, fecundity was 1.65, well less than the 3.0 required for an unchanging population (Table 11). In 2000, fecundity was 4.13, greater than the level required for the study population to serve as a source population. The pooled data (fecundity 3.74) show that over the two-year study, there is evidence that the CRFRC fields are a benefit to the larger Grasshopper Sparrow population, and are serving as a productive source of young and recruits.

Grasshopper Sparrow Movement and Territory Studies

Twenty-five territories or parts of territories were mapped in the experimental grasslands from 28 May until 23 June 2000. Although data were not collected as systematically as we had hoped, efforts were made to sample territories from all the fields.

Territory size

Twenty-one Grasshopper Sparrow territories were mapped sufficiently for analysis in 2000. The mean territory size was 4800 m^2 (SE = 445 m^2) = 0.48 hectares = 1.186 acres with an average radius of 39 meters. The maximum size was 9726 m^2 and the minimum was 1609 m^2. These territories are on average significantly smaller than the territory sizes reported by Holmes (1996) in the most dense colony in Maryland. We found no evidence that the territories in the center of the population were smaller than those on the perimeter. We had no evidence that breeding adults used the same territories in successive nesting attempts within the same season, but our studies to date were limited. Thorough monitoring of territories in 2001 is a priority now that the methodology has been established and tested.

Adult Grasshopper Sparrow Movement

Because we attempted to move the mist nets often (usually every two hours or so) and we moved what we estimated to be the distance to the next territory, we expected to maximize the number of new adults captures and minimize the number of repeated captures of adults. Our intention was to mark as many adults as rapidly as possible, and then observe the marked birds unobtrusively with optical equipment as our main method of study of individual behavior. Nevertheless, 65 different adult Grasshopper Sparrows were caught multiple times: two were caught five times, three were caught four times, twelve were caught three times, and 48 were caught twice. Twenty of the recaptures were female and 45 were male.

With few exceptions, males that were observed and captured more than once tended to remain in the confined areas we identified as territories. Our observations indicated that females were more mobile. Four females were captured at locations more than 300 meters away from where they were previously captured (Table 12). For example one female, GBFX, was captured on 26 May and again on 4 June 470 meters away, and again on 14 June 390 meters from the second capture spot and 725 meters from the original capture spot. Female GFFX was captured on 27 May and again on 4 June 435 meters away. Compared to the 39-meter radius of our average circular territory, recapture data indicated these females were traveling over multiple territories in short periods of time. The function of these travels is unknown (e.g. whether extra-pair copulations were achieved). We have no evidence yet that these females were actively nesting at the time, but it was during the height of the breeding season. We must note that our sample is biased to individuals that move more - more active females will be more likely caught in mist nets.

V. FUTURE STUDIES

Territorial male Grasshopper Sparrows sing at extraordinarily high pitches compared to other songbirds: they produce vocalizations almost exclusively in the 8 kHz range (Rising 1996, Vickery 1996, pers. obs.). In most small birds, including some other sparrows, auditory sensitivity is at a maximum between 2-3 kHz and declines rapidly above 6 kHz (Dooling *et al*. 2000, Fay 1988, Okanoya & Dooling 1987). Moreover, the decay in audibility with distance is greater (steeper) with high-pitched signals than with lower frequencies. This raises the question: How do conspecific Grasshopper Sparrows and even the singing male itself hear advertising songs? At present we know little about the hearing abilities of Grasshopper Sparrows. Because bird hearing is relatively uniform across species (Dooling *et al*. 2000), we presume that auditory sensitivity of Grasshopper Sparrow is similar to that of other small birds. Thus, the extra high frequency of the advertising songs may pose serious constraints on the distances over which they can communicate. As compensation of the high frequency, the birds have two choices, either the power (decibels) of the sound production is increased so that the song carries a normal distance, or Grasshopper Sparrows reduce the territory sizes and advertise closer to neighbors. The fact that our preliminary estimates of territory size are smaller than other grassland birds supports the latter hypothesis.

We shall examine several aspects of song variation in grasshopper sparrows in order to understand the territorial behavior in this species. Specifically, we will:

1. Describe variation in grasshopper sparrows with respect to the measurable physical features of song. Use measures from audiotape recordings to examine the relationship of within-individual variation to between-individual variation for birds sampled from this small population.

2. Record other birds and insects emitting sounds in the restored grasslands. Examine the relationship of the physical characteristics of these sounds to those of Grasshopper Sparrow vocalizations, particularly with respect to the frequency bands occupied by these other species.

3. Perform song playback tests in the local population using songs that have had specific features altered in order to test whether variation in song perception matches that of song production. In particular, test songs that have been shifted to lower (presumably audible) frequencies that may overlap with those of insect signals, and higher (perhaps less audible) frequencies that do not.

VI. MANAGEMENT OPTIONS AND RECOMMENDATIONS

Grassland Management Regimes

Maintaining a grassland community requires regular disturbance (Loucks *et al*. 1985, Dudley and Lajtha 1993). Managers interested in promoting Grasshopper Sparrow and other grassland birds have an array of options for creating the necessary levels of disturbance including regimes of fire, mowing, herbicides, and grazing. Published literature presents conflicting information on the nesting requirements of Grasshopper Sparrows, leaving land managers without a clear protocol for success for management of the species.

Grasshopper Sparrows from different regions appear to require different habitats and thus a localized research and management approach would provide the greatest success. Herkert (1998) reports that Grasshopper Sparrows are negatively impacted by a deeper litter layer while others report that suitable habitat requires only moderately deep litter (Smith 1968, Wiens 1969, Dechant *et al.* 1998). Whitmore (1979) and Bollinger (1995) state that Grasshopper Sparrows require sparsely vegetated grasslands in West Virginia and New York, but Schneider (1998) reports that Grasshopper Sparrows associate positively with percent grass cover in North Dakota. The results presented from the studies at CRFRC have not been entirely consistent with any similar studies from the Midwest or the Northeast.

Land managers must also be aware that managing the grasslands for one species of bird might negatively affect the breeding success of other bird species of concern. Grasshopper Sparrows and Upland Sandpipers require open fields with low vegetation while Dickcissels favor denser and higher vegetation associated with less frequent burning (Hughes *et al.* 1999). The following sections address the effects of some of these options on grassland bird species and grassland ecology.

Burning

Prescribed burns impose a variety of effects on warm-season grassland communities. Dominant species of grasses known to be native to eastern grassland communities, including all of the warm-season species recommended in CRP and CREP plans and those planted at the Experimental Grassland Restoration Project, are fire-tolerant. In most cases the meristems are below ground and will not be damaged by the slight soil temperature increases occurring in a low intensity fire. Prescribed burning increases above ground biomass in most C_4 (photosynthetic pathway) vegetation, eliminates woody successional competitors and standing dead vegetation, increases species richness, and reduces litter layer (Collins 1987, Madden *et al*. 1999, Mitchell *et al.* 2000). Possible negative effects of burning include reduction of arthropod abundances that act as a food source for Grasshopper Sparrows (Rodenhouse *et al*. 1995, Davis *et al*. 2000) and dormant-season burns may encourage dominant C_4 grasses resulting in sub-optimal diversity, and inhibit establishment of rare prairie plants that have adapted to summer fires (Howe 1994).

Timing of burning (dormant season, mid growing-season, and late growing-season) has produced a variety of effects on vegetation and nutrient levels (Howe 1994, Engle *et al*. 1998, Madden *et* *al*. 1999, Davis *et al*. 2000). Tallgrass prairie diversity and productivity in the Midwest are fundamentally limited by nitrogen levels (Blair 1997). Nitrogen increases immediately following a fire, but is quickly leached into the lower soil zones and remains inaccessible to plants for at least the next three years (Dudley and Lajtha 1993). Shortgrass species (Little Bluestem, Deertongue Grass and Sideoats Grama) are less tolerant of burns than are tallgrass species and may suffer decreases in productivity and biomass following burns (Engle *et al*. 1998).

Grasshopper Sparrow abundance declines the season immediately following winter burning in grassland habitats in Texas, Illinois, and Maine (Herkert 1994a, Vickery 1996, Reynolds and Krausman 1998) but has been shown to increase in subsequent years (Herkert 1994a, Vickery 1996). In North Dakota, Grasshopper Sparrows showed a clear positive response to burned habitats and were absent from unburned prairie patches (Madden *et al*. 1999). Nest predation rates were reduced in recently burned habitat in Minnesota (Johnson and Temple 1986b) presumably due to decreased predator presence. Adult abundances were not affected in Kansas following burning in wetter than average years (Zimmerman 1992).

Primary concern in a management regime that includes burning should be establishment of a heterogeneous habitat with different fields in different stages between burns. Burning should take place on a rotational basis with three to four years between burns for each particular field. Burning the experimental fields should occur before or following the breeding season as any fires during the breeding season would ensure nest failure.

Dormant season burns may not adequately simulate fire history of the Eastern Shore and several interesting species may be systematically eliminated from the restoration. Dormant season fires simulate human-managed systems that may have prevailed in pre-Columbian times, but exclude the effects of lightning-caused fires in the region. Howe (1994) found that management practices catering to the growth of the dominant species of grass were not good predictors of the success of other species of grassland plants. Late summer burns in Oklahoma have been shown to result in a short-term reduction in tallgrasses but no reduction in total production due to an increase in forbs (Engle *et al*. 1998). As long as the fires are set after mid-August, grassland bird nest mortality would be very limited. Late-summer or fall burning should be considered in CRFRC management protocols to open opportunities for flora currently suppressed by dominant C_4 grasses.

Mowing

Mowing has been recommended by some groups as a suitable alternative to burning in establishment of suitable habitat for grassland birds (Dechant *et al*. 1998, Mitchell *et al*. 2000). Mowing has some similarities to burning in that it opens the canopy structure, removes standing dead vegetation, and reduces competition from woody successional flora. In the Midwest, mowing may simulate the effects of large grazers (primarily bison) that were not abundant on the East Coast and may not be appropriate in native grassland restoration.

On the other hand, mowing at the wrong time can have detrimental effects. Mowing during the nesting season has been shown to have serious detrimental effects on nesting Grasshopper Sparrows and other grassland birds and should be avoided if possible (Bollinger *et al*. 1990, Bryan and Best 1991, Warner 1992, Kershner and Bollinger 1996, Vickery 1996). Grasslands on the East Coast may be more productive than in the Midwest (Bollinger 1995, Mitchell *et al*. 2000) and mowing without haying may increase litter. As mentioned previously, deeper litter can be a negative feature of Grasshopper Sparrow habitat (Bollinger 1995). Recommended times for mowing would be in August, after the majority of the nesting season, and haying would be advisable.

In the first two years of establishment of the Experimental Grassland Restoration Project, mowing has been a necessary technique to reduce weed competition for establishment of warm-season grasses. CRP and CREP administrators require this short-term management for enrolled acreage. Once the perennial grasses have become established, mowing is not recommended as a management tool for native prairie restoration due to increased litter buildup.

Increasing Habitat

Grasshopper Sparrows are loosely colonial and small populations appear to be somewhat ephemeral (Smith 1968, Holmes 1996). Population Viability Analyses show that populations of Grasshopper Sparrows show clear relationships between carrying capacity and population persistence (Wells 1997; Dodge, unpublished). Larger habitat carrying capacities would allow populations to grow large, better withstand variability in reproductive success, and buffer against environmental stochasticity. Increasing habitat available to Grasshopper Sparrows in the form of large habitat blocks, like those at CRFRC, would certainly increase the chances of the population persistence.

The apparent vigor with which Grasshopper Sparrows colonize new habitat blocks provides strong support for increasing habitat as a crucial management component. At our study site, two months after the conversion of marginal croplands to grasslands the population of Grasshopper Sparrows in the vicinity increased from approximately 10 mating pairs (J. Gruber, pers. comm.) to 75 mating pairs. We surmise that some of the 65 new males in the area were returning from the past breeding season, but that most were new immigrants. The implication is that site fidelity is not necessarily as strong in males as others (Wells 1997) have suggested, and that birds returning from their migration in the spring can be attracted to new, preferred habitat. Thus, suitable habitat sites are likely to be rapidly colonized.

Grasshopper Sparrow populations appear to be to relatively stochastic in nature. Small populations have a low probability of persistence in years of high mortality. Much of the grassland habitat that has been restored on the Eastern Shore has been in linear strips adjacent to croplands and these can accommodate only very small populations. The high probabilities of population extinction projected in PVAs for populations of 25 breeding pairs or less (estimated 25 hectares of habitat) indicate that a block of habitat at least 50 hectares in size is necessary to increase persistence. This is empirically substantiated by reports of decreased reproductive success in strip/linear habitats with a high edge/area ratio (Delisle *et al*. 1996 as reported in Vickery 1996, Herkert 1998, Warner 1992, Johnson 1986). Current management recommendations for the Midwest and for New England incorporate minimum size habitat blocks (Johnson and Temple 1986a, Herkert 1994a, Vickery *et al*. 1994). Additionally, the empirical evidence showing population persistence to be related to larger grasslands (i.e.

airports) and large weedfields is consistent with the PVA results (Vickery *et al*. 1994, Wells 1997).

Small populations, even with high levels of dispersal, are subject to levels of stochasticity too great to maintain a high probability of persistence. For several theoretical and practical reasons multiple small habitat patches are not a replacement for a few larger ones. However desirable they are, large plots of land are often not available for wildlife managers. If only small (less than 50 hectare) habitat areas are available, they would have to be numerous and connected by metapopulation structures (including corridors that allow immigration and emigration between the habitat areas) to minimize the chances that all subpopulations would go extinct simultaneously.

Maryland's CRP and CREP, with federal funding, have the directive of encouraging and compensating farmers to reduce agricultural production for the purpose of enhancing wildlife habitat. Little has been done to study the effects of each program's actions on wildlife populations in Maryland or in any Mid-Atlantic state. Results from CRFRC and other studies on Grasshopper Sparrows have indicated that large blocks of habitat are beneficial to population growth and persistence. To date, CRP and CREP efforts that have concentrated on installing linear strip habitat have little positive effect on grassland birds. Enrolling more block areas of land in conservation projects dedicated to declining grassland bird species is not an unreasonable request for the state of Maryland. Grasshopper Sparrows are but one of several declining species to benefit: Short-eared Owl, Bobwhite Quail, Upland Sandpiper, Dickcissel, Bobolink, Eastern Meadowlark, Vesper Sparrow, and Henslow's Sparrow are some of the others.

VII. DICKCISSELS AT CRFRC

Results and Discussion

One of the bigger surprises of the 2000 season was the invasion and nesting of Dickcissels at the Grassland Restoration Project. A total of sixteen Dickcissels were banded in the project fields in 2000, including eight AHY males, four AHY females and four nestlings; in addition, at least one unbanded adult female with young was observed in August. From 1983-1987 only four Dickcissel nesting sites were confirmed in the state of Maryland. Another eleven sites were listed as probable and yet another eleven as possible totaling only 26 observed nesting attempts over a five-year period (Smith 1996). Dickcissels can be quite irruptive in their population behavior during nesting season (Kaufman 1996). They have been known to inhabit an area one summer, and then be absent from that site in future years. Their range is centered in the open country of the Great Plains in central North America, but they may disperse to peripheral regions during droughts in the Midwest (J. Gruber, pers. comm.). The Dickcissel presence at CRFRC grasslands coincided with an extensive drought throughout the central North America in 2000.

Habitat requirements for Dickcissel include taller, more heterogeneous vegetation than the Grasshopper Sparrow (Zimmerman 1982, Smith 1996, Mitchell *et al.* 2000). Other habitat requirements for Dickcissel include elevated song perches (Smith 1996). Dickcissels are attracted to grasslands with a woody border that can be used as song perches (Hughes *et al.* 1999). Dickcissels tend to be less sensitive to habitat size and fragmentation than Grasshopper Sparrows (Herkert 1994b, Smith 1996).

We found five nests in July and have observations of three additional successful nestings. We can say for sure that only one of these five nests successfully fledged young. One other nest could possibly have fledged early, but we neglected to monitor it adequately. On 15 August three groups of recently fledged young attended by females that were defensively chipping and carrying food were observed in Field 3, 7 and 8. Two of the females seen caring for young in August were banded, and possibly represented renesting activity; the third active female was unbanded. Out of a total of eight known nesting attempts, at least four were successful.

Dickcissels nested in Fields 3, 4, 6 and 8. In Fields 4 and 8, Switch Grass was dominant and was well over one meter tall in most spots by mid-July, and two meters tall by mid-August. In Field 3, abundant Mare's-tail (*Conyza canadensis*) and sparser native grasses created similar vegetative structure during the summer. Our nest vegetation data shows that Dickcissels chose spots in our fields that were on average 35% bare and 35% live within one meter of the nest. All five Dickcissel nests active in early July were found at the base of Pokeweeds (*Phytolacca americana*). Four of the nests were firmly secured 0.5 m above the ground in the base of stiff, 2-3 cm diameter stems. Consistent with previous reports that Dickcissels generally build nests 24-34 cm above ground level (Zimmerman 1966, Smith 1996), four of the five Dickcissel nests were found in high (> 1 m) grass and pokeweed, not on the ground. A single nest in low vegetation was next to a fallen pokeweed.

There have been mixed results reported in the literature regarding vegetation structure effects on Dickcissel reproductive success. Nest survival rate was negatively associated with grass canopy covers in Kansas (Hughes *et al*. 1999) but a positive association was found in Iowa (Bryan and Best 1991). Dickcissel reproductive success was positively associated with litter depth in Kansas CRP fields (Hughes *et al*. 1999).

Management of the Grassland Restoration Project fields will be most conducive to Dickcissel colonization by maintaining tall-grass fields in a heterogeneous landscape by a sequential fire regime. Species in the tall and moderately tall planting mixtures (Big Bluestem, Switch Grass, Indian Grass, Little Bluestem, Eastern Gama Grass, and Red Fescue) are fire-tolerant and should provide adequate aboveground biomass and litter layer for nesting Dickcissels. There appears no major conflict between grassland management to provide habitat for both Dickcissels and Grasshopper Sparrows. Due to the height of Dickcissel nests, mowing during the nesting season would likely cause total nest failure. If herbicide must be applied during the summer to deter noxious weeds such as Johnson Grass or Canada Thistle, application by persons wearing portable backpacks would limit nest destruction.

VIII. OTHER BIRDS AND THEIR USES OF THE CRFRC GRASSLANDS

Killdeer were seen regularly early in both 1999 and 2000. A single nest was found in 1999.

Upland Sandpipers (a flock of 13) were observed in the study fields in August 1999. We assumed this to be a migrant group. None were observed in 2000.

Northern Bobwhite (three coveys and many adults) were observed in the fields in 1999 and 2000. A single observed nest was destroyed by a mower. Three coveys were present in late September 2000.

Eastern Kingbirds were abundant in the fields throughout both seasons. Most likely they are nesting on field borders.

Bluebirds were present in the study fields throughout the summer in both years with active breeding in surrounding nest boxes. Downy young were seen regularly in the fields.

Horned Larks actively bred in the newly planted grasslands in 1999. Three nests were found. Two nests were preyed upon 2-3 days after a mowing exercise in June 1999. In 2000 they were observed frequently in the fields early in the season. One hatchling was banded, but no nests were found.

Vesper Sparrows (an adult male and female) in breeding condition were captured in the study field in 1999, although no nest was found. Five birds were observed in the fields in 2000. Early in the season, two birds (breeding pair) were banded and one other pair was seen multiple times. Again, no nest was found.

Song Sparrows were common in the study fields near edges throughout the both seasons

Savannah Sparrows are abundant in winter and early spring.

Field Sparrows (both residents and migrants) are abundant breeders in the brush around the fields and active users of the fields for foraging. Two nests (one successful) were discovered and monitored in the fields.

Chipping Sparrows are abundant breeders in the surrounding areas to the fields and active users of the fields for foraging.

White-crowned Sparrows inhabit brush around the fields in winter. Questions remain as to the wintering site fidelity for this species.

Blue Grosbeaks are common breeders in the vegetation surrounding the fields and shrub islands were often observed foraging in the fields in both 1999 and 2000.

Indigo Buntings are common breeders in the trees surrounding the fields and commonly observed in the fields near edges in both 1999 and 2000.

Bobolinks (eight males and two females) were observed foraging in fields on 15 July 2000. Smaller groups were observed in the fields for about a week following.

Red-winged Blackbirds are abundant in fields for the entire season in both 1999 and 2000. Two nests were discovered in the fields in 2000.

Eastern Meadowlarks (a single pair) were regularly observed on Kibler Road about 1 mile from the restored grasslands in 1999. One male was singing in the fields for about a week in early June 2000.

Orchard Orioles were commonly observed foraging in fields in both 1999 and 2000. They are common breeders in the surrounding trees and in the shrub islands in the fields.

Northern (Baltimore) Orioles are common breeders in the surrounding trees and occasionally observed foraging in the fields in both 1999 and 2000.

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XI. TABLES AND FIGURES

Table 1. Conservation Status of selected grassland bird species in East Coast states.
Species legend: Grasshopper Sparrow (GRSP); Vesper Sparrow (VESP); Henslow's Sparrow (HESP); Dickcissel (DICK); Bobolink (BOBO); Eastern Meadowlark (EAME); Northern Bobwhite (NOBO); Horned Lark (HOLA); Upland Sandpiper (UPSA); Short-eared Owl (SEOW).
Status legend: Endangered (EN); Threatened (TH); Critically Imperiled (CI); Special Concern (SC); Rare (RA).

State	**GRSP**	**VESP**	**HESP**	**DICK**	**BOBO**	**EAME**	**NOBO**	**HOLA**	**UPSA**	**SEOW**	**REF.**
Maine	EN								TH	TH	(ME Dept. IFW 2001)
Vermont	SC	SC	EN						TH	SC	(VT Dept. F &W 2001)
New Hampshire	CI	RA	EN			RA		RA	EN		(NH F & G 2001)
Massachusetts	TH	TH	EN						EN	EN	(MA Div. F & W 2001)
Connecticut	EN	EN	SC			SC		TH	EN	TH	(CT Dept. Env Prot 2001)
Rhode Island	TH								EN		(RI Nat. Her. Prog. 2001)
New York	SC	SC	TH					SC	TH	EN	(NY Dept. Env. Con. 2001)
Pennsylvania				TH			SC		TH	EN	(PA Dept.. CNR 2001)
New Jersey	TH	EN	EN		TH	SC		SC	EN	EN	(NJ Div. F & W 2001)
Delaware	SC	SC	EN		SC	SC			EN	EN	(DE Nat. Her. Prog. 2001)
Maryland		SC	TH	SC					EN	SC	(MD DNR 2001)
Virginia			TH						TH		(VA Dept. F & W 2001)
North Carolina		RA	RA								(LeGrand, pers. comm)
South Carolina											(SC Herit. Trust 2001)
Georgia			SC								(GA Nat. Her. Prog. 2001)
Florida	EN										(FL F & W 2001)

Table 2a. Summary of CRP and CREP enlistment in CP2 (establishment of permanent native grasses) in Maryland Eastern Shore counties by acreage and as a percentage of total CRP and CREP enrollment 1986 - 2001 (USDA - FSA 2001).

	CRP			**CREP**		
County	**CP2 acreage**	**Total**	**%CP2**	**CP2 acreage**	**Total**	**%CP2**
Caroline	404.5	1902	0.21	0	774.3	0.00
Cecil	14.8	1944.1	0.01	4.5	843.3	0.01
Dorchester	299	5542.5	0.05	0	3133.4	0.00
Kent	637.4	3912.8	0.16	140	1044.8	0.13
Queen Annes	351.2	5752.1	0.06	9.1	2800.3	0.00
Somerset	3.8	2464.6	0.00	0	2017	0.00
Wicomico	34.6	1436.5	0.02	0	553.1	0.00
Worcester	22.6	1861.1	0.01	0	1545.6	0.00
Total	1767.9	24815.7	0.07	153.6	12711.8	0.01

Table 2b. Summary of CRP and CREP enlistment in CP21 (establishment of filter strips) in Maryland Eastern Shore counties by acreage and as a percentage of total CRP and CREP enrollment 1986 - 2001 (USDA - FSA 2001).

	CRP			**CREP**		
County	**CP21 acreage**	**Total**	**%CP21**	**CP21 acreage**	**Total**	**%CP21**
Caroline	906.9	1902	0.48	770.5	774.3	0.99
Cecil	248.9	1944.1	0.13	165.6	843.3	0.20
Dorchester	3818.1	5542.5	0.69	2947.1	3133.4	0.94
Kent	493.1	3912.8	0.13	428.4	1044.8	0.41
Queen Annes	2463.9	5752.1	0.43	2243.9	2800.3	0.80
Somerset	471.4	2464.6	0.19	394.3	2017	0.20
Wicomico	309.4	1436.5	0.22	212.7	553.1	0.38
Worcester	866.7	1861.1	0.47	743.6	1545.6	0.48
Total	9578.4	24815.7	0.39	7906.1	12711.8	0.62

Table 3. Eight species of native perennial warm-season grasses and one species of cool-season grass planted at CRFRC in March 1999.

Common Name	**Scientific Name**	**Growing Season**
Big Bluestem	*Andropogon gerardi*	Warm
Side-oats Grama	*Bouteloua curtipendula*	Warm
Deertongue Grass	*Panicum clandestinum*	Warm
Switch Grass	*Panicum virgatum*	Warm
Coastal Panicum	*Panicum amarum*	Warm
Indian Grass	*Sorghastrum nutens*	Warm
Little Bluestem	*Schizachyrium scoparium*	Warm
Eastern Gama Grass	*Tripsacum dactyloides*	Warm
Red Fescue	*Festuca rubra*	Cool

Table 4. Grass species mixtures and planting rate for CRFRC fields as planted in March 1999. In addition to the following species, Blue Grama (*Bouteloua gracilis*) was inadvertently planted in very small quantities with Sideoats Grama. Tall Fescue (*Festuca arundinacea*) was inadvertently planted in moderate quantities with Red Fescue. *Red Fescue and Tall Fescue are cool season grasses.

Field	**Seed Mix**	**Grasses**	**Seed Rate (lbs/acre)**
1, 6	Short	Little Bluestem Sideoats Grama Deertongue Grass	4 2 2
2, 7	Moderately Short	Little Bluestem Big Bluestem Eastern Gama Grass	4 2 2
3, 5	Tall	Little Bluestem Big Bluestem Indian Grass	2 2 4
4, 8	Moderately Tall	Eastern Gama Grass Switch Grass Red Fescue*	4 2 2
9-12	Mid-height	Coastal Panicum Little Bluestem Indian Grass	4 3 1

Table 5. Grasshopper Sparrows captured in mist nets on experimental grasslands in the 1999 and 2000 seasons. HY means hatching year (those birds born earlier that season). Local birds were nestlings banded in the nest.

	1999	**2000**	**Total**
Male adult	50	80	130
Female adult	23	61	84
Unknown HY	6	46	52
Local	12	84	96
	91	**271**	**362**

Table 6. Measurements and results of t-test analyses of adult Grasshopper Sparrows captured in mist nets in experimental grasslands. Wing-length, tail-length, and exposed culmen differ significantly (α =0.05) between males and females.

	Mean	**N**	**Max.**	**Min.**	**SE * 2**	**P**
Wing Length (chord)						
Male	61.2 mm	129	65.0	58.0	0.21	<.001
Female	58.5 mm	83	61.5	55.0	0.31	
Weight						
Male	17.7 g	119	20.0	15.2	0.17	0.37
Female	17.9 g	81	24.0	14.2	0.38	
Bill Length						
Male	8.2 mm	96	9.0	7.0	0.08	0.72
Female	8.2 mm	59	9.0	7.0	0.12	
Bill Width						
Male	5.7 mm	96	6.5	5.0	0.09	0.35
Female	5.6 mm	59	6.5	4.5	0.12	
Tail						
Male	43.8 mm	84	47.0	40.0	0.35	<.001
Female	42.7 mm	53	47.5	39.0	0.46	
Exposed Culmen						
Male	12.1 mm	76	13.5	11.0	0.13	0.85
Female	12.0 mm	51	13.0	10.5	0.18	
Lore Length						
Male	6.0 mm	97	8.5	3.5	0.19	<.001
Female	5.5 mm	59	8.5	3.5	0.24	

Table 7. Nest habitat of Grasshopper Sparrows from 2000 (n=30). Percent bare ground, percent duff, and percent live vegetation are presented for circles of radius one and five meters centered on the nest cup.

	One meter radius from nest			Five meter radius from nest		
	Bare %	Duff %	Live %	Bare %	Duff %	Live %
Mean	34	36	30	33	29	38
Max	70	70	65	60	56	60
Min	5	5	15	5	9	20
SD	20.16	17.8	10.7	17.9	12.8	11.2

Table 8. Number of Grasshopper Sparrow nests found in 2000 in each of the four planting mixtures comprising Fields 1-8 at CRFRC. Planting mixtures and rates are shown in Table 5.

	Short (1,6)	Mod. Short (2, 7)	Tall (3, 5)	Mod. Tall (4, 8)
	0	4	4	4
	5	9	3	0
Total	5	13	7	4

Table 9. Status of males of nests started in the first week of nesting season. 50% of these males were banded in 1999, but made up only 20% of 2000 male population.

Nest	Est. Lay Date	Male/Sire	Status
06-GRSP-01	5/13/00	ORBX	Banded 1999
03-GRSP-03	5/14/00	BTBX	Banded 1999
07-GRSP-02	5/14/00	YFBX	New
07-GRSP-04	5/15/00	MWBX	New
07-GRSP-01	5/16/00	YPBX	New
07-GRSP-03	5/19/00	OBBX	Banded 1999

Table 10. Nest observations from the Summer 2000 field season.

Nest	Begin Date	End Date	Days Observed	Outcome	Eggs Laid	Hatch	Fledge
2-GRSP-01	06/14/00	06/21/00	6	Fledge		5	5
2-GRSP-02	07/02/00	07/21/00	18	Fledge	4	4	4
2-GRSP-03	06/30/00	07/21/00	20	Fledge	5	4	4
2-GRSP-04	07/02/00	07/17/00	14	Fledge	5	5	5
3-GRSP-01	06/01/00	06/12/00	10	Predation	5		
3-GRSP-02	06/02/00	06/12/00	9	Fledge	4	4	4
3-GRSP-03	06/03/00	06/03/00	0	Fledge			3
3-GRSP-04	06/05/00	06/21/00	15	Fledge	5	4	3
4-GRSP-01	06/04/00	06/26/00	21	Fledge	5	5	5
4-GRSP-02	06/07/00	06/28/00	20	Fledge	5	5	5
4-GRSP-03	06/08/00	06/23/00	14	Fledge	5	5	5
4-GRSP-04	06/13/00	06/23/00	9	Predation	4		
5-GRSP-01	06/08/00	06/19/00	10	Predation	5		
5-GRSP-02	06/19/00	06/24/00	4	Fledge			5
5-GRSP-03	07/12/00	07/17/00	4	Fledge			5
6-GRSP-01	05/25/00	05/29/00	3	Fledge	5	3	
6-GRSP-02	06/21/00	07/04/00	12	Kill -mower	5	5	
6-GRSP-03	06/22/00	07/06/00	13	Fledge	4	4	4
6-GRSP-04	06/23/00	06/28/00	4	Fledge		5	5
6-GRSP-05	07/18/00	07/26/00	7	(unknown)	5	5	
7-GRSP-01	05/26/00	05/29/00	2	Predation	5	2	
7-GRSP-02	05/27/00	06/02/00	5	Fledge		4	4
7-GRSP-03	05/27/00	06/10/00	13	Fledge	5	5	5
7-GRSP-04	05/27/00	06/02/00	5	Fledge		3	3
7-GRSP-05	05/27/00	06/15/00	18	Fledge	5	4	4
7-GRSP-06	06/03/00	06/12/00	8	Fledge		5	5
7-GRSP-07	06/06/00	06/26/00	19	Fledge	5	5	5
7-GRSP-08	06/27/00	07/06/00	8	Predation	5	4	
7-GRSP-09	06/27/00	07/02/00	4	Fledge		5	5
9-GRSP-01	06/07/00	06/21/00	13	Fledge	5	5	3
		Total	**308**				**96**
		Mean	**10.3**		**4.81**	**4.38**	**4.36**

Table 11. Three aspects of reproductive success: probability of nest success, number fledged per successful nest, and fecundity for 1999, 2000, and pooled data.

	Reproductive Success		**Number fledged per successful nest**		**Fecundity**	
Year	Mean	SE	Mean	SE	Mean	SE
1999 (n=9)	22.8	Pending	3.8	0.37	1.65	Pending
2000 (n=30)	66.8	Pending	4.4	0.17	4.13	Pending
Pooled (n=39)	56.3	Pending	4.3	0.16	3.74	Pending

Table 12. Female Grasshopper Sparrows that were caught more than one time at distances greater than 300 meters between capture sites.

BIRD	First Capture	Recapture	Time interval	Distance (m)
GBFX	5/26	6/4	9 days	470
-GBFX	6/4	6/14	10 days	390
-GBFX	5/26	6/14	19 days	725
GFFX	5/27	6/4	8 days	435
PWFX	6/1	6/3	2 days	340
GWFX	5/25	6/4	10 days	435

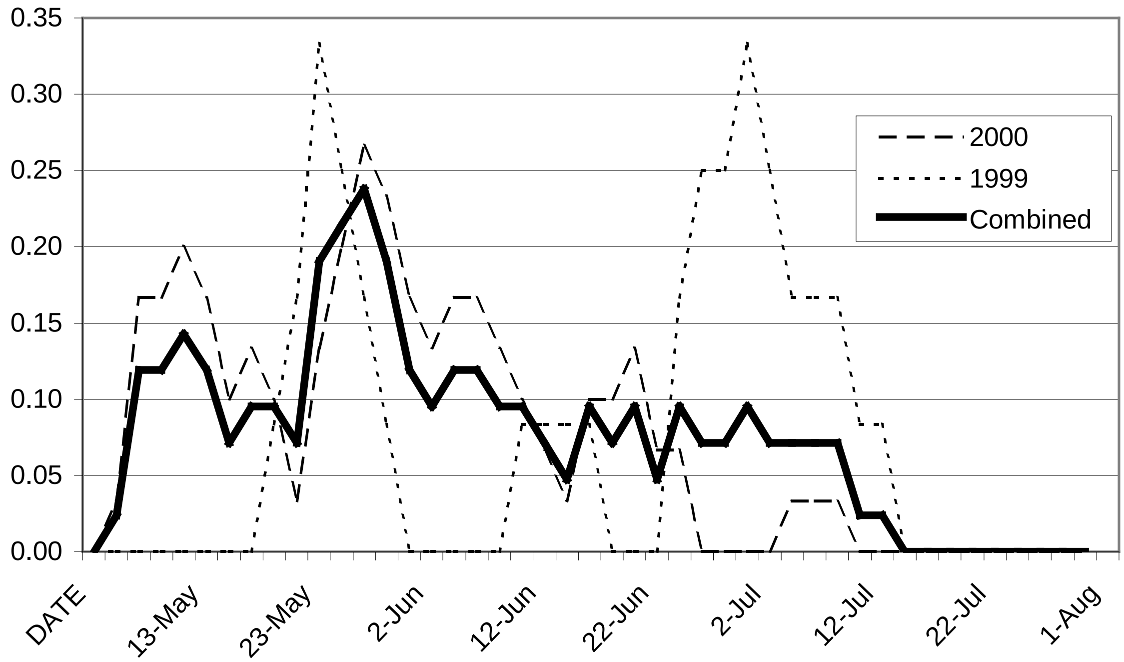

Figure 1. Beginning dates of nests on CRFRC as a percentage of season total based on data from 1999 (12 nests) and 2000 (30 nests). One outlier nest from late in the 1999 breeding season was omitted.

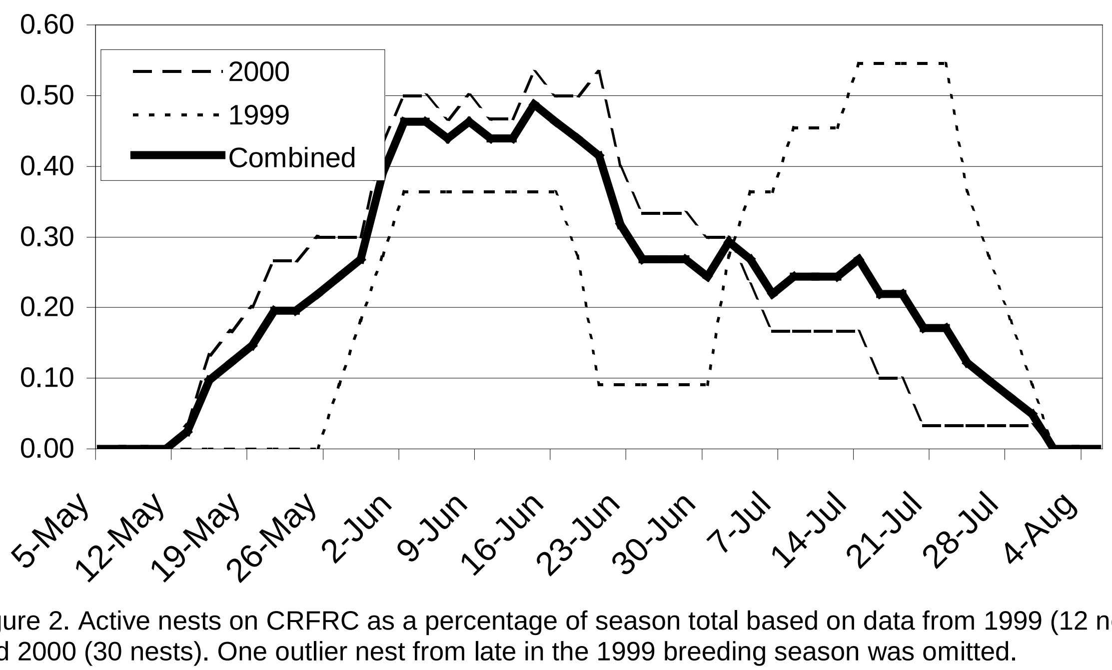

Figure 2. Active nests on CRFRC as a percentage of season total based on data from 1999 (12 nests) and 2000 (30 nests). One outlier nest from late in the 1999 breeding season was omitted.

XII. APPENDIX I

We assume that: 1) all adult females (SY and ASY) are breeding each summer, 2) each female has a maximum of four opportunities to complete a nest but can physiologically complete only two nests, 3) if a nest fails a female will renest, and continue to do so until all four nest opportunities expire, and 4) the probability of daily nest survival is constant in a season.

We model the pattern of nestings through a breeding season by females as a truncated binomial probability density function of successes (p) and failures (q = 1-p) with the constraint that only two successful nests are possible:

$(p + q)^4 = p^4 + 4p^3q + 6p^2q^2 + 4pq^3 + q^4$

where the first two terms of the expansion are not possible and deleted. The remaining three terms can be described as follows;

A. Two successful nests in a season - $6p^2q^2$

1. First two nests successful, females quits further attempts = pp--
2. First nest unsuccessful, nests #2 and #3 successful, no further attempt = qpp-
3. First two nesting attempts unsuccessful, nests #3 and #4 successful = qqpp
4. First nest successful, nest # 2 not, nest # 3 successful, quit = pqp-
5. First nest successful, nests # 2 and #3 not, nest #4 successful = pqqp
6. First nest not successful, nest #2 successful, nest #3 not, nest # 4 successful = qpqp

B. One successful nest in a season - $4pq^3$

1. First nest successful, all subsequent ones failures = pqqq
2. First nest unsuccessful, second nest successful, nest #3 and #4 failures = qpqq
3. First and second nest unsuccessful, third successful, nest #4 failure = qqpq
4. First three nests unsuccessful, fourth attempt successful = qqqp

C. No successful nest in a season - q^4 = qqqq

These patterns are mutually exclusive.

D. Reproductive Success of Grasshopper Sparrows on the restored grasslands

The total number of female fledglings produced from all successful nests by a female in a season is our definition of fecundity (F). If a female has two successful nests her reproductive success is 2 x females fledglings per nest x probability of having two successful nests. A female with only one successful nest (out of 4 attempts) has reproductive success of 1 x female fledglings per nest x probability of having one successful nest. In principle, these reproductive successes are then averaged over the number of females having two, one, or zero successes.

Year	F	p	q	$6p^2q^2$	$+ 4pq^3$	$+ q^4$
1999	1.9	0.228	0.772	0.1859	0.4196	0.3552
2000	2.2	0.668	0.332	0.2951	0.0978	0.0121
Pooled	2.15	0.563	0.437	0.3632	0.1879	0.0365

We do not yet have nest records of each female and her pattern of successes and failures over the season. We do have record of the number of successful nests (S) and number of failures (U) as a composite for the season. If we use the probability values p and q instead of the combinatorics, we can calculate crude estimates of reproductive success per nest. Reproductive success = (SpF)/(S + U). Reproductive success is the average number of daughters successfully fledged per female

Average Reproductive Success:

	Successes (S)	Unsuccesses (U)	Average Reproductive Success (SpF)
1999	5	4	0.24
2000	24	6	1.18
Pooled	29	10	0.90