POST-FLEDGING DISPERSAL OF GRASSHOPPER SPARROWS (AMMODRAMUS SAVANNARUM) ON A RESTORED GRASSLAND IN MARYLAND

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ABSTRACT.—Little is known about the post-fledging period in most bird species, and almost nothing has been reported for the family Emberizidae, including New World sparrows. We report here, for the first time, the sizes (wing length and body weight) of, and the distances traveled by fledgling Grasshopper Sparrows within their hatch summer in a restored Atlantic Coastal grassland in Maryland. In the years 2002–2009, we recaptured 24.3% of the 799 banded nestlings in the grasslands at least once within their hatch year. Body weight was not correlated with wing length, wing length did not change with time of recapture, and the average fledgling gained weight by 14% in 100 days. Smaller than average birds were missing from late summer recaptures. As expected, the distance traveled increased significantly with time, but the average fledgling was recapture 346 m from its nest. The average time of recapture was 33 days after fledging; the youngest recapture was 5 days after fledging and it dispersed a net 580 m from its nest; the longest and fastest distance recorded was 1,615 m from the natal nest in no more than 20 days; the longest recorded retention was 97 days by a local that moved a net distance of 753 m. We conclude that most fledglings in this population of Grasshopper Sparrows remain within their natal habitat for most of the months prior to their pre-formative molt, and that at least 1:4 of them survive at remarkably high rates. *Received 13 July 2012. Accepted 13 November 2012.*

Key words: Ammodramus savannarum, Chester River Field Research Center, Grasshopper Sparrow, post-fledging dispersal, restored grassland.

The post-fledging period is probably the most challenging time in the life of most birds departure from the protection, thermoregulation, and allo-feeding in the nest by social parents brings abrupt exposure to the hostilities of predators, parasites, adverse ambient climates, and imminent starvation. In songbirds, the several weeks after fledging also include the critical receptive period of learning and discriminating the sound environment, often necessary to avoid predators, secure mates, and reproduce in adulthood (Soha et al. 2009). For most bird species, study of fledglings is notoriously difficult, and the behavior and ecology of fledglings are largely unknown. Fledglings usually disappear from sight, are cryptic and secretive, and presumably disperse increasing distances from their nest sites; hence re-locating them at all becomes exponentially more difficult with time. In contrast to the substantial literature on the return rates of nestlings to natal sites (and the observed dispersal and settling away from natal sites) as breeding adults in subsequent years, little is known about dispersal distances and timings of departure of post fledgling songbirds within their hatch-year.

We report here the results of recapturing juvenile Grasshopper Sparrows, (Ammodramus savannarum pratensis; GRSP) after they fledged within the summer of their hatching on an experimentally restored, coastal grassland in Maryland. Based on large sample sizes of banded nestlings and daily efforts of recapture, our results are the most quantitative estimates of distances and time of retention of fledglings at their natal sites in the species in the genus Ammodramus. Except for a brief comment by Perkins and Vickery (2001) that five of 50 nestling Florida Grasshopper Sparrows were resighted within 2,000 m of their nests, no other reports have been published that change Vickery's (1996) summary that nothing is known about post-fledgling activity of Grasshopper Sparrows. We found no reports of post-fledging activity for any other species of Ammodramus. For the sparrow family Emberizidae, only Arcese (1989) reported that fledglings of non-migratory Song Sparrows (Melospiza melodia) on Mandarte Island establish winter residencies (home ranges) a couple of

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territories away from their birth-place shortly after their post-juvenal molt. Our study is the first quantitative report on fledgling activity in a migratory emberizine species prior to the preformative molt. Exceptionally detailed among the few reports of post-fledging activity and withinhatch-year dispersal of other passerines, Dhondt's (1979) observations of fledgling non-migratory Great Tits (*Parus major*) in Holland found that females travel farther from nests than males, and that neither brood size, fledgling date, nor fledgling size had any effects on movement.

We asked the questions: (1) Do fledglings disperse gradually from their birth places or do they reside for months in their natal habitat, the vicinity of their site-faithful, multi-brooded parents until autumn migration? (2) Do fledglings from early summer nests (first nests of multibrooded parents) disperse faster and farther, or conversely linger in natal areas longer, than fledglings from later summer nests? and (3) How do measures of condition (size, mass) change during the post-fledging period?

METHODS

Study Site.—The Chester River Field Research Center (CRFRC) was established in 1999 on CRP portions of Chino Farms, Inc., located in Queen Anne's County in eastern Maryland, USA (39.13 N, 79.00 W). Part of a large-scale, experimental effort to restore the mid-Atlantic coastal grasslands, an extinct ecosystem that once prevailed on the eastern North American seaboard (Askins 1999), the CRFRC grasslands comprised 91.7 ha and were subdivided into 12 contiguous experimental fields. Gill et al. (2006) give details about climate of the area, vegetation changes in the grasslands, and bird colonization during the first 6 years of grassland establishment.

CRFRC Grasshopper Sparrow.—Field studies of all the birds using the 91.7 ha of restored CRFRC grasslands have been conducted since the site's creation in 1999. GRSP have sustained a breeding population of 80 ± 10 pairs annually. We banded 2,284 GRSPs from 2002 to 2009 by using mist nets and finding nests. Long-lived (Small et al. 2009b) and new adult GRSPs appeared in the third week of April each year from unknown wintering grounds. Nesting commenced by early May, and pairs initiated multiple broods until early September. Thus 2–3 clutches of GRSP were regularly produced by socially monogamous adults (Small et al. 2009a) in a summer. Demographic and social structure, mate fidelity, and rates of extra-pair fertilizations will be reported elsewhere. GRSPs have not been recorded yet on the CRFRC Grasslands from November to mid April.

Finding Nests.—Our technique of finding GRSP nests changed over the 11-year study. From 1999 through 2002, nests were found by observers watching for nesting behavior (parents persistently chipping and/or carrying food or fecal sacs) or accidently flushing females when walking through fields. In 2001–2003, lines of people spaced 5-10 m apart marched across all fields in parallel contiguous transects intent on flushing brooding females from hidden ground nests. In 2003-2007, the spacing between investigators was tightened to shoulder-to-shoulder because we discovered GRSP females on nests often failed to flush between observers in the wider spaced lines. This simple change led to a 5-fold increase in nests found, especially in densely populated fields. In 2007-2009, we returned to patient observation of adult activity to find nests because the established prairie grasses had become thick and 2 m tall, making the marching-line technique ineffective. In 2009, a weighted rope was dragged across the short grass areas of an airstrip to flush females off nests (Koford 1999). The locations (latitude/longitude) of nests and their contents were recorded as waypoints by a hand-held Garmin GPS 12XL. At age 7 ± 1 days posthatching, nestlings were banded with USGS aluminum bands, bled for genetic parentage tests, and put back directly into the nest; weights were not taken at these times.

Recapturing Fledglings (Hatch-Years = HYs).— After target netting and color-banding adult GRSP in April and May, long rows of 4-shelf, 12 m long, 2.6 m high, 30 mm mesh, nylon Japanese mist nets (Manomet Bird Observatory, MA) were set up along the internal edges of the restored grassland fields to capture resident, foraging, and transient birds. Sixteen nets were strung in tandem on 3.1 m poles anchored on temporary 1.5 m rebars that were pounded 1 dm into the sandy soil. On 1 June of each year and starting along the margin of the westernmost field, we moved the row of 16 mist nets sequentially along the clover-covered firebreaks and access roads between fields until the easternmost field was reached 4.5 weeks later. Birds were mist-netted routinely for 2 days at each location in early summer, but occasionally a third day was added if the location was productive. In

early July, a second round was started again on the western side of the grasslands and followed the same course as the first round until the end of August. Because numerous HYs were in the Grasslands in late summer, the mist nets were kept in place during the second round for a minimum of 3 days. Sometimes additional nets were placed in "hot spots" between fields where large numbers of HYs were concentrated. Nets were routinely opened 30 min before sunrise and closed in late morning when temperatures became hot or wind too strong. We consider putative biases in this protocol on the site locations of recaptures in Discussion. When recaptured as free-flying banded HYs, local GRSPs were identified, measured, and released immediately; free-flying unbanded HYs were processed but not included in this analysis because their nest of origin and parentage were unknown. The locations at which the free-flying HY GRSPs were caught in the net were recorded as GPS waypoints. High resolution GPS units became available in 2002; therefore, we have no accurate locations for recaptured birds for years 1999, 2000, and 2001. Data from Microsoft Excel sheets were transferred to ESRI Arcview v3.2 maps, where the distance tool was used to measure the distance between nest sites and recapture sites of fledglings banded as nestlings.

RESULTS

Seven hundred and seventy-four of the 791 nestling GRSP (Locals) banded in the nest in 2002 to 2009 fledged successfully. The number of banded fledglings each year was 97% predictable from the number of nests found each year. The 194 Locals captured at least once after fledging vielded 257 recapture records; 75% of fledglings were never recaptured. The numbers of individual fledglings (number of total recaptures) recaptured by year were: 2002 - 2(2); 2003 - 0(0); 2004 - 2(2); 200468(87); 2005 - 45(65); 2006 - 3(4); 2007 - 7(10); 2008 - 41(51); 2009 - 28(38). The frequency distribution of the fledgling repeat records was: only once 142, twice 42; three times 9; four times 1. In addition to these Locals we banded exactly 1,000 free-flying HYs of unknown nest origin on the Grassland study site in the years 2002–2009.

The distance fledglings dispersed from their nests was positively correlated with time (Fig. 1). The mean number of days a repeat fledgling was found on the Grasslands was 33 days \pm 2 SD 28 days) after fledging. The mean net distance a repeat local traveled within the grasslands was

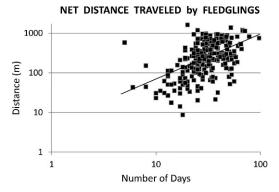


FIG. 1. The distance traveled by fledglings in their HY summers 2002–2009 was a very highly significant positive function with time: y = 1.14x + 1.57, $r^2 = 0.255$, n = 257, F = 40.96, P < 0.001.

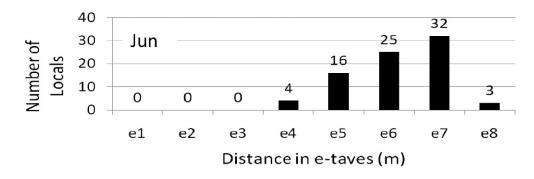
346 m±581 m. The youngest bird was recaptured 5 days after fledging and had traveled a net 510 m. The longest distance traveled by a fledgling was 1,615 m and accomplished in no more than 20 days in 2008; the shortest net distance was only 9 m after 18 days. Our longest recorded resident fledgling on the grassland stayed at least 97 days and traveled a net minimum 753 m away from its nest in 2002. Birds that fledged from their nests in early summer (June, Fig. 2A), mid-summer (July, Fig. 2B), and late summer (August, Fig. 2C) had similar monomodal frequency distributions of dispersal distances, but the shift in the mode to the left from June to August was very highly significant (Contingency $\chi^2 = 28.4$, df = 6, P < 0.001).

The weights of fledglings were positively correlated with the time of their recapture; because no weights of nestlings at day 6–7 were taken, these weights are only a pooled sample of the 8 year populations of free-flying HYs of known age and nest origin. Birds of less than average weight were noticeably absent later in the summer (Fig. 3A). There was no change in the length of wing chord with time of recapture (Fig. 3B), and there was no correlation of body weight with wing length in recaptured fledglings (Fig. 3C).

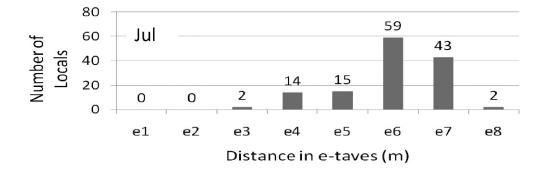
DISCUSSION

Production of fledglings varied greatly across years. Especially poor years were 2002 and 2006 which were record-breaking drought years vegetation on the grasslands was brown and









С

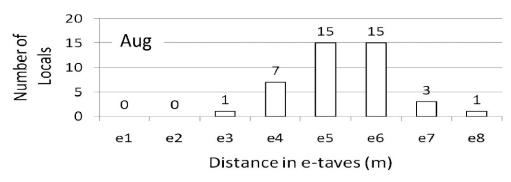


FIG. 2. Frequency distribution of fledgling distance traveled from nest by month in 2002–2009. Abscissa is in e-taves (i.e., powers of e, the base of natural logarithms, e = 2.71828: $e^1 = 1-3$ m, $e^2 = 4-7$ m. $e^3 = 8-20$ m, $e^4 = 21-55$ m, $e^5 = 56-148$ m, $e^6 = 149-403$ m, $e^7 = 404-1,097$ m, $e^8 = 1,098-2,981$ m). Note the different scales of the ordinates. A. Fledges in June. B. Fledges in July. C. Fledges in August.

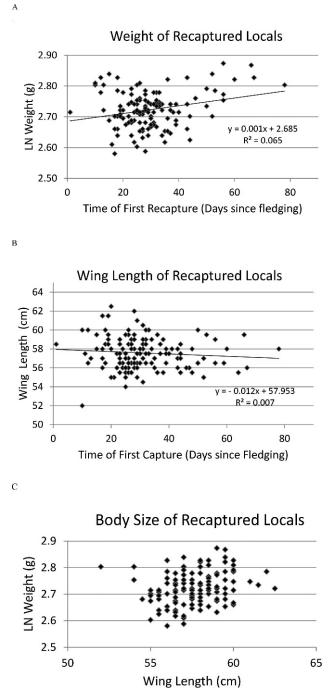


FIG. 3. Size (wing chord length) and condition (weight) of locals upon first recapture as fledglings in their HY summers 2002–2009. A. The natural logarithm of weights of Locals upon first recapture. The weights of recaptured Locals increased significantly with time of recapture: n = 131, F = 3.92, P = 0.048. Fledglings of greater weight stayed in the grasslands longer than fledglings of lighter weight. B. Wing length of GRSP fledglings upon first recapture. The regression was not significant: n = 148, F = 1.17, and P = 0.13. C. The body size in two dimensions (ln weight and wing length) of GRSP locals upon first recapture. The coefficient of determination $r^2 = 0.051$ was not significant: n = 130, F = 0.002, P = 0.078.

wilting by mid July, insect densities were low, and we presume mortality of fledglings was exceptionally high. Also a poor production year, 2003 was the coldest and wettest summer on record - the Grasslands were flooded, and ground-nesting birds suffered high nest failures. Our data are therefore concentrated on the five "normal" years of moderate temperatures and rain, namely 2004, 2005, 2007, 2008, and 2009 when large numbers of chicks fledged and were recaptured. The relative low frequency (1–4) of recaptures per individual was unquestionably because of our protocol of sampling the entire grasslands only twice each summer with short 2–3 day efforts at each locality.

As we expected, fledglings were captured at greater distances with time. On average, the weight of fledglings was greater the longer they were away from the nest, but this gain of weight was, quite unexpectedly, independent of body size as measured by wing chord of the juvenal remiges. We surmise that remiges grow to full length quickly and body mass increases more slowly during the post-fledging period. We interpret the noticeable absence of light weight juveniles in late summer compared to early summer as indicating light-weight fledglings suffer higher mortality in the weeks after fledging than do heavier-weight juveniles. The alternative explanation, that runts and/or undernourished juveniles would disperse greater distances, or leave the natal grassland habitat faster than wellnourished young, seems unlikely.

Most recaptured fledglings were encountered within a couple hundred meters of their natal nests throughout the summers (Fig. 2); the logarithmic distribution of dispersal distances (Figs. 2A, B, C) did change according to the month of fledging (Contingency $\chi^2 = 28.4$, df = 6, P < 0.001). The mode of the distributions shifted left as the summers progressed simply because the time between fledging and possible recapture was shorter within August (Fig. 2C) than from June to August (Fig. 2A). We interpret the unimodal distance distributions of each month's fledglings as reflecting the natural behavior of fledglings, because we can discern no bias in our capture technique with the moving line of mist nets. At any point in time, the nets were close to some nests but varying (including long) distances from most other nests in the grasslands. Hence, every day the nets were as likely to intercept moderate and long distance dispersers as they would fledglings close to their nests. Juvenile HY#546 dispersed from one end of the Grasslands to the other end in a mere 20 days, while HY#165 dispersed about half the length of the Grasslands in the opposite direction, was recaptured twice at that new site, and stayed in the grasslands for at least 97 days.

That 25% of Locals were recaptured at least once after fledging indicates a surprisingly high rate of survival of post-fledged young and that most surviving fledgling GRSPs stay within a couple hundred meters of their natal nests for the months before their pre-formative (post-juvenal) molt in early autumn. For this reason, we interpret that most of the 1,000 free-flying HYs (in addition to the Locals) that we capture in the grasslands were probably fledged from nests in the Grasslands that we failed to find. Interestingly, our change in nest-finding technique in 2007-2009 reversed the ratio of banded HYs/Locals: from 2002-2006 the ratio was 815/403, whereas 2007-2009 the ratio was 185/388. It seems in recent years, we succeeded in banding a greater proportion of total GRSP production in the nest before they fledged. This short distance dispersal or intimate positioning coincides with the site fidelity of adults (their social parents) on the Grassland even though the parents are multiplebrooding (Small et al. 2009a). A project planned for upcoming field seasons is to place transmitters on fledglings and their parents to record daily movements and determine precisely the social associations fledgling GRSP are making during their sensitive receptive and learning stages.

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