

MOVEMENT PATTERNS OF WINTERING GRASSLAND SPARROWS IN ARIZONA

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ABSTRACT.—I used mark-recapture analysis and radio telemetry to characterize winter movement patterns of six grassland sparrows in southeastern Arizona. Mark-recapture data were generated by banding birds captured during repeated flush-netting sessions conducted on a series of 7-ha plots over three consecutive winters. This resulted in 2,641 captures of 2,006 individual sparrows of the six species. Radio telemetry was conducted concurrently on 20 individuals of four of these species. Recapture data and radio telemetry indicated that Cassin's Sparrow (*Aimophila cassinii*) and Grasshopper Sparrow (*Ammodramus saviarum*) were the most sedentary, followed by Baird's Sparrow (*Ammodramus bairdii*), Vesper Sparrow (*Poocetes gramineus*), Savannah Sparrow (*Passerculus sandwichensis*), and Brewer's Sparrow (*Spizella breweri*). Grasshopper, Baird's, Savannah, and Vesper sparrows tended to remain within fixed home ranges during winter. With the exception of Savannah Sparrows, whose movement behavior varied among study sites, movement patterns remained constant within species across years and study sites despite radical fluctuations in the absolute and relative abundances of all species. Interspecific differences in movement pattern suggest that species in this system partition niche space according to the regional-coexistence mechanism. Abundances of the most sedentary species, Cassin's, Grasshopper, and Baird's sparrows, were poorly or negatively correlated with summer rainfall at the between-year landscape scale, whereas abundances of the more mobile Savannah, Vesper, and Brewer's sparrows were strongly positively correlated. This is consistent with the theoretical prediction that movement constrains large-scale habitat selection, favoring mobile species in fragmented environments. Received 28 April 1999, accepted 10 February 2000.

THE MOVEMENT BEHAVIOR of an organism determines the scale at which it perceives and responds to the spatial subdivision of its environment (Wiens 1976, Levin 1992). Movement also is a fundamental element of population-level processes such as metapopulation dynamics, gene flow, habitat selection, and foraging behavior. Understanding the patterns, constraints, and adaptability of movement behavior is an important step toward understanding the dynamics of an organism's ecological relationships.

The range of movement patterns in nature can be viewed as a continuum ranging from random wandering to movements within a fixed home range. Random wandering is well suited for exploiting unpredictable, patchy resources. In such cases, the cost of exploratory movement is offset by the benefit of increased encounters with resource patches (Noy-Meir 1973, Andersson 1980, Sinclair 1984). This rationale has been used to explain the high degree of nomadism among granivorous birds in

desert environments, where the unpredictability of rainfall creates seed distributions that are highly patchy in time and space (Davies 1984, Clark 1997, Dean 1997).

In contrast, an organism with a fixed home range moves around repeatedly within an area that is small relative to its ability to travel a given distance. Such home ranges may or may not be defended against conspecifics. This type of movement is suited for exploiting relatively predictable resources. In such cases, gaining familiarity with a particular area is more cost effective than engaging in long-distance exploratory movements (Sinclair 1984).

Although random wanderings and fixed home-range movements generally are linked to distinct types of resource distributions, both strategies can be viable in many environments. Indeed, the use of multiple movement strategies for exploiting single resources in particular landscapes has received a great deal of attention (e.g. Hutchinson 1951, Levins and Culver 1971, Horn and MacArthur 1972, Tilman 1994). In models of regional coexistence, ecologically similar species coexist via a tradeoff

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between widespread exploration for and local exploitation of resources (Brown 1989, Tilman 1994). This tradeoff implies that increased efficiency at seeking new patches can only be gained by some sacrifice of an organism's within-patch efficiency, and vice versa. This concept has been invoked to explain niche differences among granivorous mammals and birds in desert ecosystems (Mares and Rosenzweig 1978, Brown et al. 1979, Thompson et al. 1991). In such cases, granivorous birds are described as "cream-skimmers" that explore large areas to find the richest patches in the landscape. This implies that birds distribute themselves to match the production of resources at the landscape scale. Granivorous rodents, in contrast, are more sedentary but are more locally efficient, such that they can survive on resource densities too low to support birds. This notion of birds as highly mobile cream-skimmers is consistent with patterns of nomadism that have been documented in many seed-eating birds of arid regions of Australia (Davies 1984, Clark 1997) and South Africa (Dean 1997). Movement patterns of granivorous birds in the American southwest have never been documented.

Rather than falling on a fixed point along the nomadism/home-range continuum, an organism may adjust its movement strategy in response to shifting environmental conditions. Behavioral plasticity is particularly valuable in highly fluctuating and unpredictable environments where the benefits of flexibility outweigh the costs of not being able to specialize on, and thereby maximize efficiency for, one particular strategy (Tripp and Colazo 1997). Plasticity of behavior and/or growth form has been found in a variety of desert organisms (Fox 1990, Pfennig 1992).

Given the variability and heterogeneity of their environment, plasticity would appear to be advantageous for sparrows wintering in Arizona grasslands. Productivity in these ecosystems is largely limited by rainfall (McClaran 1995). The rainfall that occurs during the summer monsoon season largely determines the distribution of habitat conditions for wintering sparrows. Summer rainfall controls the production of grass seeds that comprise the sparrows' primary food source (Pulliam 1983, C. Gordon unpubl. data) and the vegetative cover that provides important protection from predators (Pulliam and Mills 1977, Lima and Valone

1991). Summer rainfall in this region is patchy at the scale of thunderstorm cells that are 2 to 8 km wide and is highly variable and unpredictable among years (Noy-Meir 1973, McClaran 1995). For this reason, these sparrows may be faced with radically different spatial distributions of suitable habitat from winter to winter. Pulliam and Parker (1979) measured seed production at two grassland study plots in southeastern Arizona over four successive years and found that fluctuations exceeding an order of magnitude were common. On one plot, seed production increased more than two orders of magnitude in response to a 64% increase in summer rainfall between years.

My study addresses two major questions. First, can variation in movement patterns explain the coexistence of several ecologically similar species in this system? Second, does movement behavior constrain habitat selection in this system? To these ends, I develop new field and analytical techniques for studying the local movement behavior of grassland sparrows. I use these in conjunction with radio telemetry to characterize movement patterns of six species of granivorous sparrows on their wintering grounds in the grasslands of southeastern Arizona during three consecutive winters. In particular, I focus on overall sedentariness, the tendency toward fixed home-range versus nomadic movements, and plasticity of within-season movement patterns. I discuss the observed movement patterns as strategies that are more or less adapted for the spatiotemporal distribution of resources, patches, and biological interactions in the environment.

MATERIALS AND METHODS

Study sites.—Field work was conducted at three study sites in southeastern Arizona. The Research Ranch (TRR) is a 3,200-ha preserve located 8 km southeast of the town of Elgin in Santa Cruz County, Arizona. TRR is dominated by upland grassland vegetation and lies at the edge of a large (ca. 900 km²) region of grassland in the Sonoita Valley. TRR has not been grazed by cattle since 1967. Study plots were located in the northwestern quarter of TRR between 1,450 and 1,500 m elevation. The Empire Cienega Resource Conservation Area (EC) is also located within the Sonoita Valley grasslands, roughly 10 km from TRR. It lies in Pima and Santa Cruz counties and is leased to a private rancher for cattle grazing. Within the EC, fieldwork was conducted in the southeastern corner of the Davis Pasture, which is lo-

cated roughly 3 km west-northwest of Elgin between 1,450 and 1,480 m elevation. The Buenos Aires National Wildlife Refuge (BANWR) is located in the southern Altar Valley in Pima County roughly 150 km west of the previous study sites. This valley contains a much smaller patch of grassland habitat (ca. 100 km²) that occurs almost entirely within the refuge. BANWR has not been grazed by cattle since 1985. Study plots were located in the Borrego Grasslands section of the refuge between 1,050 and 1,210 m elevation.

Vegetation.—All three study areas were located in open semidesert or plains grassland vegetation (McClaran 1995). Rainfall fluctuates widely in this habitat, ranging between 200 and 400 mm per year; 50 to 60% of the rainfall usually falls during the summer monsoon season from July to September (McClaran 1995). This habitat is dominated by a variety of perennial bunchgrasses, although many forbs and several small woody perennials also are common. The most abundant grasses include several species of *Bouteloua* and *Eragrostis*, including the widespread exotic *Eragrostis lehmanniana*. The only woody plants taller than 1 m on the study plots were a few small mesquite trees (*Prosopis velutina*). These were more abundant at the slightly lower and drier BANWR site, where they tended to be concentrated in arroyos off of study plots. Several species of oaks (*Quercus*) occurred in arroyos near study plots at TRR.

Study species.—The study taxa consisted of six species of New World sparrows (Emberizinae): Cassin's Sparrow (*Aimophila cassinii*), Brewer's Sparrow (*Spizella breweri*), Vesper Sparrow (*Poocetes gramineus*), Savannah Sparrow (*Passerculus sandwichensis*), Grasshopper Sparrow (*Ammodramus savannarum*), and Baird's Sparrow (*Ammodramus bairdii*). Except for the smaller Brewer's Sparrow, these species exhibit a great deal of overlap in body size and bill size, which suggests a high degree of overlap in the seeds that comprise their winter diet (Pulliam 1983, C. Gordon unpubl. data). All of these species co-occur in mid-elevation grasslands of southeastern Arizona.

Baird's, Savannah, Vesper, and Brewer's sparrows are long-distance migrants that do not breed locally. They begin to arrive in southeastern Arizona in late August and are absent from the area by early May (Phillips et al. 1964). Cassin's Sparrows breed locally, but it is unknown whether the wintering individuals I studied were local breeders. Grasshopper Sparrows wintering in southeastern Arizona are composed of locally breeding (C. Gordon unpubl. data) and migrant birds, but the proportional representation of these two groups is unknown. Grasshopper, Baird's, and Cassin's sparrows are non-flocking species that are exclusively (Grasshopper and Baird's sparrows) or largely (Cassin's Sparrow) restricted to grassland habitat (Rising 1996). Savannah, Vesper, and Brewer's sparrows are flocking species that use a wider spectrum of vegetation types including shrubby and

weedy habitats as well as grassland (Rising 1996, C. Gordon pers. obs.).

Flush-netting.—At BANWR and TRR, I established six permanent 7-ha flush-netting plots. Each plot consisted of a 96-m net line with a 3.5-ha flushing zone fanning out on each side. For each day of flush-netting, crews of 13 to 30 people (average 22) assembled at 0830 MST at the field site to perform the following field protocol. Eight mist nets (2 × 12 m, 36 mm mesh) were set up along the net line at the first of the six plots. When nets were ready, the field crew fanned out along the 300-m back edge of one flushing zone. With people spread out evenly along the periphery of the flushing zone, a signal was given and the group walked through the flushing zone toward the net line, causing sparrows to flush toward the nets. The crew repeated the procedure for the second flushing zone on the other side of the net line.

After working both sides of a study plot, each netted bird was banded with individually numbered aluminum leg bands or their band number recorded if a recapture. We then disassembled the nets at the first plot and repeated the procedure at the next plot. In this way, we flush-netted all six plots at a study site in random sequence on each day of netting.

Between the first week of January and the first week of March 1996, flush-netting crews performed the above procedure on seven Mondays at TRR. At the same time of year in 1997 and 1998, flush-netting was done on seven Wednesdays at TRR and on nine Saturdays at BANWR. Between January and early March 1999, three flushing days were conducted on the same study plots at TRR and BANWR.

Radio telemetry.—I placed radio transmitters on three Baird's Sparrows and two Grasshopper Sparrows in late February 1997 at the EC and TRR study sites. I attached 1.0 g radio transmitters (model BD-2, Holohil Systems Ltd.) over the rump with leg-loop harnesses (Rappole and Tipton 1991) made of cotton candlewick. The radios have a battery life of six to eight weeks. Beginning the day after radios were attached, I attempted to locate each bird once per day on 12 days over a seven-week period. Locations of initial netting and all subsequent relocations were recorded using a global positioning system (GPS) unit accurate to within 2 m but not corrected for military signal scrambling. I conducted this same procedure on seven Vesper Sparrows and eight Savannah Sparrows between late January and early March 1998 at BANWR.

Recapture analysis.—Goodness-of-fit tests from program RELEASE (Burnham et al. 1987) showed that the mark-recapture data sets did not fit the assumptions of the Jolly-Seber models used in current mark-recapture analyses ($P < 0.01$ for all data sets). Therefore, I created a statistic called the recapture event rate (RER) that I used as an index of sedentariness, with higher RER values reflecting sedentary behavior and/or lower mortality during the study

period. RER is defined simply as the number of recapture events divided by the number of recapture opportunities. The number of recapture opportunities for a given bird is the number of netting days subsequent to the initial capture of that bird during a given season. This statistic measures the overall tendency of birds to be recaptured.

I tested the significance of differences in RER between data sets with a Monte Carlo simulation procedure. For each simulation, I compared a pair of data sets by preserving the mark-recapture patterns of individual birds but randomly reshuffling individuals between the two data sets. The RER statistic was then recalculated for the two sample data sets. This procedure was repeated 1,000 times for each pairwise test and then the observed RER values were compared with the distributions of RER values generated by the simulations.

Net learning potentially could confound RER statistics by reducing capture probability for previously captured birds. For data sets with large numbers of recaptures (>20), I tested for net learning effects by creating an expected binomial distribution of captures under the null hypothesis of no net learning (capture probabilities are independent of previous capture). To do this, I generated maximum-likelihood estimates of binomial parameters as outlined below.

A preliminary value of N (population size) was visually estimated from the asymptote of a plot of cumulative individual birds banded with time. The probability of capturing a given bird in a given flush, p , was calculated as x (the average number of birds captured on a sampling date) divided by N , and $1 - p = q$ was the probability of not capturing a given bird in a given flush. The probability of not capturing a given bird in i sampling dates is q^i , and $q^i N$, therefore, is the number of birds in the population that were never captured in i sampling dates. This number was then added to the total number of birds that were actually captured at least once in the sampling period to produce a new estimate of N . This procedure was then iterated with the new estimate of N until the parameter estimates converged on values that did not change in subsequent iterations. These parameters were then used to generate expected binomial frequency distributions for the number of captures for each bird in the data set. Observed distributions were then compared with the expected distributions using chi-square goodness-of-fit tests.

I calculated RER statistics for each data set by lumping all recapture events and opportunities over all individuals within data sets. This weights each recapture opportunity equally, but individual birds with more recapture opportunities (first captured earlier in the season) are weighted more heavily than individuals with fewer recapture opportunities (first captured later in the season). An alternative is to take

the average of the RER values of each individual in the data set. This statistic weights all individuals equally and might be called the average individual recapture event rate (AI). If individuals are drawn from a homogeneous population, these two statistics should be identical. However, if birds captured early in the season behave differently from those captured late in the season, these statistics would differ. The early birds have more opportunities to be recaptured than the late birds and are, therefore, heavily weighted in the RER but not in the AI.

I used a simulation procedure to test for statistically significant differences between the RER and AI statistics for all data sets with at least 20 recapture events. For each simulation, I preserved the exact structure of initial captures by date for all individual birds within a given data set. I simulated recapture data for each data set by setting the probability of recapture at each opportunity equal to the RER for that data set. I repeated this procedure 1,000 times and compared observed differences between AI and RER with the sampling distributions of these statistics generated by the simulations.

RESULTS

Flush-netting.—Analysis of movement pattern was based on the first three field seasons of flush-netting, which yielded 2,641 captures of 2,006 individual sparrows among the six focal species and two study sites as listed in Table 1. Of the 574 within-season recaptures, only seven occurred at a plot other than the one in which the bird had been initially banded. Only two of these (one Grasshopper Sparrow and one Savannah Sparrow) required movement of more than 100 m. Therefore, I based subsequent analyses of movement patterns from the banding data on same-plot recaptures as described above.

The simulation tests showed pronounced interspecific differences in RER (Table 2). Cassin's Sparrows and Grasshopper Sparrows were the most sedentary, followed by Baird's Sparrows, Vesper Sparrows, and finally Savannah Sparrows and Brewer's Sparrows. Within species, RER varied little among data sets (Table 3). I found no significant differences in RER between data sets (year \times study site) for any species except Savannah Sparrow, which was significantly more sedentary at the TRR study site than at BANWR. This pattern was consistent across years.

Five data sets (four for Grasshopper Sparrow, one for Cassin's Sparrow) contained

TABLE 1. Number of individuals captured and within-season recaptures for six grassland sparrows. Data are number of individual birds, with number of recapture events in parentheses. TRR = The Research Ranch, BANWR = Buenos Aires National Wildlife Refuge.

Study site	1996	1997	1998	Total*
Cassin's Sparrow				
TRR	0 (0)	0 (0)	2 (3)	53 (34)
BANWR	—	9 (3)	43 (28)	
Grasshopper Sparrow				
TRR	164 (71)	16 (8)	388 (149)	989 (466)
BANWR	—	278 (153)	189 (85)	
Baird's Sparrow				
TRR	36 (5)	15 (3)	28 (7)	100 (21)
BANWR	—	9 (2)	18 (4)	
Vesper Sparrow				
TRR	1 (0)	7 (0)	141 (14)	420 (37)
BANWR	—	194 (15)	83 (8)	
Savannah Sparrow				
TRR	29 (2)	7 (0)	105 (9)	365 (14)
BANWR	—	106 (1)	119 (2)	
Brewer's Sparrow				
TRR	0 (0)	0 (0)	0 (0)	79 (2)
BANWR	—	72 (2)	8 (0)	

* Species totals for both study sites. The total number of individuals captured for each species is slightly less than the sum of subtotals because individuals captured in multiple field seasons are counted separately in each data set in which they occurred, but only once in the totals.

enough recapture events to use the maximum-likelihood net-learning tests described above. In all of these data sets, observed distributions of captures were not significantly different from those expected under the null hypothesis of independence of capture events (Table 4). This suggests that a strong net-learning effect was not present for Cassin's Sparrows and Grasshopper Sparrows.

Each recapture event and opportunity for recapture can be defined by the amount of time elapsed between it and the initial capture of an individual bird. Thus, the RER statistic can be

broken down by weekly intervals to examine the probability of recapturing individuals as a function of the increasing time between first and subsequent captures. For a randomly wandering individual, the probability of recapture should decrease with time as it "diffuses" away from its starting point. Sparrows with fixed home ranges may experience some decrease in recapture probability due to mortal-

TABLE 2. Interspecific differences in sedentariness of sparrows as measured by recapture event rate (RER). CASP = Cassin's Sparrow, GRSP = Grasshopper Sparrow, BAIS = Baird's Sparrow, VESP = Vesper Sparrow, SAVS = Savannah Sparrow, BRSP = Brewer's Sparrow.

Species	RER	CASP	GRSP	BAIS	VESP	SAVS	BRSP
CASP	0.1110	—					
GRSP	0.0943	ns	—				
BAIS	0.0446	*	**	—			
VESP	0.0179	**	**	**	—		
SAVS	0.0085	**	**	**	*	—	
BRSP	0.0044	**	**	**	*	ns	—

ns, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$ (Monte Carlo simulations).

TABLE 3. Intraspecific variation in recapture event rate (RER) among years and between study sites for four grassland sparrows. Only data sets with at least 15 individuals and species with at least two such data sets are listed.

Species	1996	1997	1998
The Research Ranch			
Grasshopper Sparrow	0.1100	0.1270	0.0917
Baird's Sparrow	0.0382	0.0455	0.0588
Vesper Sparrow	—	—	0.0234
Savannah Sparrow*	0.0220	—	0.0216
Buenos Aires National Wildlife Refuge			
Grasshopper Sparrow	—	0.1000	0.0777
Baird's Sparrow	—	—	0.0404
Vesper Sparrow	—	0.0146	0.0192
Savannah Sparrow	—	0.0018	0.0036

* RER was significantly higher at The Research Ranch than at Buenos Aires NWR ($P < 0.05$; Monte Carlo simulations).

TABLE 4. Estimated binomial parameters and chi-square goodness-of-fit tests for net-learning effect in sparrows. The test compares observed distributions of individuals in capture frequency classes with expected distribution based on the assumption of independence of capture probabilities (no net learning).

Species	Data set	N^a	p^b	P
Cassin's Sparrow	1998 Buenos Aires National Wildlife Refuge	65	0.121	0.67
Grasshopper Sparrow	1998 Buenos Aires National Wildlife Refuge	315	0.097	0.30 ^c
Grasshopper Sparrow	1998 The Research Ranch	686	0.112	0.47 ^c
Grasshopper Sparrow	1997 Buenos Aires National Wildlife Refuge	415	0.116	0.25 ^c
Grasshopper Sparrow	1996 The Research Ranch	265	0.129	0.20

^a Estimated population size.

^b Estimated probability of capture of given individual on given netting day.

^c A single trap-happy individual removed from analysis.

ity, but otherwise the probability of recapture should remain relatively constant through time.

The probability of recapturing Grasshopper Sparrows (all data sets combined) decreased with time (Fig. 1). However, the RER at the longest time interval (eight weeks) was still higher than the total RER of the next-most sedentary species, Baird's Sparrow (Table 2). In the 1996 TRR data set for Grasshopper Sparrows and the 1998 BANWR data set for Cassin's Sparrows, RER remained almost constant through time (Fig. 1). In these cases, individuals were just as likely to be recaptured eight weeks following initial capture as in the first week post-capture. This demonstrates a strong tendency

for Grasshopper Sparrows and Cassin's Sparrows to remain within fixed home ranges during this time period. It also demonstrates that mortality was not significant in these cases. Grasshopper Sparrows and Cassin's Sparrows were the only species with enough recapture events for this analysis to be performed.

Cassin's Sparrows (1998 BANWR data set) did not show a significant difference between AI and RER, but Grasshopper Sparrows did show this difference. For all four of the large data sets for Grasshopper Sparrows, AI values were significantly lower than the RER ($P < 0.05$ for 1998 at BANWR; $P < 0.01$ for 1998 at TRR, 1997 at BANWR, and 1996 at TRR). Grasshopper Sparrows that were captured early had higher probabilities of recapture than birds that were not initially captured until later in the season.

Radio telemetry.—Of the 20 birds that received radio transmitters, three disappeared before the battery should have expired, and 10 were found dead before the battery expired, having been killed by predators. I relocated 18 birds at least twice for a total of 115 relocations.

To characterize movement patterns, I plotted net distance moved between each pair of locations as a function of time and performed linear regression (Fig. 2). The regressions for all four species had slopes below 2.6 m per day and R^2 values below 0.029. This suggests that individuals of all four species tended to remain within fixed home ranges. Thus, interspecific variation in sedentariness may have resulted from variation in home-range size among species.

To describe the extent of movement, I also compared the average net distance moved between all pairs of locations for individuals of each species. Because net distance moved was not correlated with time, these distances can be

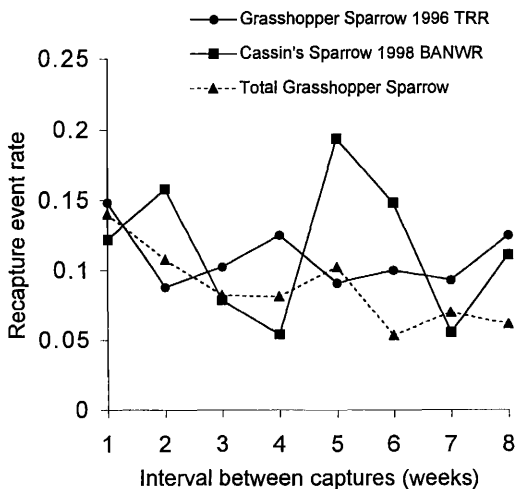


FIG. 1. Recapture event rate as a function of the time interval between first and subsequent recapture events for total Grasshopper Sparrows and Grasshopper Sparrows in 1996 at The Research Ranch (TRR) and Cassin's Sparrows at Buenos Aires National Wildlife Refuge (BANWR).

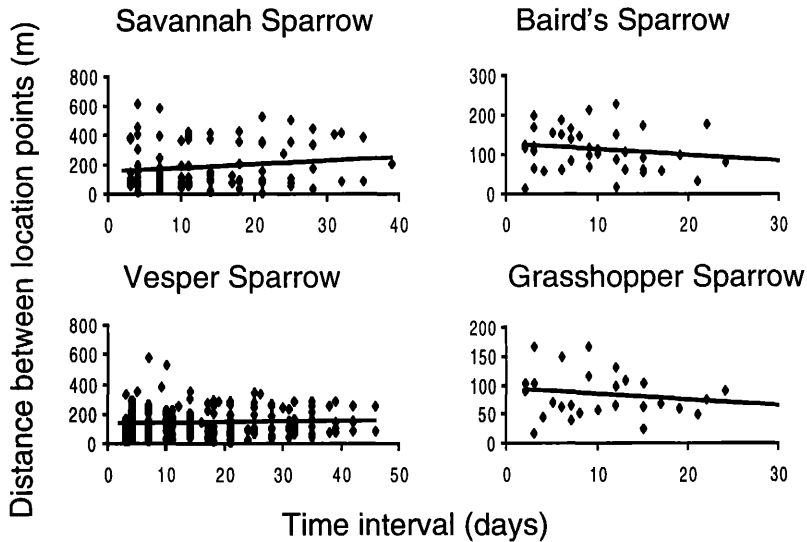


FIG. 2. Net distances (distances between each pair of radio telemetry relocations) moved with time for four grassland sparrows.

thought of as the net distance moved between any two locations of a bird. These data ranked species from most to least sedentary in exactly the same order as the RER from the netting data in Table 2. The Grasshopper Sparrow was the most sedentary with an average net movement of 84 m, followed by Baird's (113 m), Vesper (142 m) and Savannah (186 m) sparrows. All interspecific differences were significant (two-tailed t -tests, $P < 0.05$). These observed average distances were overestimates because of GPS signal scrambling and the error of the GPS unit. GPS locations for a fixed point taken on the days of radio telemetry showed an average net movement of 50.2 m.

It is important to note that mortality cannot be distinguished from emigration as sources of low RER. Corroboration of interspecific differences in RER by the telemetry data suggests that RER does indeed reflect differences in mobility among species. Furthermore, the constancy of RER with weekly intervals suggests that the amount of mortality that occurred during the study period was extremely small, at least for Cassin's Sparrows and Grasshopper Sparrows (Fig. 1).

DISCUSSION

Variation among individuals.—One possible explanation for differences in recapture probab-

ity among individual Grasshopper Sparrows is that two types of individuals are present in winter, some with fixed home ranges and others that move nomadically. This is consistent with many territorial systems which "floaters" represent an excess of individuals relative to the number of available territories (Shutler and Weatherhead 1994, Stutchbury 1994, Westcott and Smith 1994). A discrepancy in movement behavior among individual Grasshopper Sparrows also may correspond to a difference between migrant and resident populations that coexist on these study sites in winter. It is also possible that differences in recapture probabilities among individuals were caused by other behavioral differences that could lead to different capture probabilities, such as different flushing responses or flying heights.

Extent of movement.—Cassin's Sparrows and Grasshopper Sparrows, and to a lesser extent Baird's Sparrows, were the most sedentary species. The extent and pattern of movements in these sparrows are consistent with those observed for desert rodents (Brown 1989, Brown and Zeng 1989). Thus, the notion that these birds are highly mobile "cream-skimmers" in this system may not be accurate (Mares and Rosenzweig 1978, Brown et al. 1979, Thompson et al. 1991). Some birds, particularly Cassin's Sparrows and grassland-obligate Baird's Spar-

rows and Grasshopper Sparrows, may behave more like the rodents in the above models of desert granivore coexistence, playing the roles of highly sedentary but highly efficient foragers.

The sparrows in this study exhibited significant interspecific variation in movement patterns. Nonetheless, telemetry data indicated that even the least sedentary species tended to remain within fixed home ranges (Fig. 2). This pattern might seem to conflict with the nomadic behaviors that have been documented in seed-eating birds in other rainfall-limited ecosystems (Davies 1984, Clark 1997, Dean 1997). In such systems, nomadism has been suggested as a way for consumers to cope with extreme spatial and temporal variability in resource distribution (Noy-Meir 1973, Davies 1984, Clark 1997, Dean 1997). Nonetheless, the observed sedentariness of sparrows in this study was not inconsistent with nomadic movements at different scales of time and space. In fact, sparrows may have combined between-year regional scale mobility with within-winter sedentariness to effectively exploit the specific scales of environmental heterogeneity and variability in this system. The dramatic fluctuations in sparrow abundance across sites within years and across years within sites (Table 1) suggested that the distributions of sparrows varied significantly between years at a regional scale. This pattern could result if sparrows underwent a brief period of exploratory movement upon arriving on the wintering grounds. This would allow them to match their distribution to the variable and patchy distribution of resources in any given year, driven by the summer rains.

In contrast to the between-year variability of the summer rainfall pattern, the pattern of summer rainfall remains fixed over the course of any given winter. For this reason, the distributions of seeds and grass cover remain relatively constant during the course of a winter. It is unlikely that sparrows alter this distribution significantly during the course of most winters, because they consume only 20 to 30% of the seed resources in many winters (Pulliam and Dunning 1987). Fixed home ranges during midwinter may be an adaptation to exploit this within-winter constancy by remaining sedentary and conserving energy.

Plasticity of movement patterns.—Although Sa-

vannah Sparrows showed significantly different local movement patterns between study sites, movement patterns of Grasshopper, Baird's, and Vesper sparrows were fixed across years and study sites (Table 3). This behavioral constancy is remarkable given the radical fluctuations (up to 20-fold) in abundance of sparrows across sites and years (Table 1). Fluctuations near an order of magnitude were observed for all focal species. Given the importance of densities of interspecific and intraspecific competitors on habitat selection in various theoretical and empirically demonstrated situations (Fretwell and Lucas 1970, Rosenzweig 1981, Pimm et al. 1985), it is surprising that such variation in the density of potential competitors would have no effect on movement behavior. One potential explanation for this pattern is that competition among sparrows may not be an important ecological factor in this system. Another possibility is that the movement behavior of Grasshopper, Baird's and Vesper sparrows is fixed because of various physiological, morphological, or other constraints, and that these species are unable to adapt their movement behavior quickly enough to track rapid changes in their environment. A third possibility is that the density adjustments that birds make in response to environmental variability obviate the need for additional behavioral adjustments.

Movement patterns and community structure.—Following Hutchinson's (1951) concept of a fugitive species, several theoretical studies have suggested that variation in movement patterns functions as a niche axis, allowing the coexistence of otherwise ecologically identical species in competitively structured communities (e.g. Levins and Culver 1971, Horn and MacArthur 1972, Tilman 1994). This coexistence is permitted by a tradeoff between efficiency at exploring for new patches and efficiency at exploiting a particular patch (Brown 1989, Tilman 1994). In other words, the best colonizer of new patches cannot also be the best competitor within patches.

In recent decades, the validity of equilibrium-based, competition-structured coexistence theories has been questioned (Connell 1975, Connor and Simberloff 1979, Strong 1983), particularly in highly fluctuating environments such as grassland and shrubsteppe (Wiens 1974, Rotenberry and Wiens 1980). The ratio-

nale for this argument is that in communities where biological interactions never reach equilibrium and consumers do not saturate resources, competitive pressure should be low. Without competition, no reason exists for niches to be competitively structured. Resource partitioning is not required for species to coexist. The wide fluctuations in sparrow abundance across time and space (Table 1) suggest that winter grassland sparrow assemblages indeed are far from being in equilibrium. Furthermore, sparrows are not believed to saturate seed resources during most winters (Pulliam and Brand 1975, Pulliam and Parker 1979, Pulliam and Dunning 1987). Therefore, it may not be appropriate to invoke the notion of resource partitioning to explain the significant differences in movement patterns among species recorded in this study. In short, the notion of competitive coexistence may not apply to coexisting species of grassland sparrows.

Nonetheless, competitive structuring should not be ruled out completely. Competition does not need to be intense or constant to affect the distribution of niches in a community (Connell 1980). Pulliam (1985) suggested that competition and resource partitioning among sparrows wintering in Arizona grasslands are important only in rare years when seed production is extremely low and competition for seeds may be especially intense. Furthermore, even if predators limit sparrow populations below their ability to saturate food resources, niche partitioning may be required for coexistence (Holt 1977). Therefore, differences in movement patterns may function as an important coexistence mechanism for ecologically similar grassland sparrows wintering in Arizona grasslands.

Even in the absence of niche partitioning in response to competition, the tradeoff between within-patch efficiency and among-patch searching may pose significant constraints for sparrows. Species that sacrificed some ability to explore the landscape may have done so to gain efficiency at the local scale. Indeed, the three most sedentary species in my study, Cassin's Sparrow, Grasshopper Sparrow, and Baird's Sparrow, are short-winged relative to other sparrows and are known to be weak fliers (Rising 1996). This leads to the prediction that these sedentary species are more locally efficient than are the more mobile sparrows, and

that they should be able to make a living on patches with lower resource densities.

Significance of movement strategies in a fragmented landscape.—Recent models have shown that sedentary species, including competitive dominants, are more adversely affected by landscape fragmentation than are more mobile species (Dytham 1994; Tilman et al. 1994, 1997; Moilanen and Hanski 1995). If suitable patches become widely separated in space, sedentary species are unable to find and colonize them. Danielson (1991) and Pulliam and Danielson (1991) modeled the effect of sedentary behavior on habitat selection by varying the amount of patches that individuals sampled before they chose a patch to inhabit. In their simulations, individuals that sampled a high number of patches occupied a higher percentage of the better habitat than individuals with low patch sampling. In landscapes where high-quality habitat patches were rare, the ability to find good patches limited population growth, and a high level of exploratory patch sampling was necessary for species to survive.

This has an important implication for the management of highly sedentary species such as Grasshopper Sparrows, Baird's Sparrows, and Cassin's Sparrows. In addition to being affected by pure increases or decreases in their preferred habitat types, sedentary species may suffer increased adverse effects relative to more mobile species if the distribution of suitable habitat becomes fragmented. One important caveat is that in this study, the mobility of sparrows was measured at the scale of several hectares. This small scale may not accurately reflect regional movements, which perhaps are more appropriately matched to the spatiotemporal scale of environmental variability in this system. Figure 3 suggests that these local, within-year mobility differences indeed reflect movement constraints at the regional scale as well. At the between-year and between study site scales, abundances of the more locally sedentary species were more poorly correlated with summer rainfall (a negative correlation in the case of Baird's Sparrow) than were abundances of the more mobile species. Alternative hypotheses cannot be ruled out, but a likely explanation for this pattern is that sedentary behavior constrains the ability of Grasshopper Sparrows, Baird's Sparrows, and Cassin's Sparrows to match their winter spatial distributions to

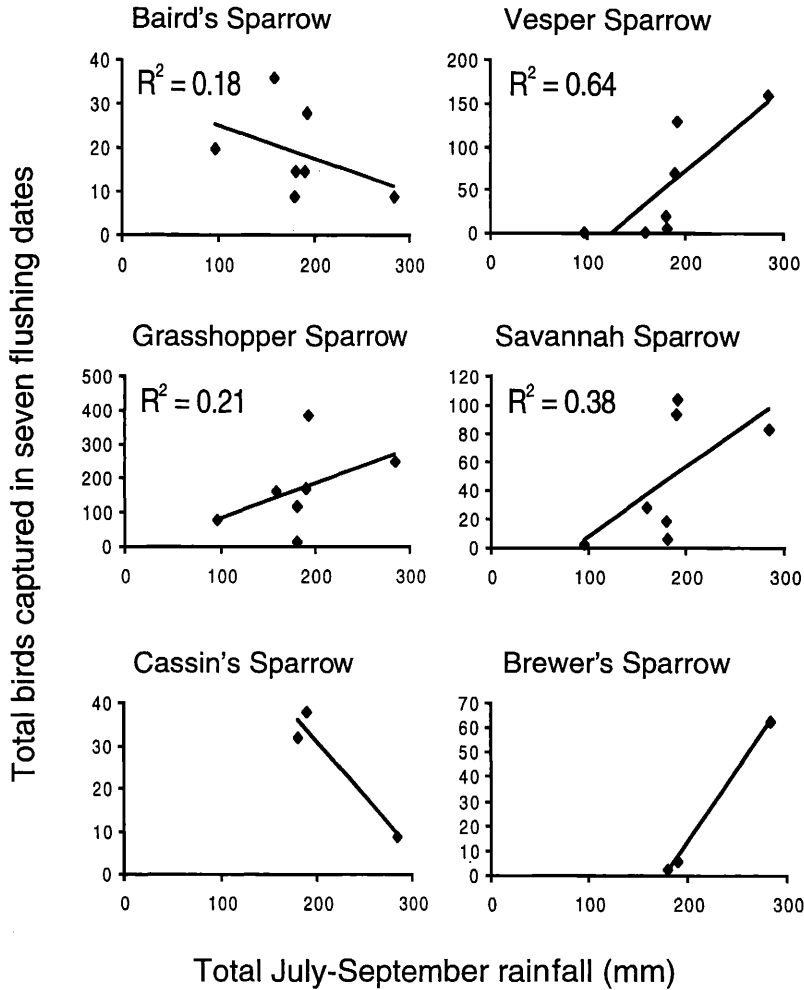


FIG. 3. Relationship between summer rainfall and sparrow captures in subsequent winter from January to March 1996 to 1999. The three most sedentary species at left are much more poorly (or negatively) correlated with rainfall than the three more mobile species at right, suggesting that movement constraints play an important role in large-scale habitat selection. Each data point represents the total number of individuals captured in seven flush-netting sessions at a single study site per winter. The 1997 and 1998 BANWR data sets were standardized to seven flush-netting dates by discarding data from the eighth and ninth netting sessions. I extrapolated the 1999 totals from three to seven dates by dividing the three-week totals by the average proportion of birds in a seven-week data set captured by the third week. To calculate these averages, I divided the total number of birds caught by the third week by the total number of birds that had been caught by the seventh week in all data sets with at least seven netting dates. July to September rainfall data are from rain gauges at the headquarters of TRR and BANWR, 1 to 5 km from all study plots. R² values are given only for species with seven data points. Brewer's Sparrows and Cassin's Sparrows do not occur regularly at the higher-elevation TRR study site; hence, only three data points representing three flush-netting seasons at BANWR are presented.

the distribution of preferred conditions (high rainfall areas) in the landscape.

The grassland-obligate Grasshopper Sparrows and Baird's Sparrows undoubtedly have suffered from widespread conversion of grass-

lands to shrublands in southeastern Arizona over the past 120 years (Bahre 1991). The sedentary behavior of these species suggests that managers need to consider the distribution of habitat patches in the landscape, as well as the

structural composition of the patches. In other words, it's not just a question of creating the right conditions in a particular patch: it also may matter where the patch is relative to other patches within the range of existing populations of sparrows. Managing for relatively sedentary species such as Cassin's Sparrow, Baird's Sparrow, and Grasshopper Sparrow may require maintaining a landscape with aggregated patches of suitable grassland, or core areas, as opposed to a landscape with an equal area of grassland spread out among widely separated small patches.

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