

Agricultural management affects evolutionary processes in a migratory songbird

NOAH G. PERLUT,[†]§ COREY R. FREEMAN-GALLANT,[‡] ALLAN M. STRONG,[§]
THERESE M. DONOVAN,^{§*} C. WILLIAM KILPATRICK[¶] and NATHAN J. ZALIK[§]

^{*}United States Geological Survey, [†]Vermont Cooperative Fish and Wildlife Research Unit, Burlington, VT 05405, USA, [‡]Department of Biology, Skidmore College, Saratoga Springs, NY, 12866, USA, [§]The Rubenstein School of Environment and Natural Resources, [¶]Department of Biology, University of Vermont, Burlington, VT, 05405, USA

Abstract

Hay harvests have detrimental ecological effects on breeding songbirds, as harvesting results in nest failure. Importantly, whether harvesting also affects evolutionary processes is not known. We explored how hay harvest affected social and genetic mating patterns, and thus, the overall opportunity for sexual selection and evolutionary processes for a ground-nesting songbird, the Savannah sparrow (*Passerculus sandwichensis*). On an unharvested field, 55% of females were in polygynous associations, and social polygyny was associated with greater rates of extra-pair paternity (EPP). In this treatment, synchrony explained variation in EPP rates, as broods by more synchronous females had more EPP than broods by asynchronous females. In contrast, on a harvested field, simultaneous nest failure caused by haying dramatically decreased the overall incidence of EPP by increasing the occurrence of social monogamy and, apparently, the ability of polygynous males to maintain paternity in their own nests. Despite increased social and genetic monogamy, these haying-mediated changes in mating systems resulted in greater than twofold increase in the opportunity for sexual selection. This effect arose, in part, from a 30% increase in the variance associated with within-pair fertilization success, relative to the unharvested field. This effect was caused by a notable increase (+110%) in variance associated with the quality of social mates following simultaneous nest failure. Because up to 40% of regional habitat is harvested by early June, these data may demonstrate a strong population-level effect on mating systems, sexual selection, and consequently, evolutionary processes.

Keywords: agricultural management, evolutionary processes, female breeding synchrony, Savannah sparrow, sexual selection, social and genetic mating systems

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Introduction

As humans exert greater influences on ecological systems (Hannah *et al.* 1995), co-evolved relationships between vertebrates and their breeding habitats can become decoupled. Although human-mediated effects on ecological processes have been well documented (Vitousek *et al.* 1997; Parmesan & Yohe 2003), in general, little is known about the evolutionary consequences of anthropogenic activities on vertebrate populations. One widely cited example of negative ecological effects is that of agricultural grasslands

and the songbirds that use these habitats for breeding (Bollinger *et al.* 1990; Perlut *et al.* 2006). In fact, breeding in agricultural grasslands is thought to be a main contributor to long-term grassland bird population declines (Bollinger & Gavin 1992; Peterjohn & Sauer 1999; Murphy 2003), as all active nests fail due to the harvest (Perlut *et al.* 2006). Additionally, haying alters resource abundance and distribution by removing biomass and food. However, the evolutionary effects remain unknown. In this study, we explore the evolutionary consequences of agricultural management practices on breeding songbirds.

Hay harvests, by altering the distribution of resources and the synchrony of breeding females, may influence mating systems (Verner & Willson 1966; Emlen & Oring

Correspondence: Noah G. Perlut, Fax: 802.656.8683; E-mail: nperlut@uvm.edu

1977; Fishman & Stone 2005). Most polygynous avian species, in which males establish social pair bonds with multiple mates, are found in habitats with high resource variation among territories, with the best territories holding sufficient food resources for multiple mates (Emlen & Oring 1977). When a small percentage of males monopolize resources and multiple females, a greater opportunity for sexual selection and increased variance in male fertilization success arises (Emlen & Oring 1977). However, if females become highly synchronous (with overlapping fertile periods; Kempenaers 1993), the social monogamy rate may increase because males have little opportunity to seek additional mates (Emlen & Oring 1977), resulting in low variance in male fertilization success. Thus, while resource abundance and distribution define a habitat's polygyny potential, female synchrony may determine whether this potential is realized.

Variance in male fertilization success, however, is not always explained by the social mating system. At the individual pairing level, parentage is often incorrectly assigned as a result of extra-pair paternity (EPP), which occurs when an egg is fertilized by a male other than the social mate. EPP defines the genetic mating system of a breeding population and female breeding synchrony is a critical component either increasing or decreasing the EPP rate (Stutchbury & Morton 1995). Synchrony increases EPP rates if females can assess male quality simultaneously and mate accordingly (Stutchbury *et al.* 1997); offspring are sired by a small proportion of available males, increasing variance in fertilization success. Alternatively, synchrony decreases EPP if males increase time spent mate guarding, decreasing the amount of time seeking copulations (Kempenaers 1997; Weatherhead 1997); high synchrony results in low social and genetic polygyny, lowering variance in fertilization success.

Because the extent of social and genetic polygyny influences variation in male fertilization success, mating systems can affect evolutionary processes. The extent of variation in male fertilization success affects the magnitude of sexual selection (Webster *et al.* 1995); therefore, mating systems can directly influence the strength of selection on phenotypes important to male–male competition and female choice. Changes in the ecological conditions that shape social and genetic mating systems may alter the characteristics that define sexual selection, thereby influencing a species' evolutionary trajectory.

Birds breeding in managed agricultural systems provide a unique natural experiment with which to determine how altering resource distribution and breeding synchrony influence both ecological and evolutionary processes. Within this model, we studied the Savannah sparrow (*Passerculus sandwichensis*), a species with a mixed-mating strategy, asynchronous settlement, and biparental care (Wheelwright & Rising 1993; Freeman-Gallant 1998; Perlut *et al.* 2006).

Our objective was to identify plasticity in Savannah sparrows' social and genetic mating systems as a result of hay harvest and to determine the evolutionary significance of these behavioural responses.

From 2002 to 2005, we studied Savannah sparrows in one harvested field, first harvested ~1 June, and one unharvested field, where the field was managed after the breeding season. In the harvested field, we compared the social and genetic mating systems pre- and post-cutting (two discrete 'haying intervals') and quantified potential mechanisms, changes in breeding synchrony and resource distribution between the two periods. In the unharvested field, we followed settlement patterns throughout the season and determined how breeding synchrony, resource distribution, the social mating system, and the genetic mating system changed over time.

Materials and methods

Our research took place in the Champlain Valley of Vermont, USA, which contains 146 000 ha of managed grasslands (NASS 2007). We followed breeding adults in one harvested field (18.5 ha) and one unharvested field (17.6 ha). The two fields were 1.5 km apart, no birds switched fields within any given year, and female densities were similar between fields (see Perlut *et al.* 2006 for vegetation characteristics). These fields were representative of a majority of the Champlain Valley's hayland habitat, where 23% was managed in the harvested scheme (cut by early June) and 45% in the unharvested scheme (cut after the breeding season), and with similar breeding densities (female densities on harvested and unharvested fields across the valley were 0.30 and 0.29 per ha, respectively; Perlut 2007).

Adult birds were captured with mist nets and fitted with unique combinations of coloured leg bands and one metal US Fish and Wildlife Service (USFWS) band. We obtained a small (20–60 µL) sample of blood from the brachial vein of each adult. Blood samples were taken from all nestlings in each brood when they were banded (USFWS only) on day 6–7. Additionally on the harvested field, blood samples were taken from nestlings aged 0–7, as all nests would eventually fail due to harvest (Perlut *et al.* 2006). Blood was put in a solution following Seutin *et al.* (1991), and stored in a freezer or placed on a Watman disc filter paper, allowed to dry, stored in plastic zip-loc bags with silica desiccation beads, and kept in a freezer until extraction.

We attempted to find the nests of all females on each field, and monitored the contents of each nest every 1 to 2 days until the young fledged or the nest failed. The social mating system was determined through intensive nest observations. Since incubation is a female-only behaviour, female association was identified by flushing incubating birds off the nest. Male association was identified by feeding and territory defence behaviour (Wheelwright & Rising 1993).

Statistical analysis was performed in SAS 8.2 (SAS Institute) using the generalized linear models (GENMOD) and general linear model (GLM) procedures. Here, patterns in social and genetic mating systems were compared with generalized estimating equation (GEE), testing differences among levels of a categorical factor using empirical standard error estimates within and between treatments. Pairwise comparisons of the GEE parameter estimates were performed by chi-square tests with 1 degree of freedom (GENMOD), or for the GLM procedures, *F* tests. These models controlled for repeated measures, as different broods by a given female were sampled between or within years. To account for varying brood size, for analyses of the genetic mating system, the sampling unit was determined as the percentage of extra-pair offspring in a given brood. Where appropriate, to understand the effect of haying, statistical comparisons were made between the unharvested field and post-harvest re-nests because sample size for some variables on the harvested field pre-harvest were too small. Importantly, the unharvested field served as an appropriate control for these variables, as settlement and behavioural patterns were not statistically different over time (see Results under the headings Social mating system and Genetic mating system, and legend for Fig. 1).

Female breeding synchrony was calculated with Kempenaers's (1993) breeding synchrony index (SI). SI determines the average proportion of fertile females on a given day within a population, requiring information on the breeding stage of every nesting female on a field. The fertile period included 5 days prior to laying the first egg until the day the last egg was laid (Kempenaers 1993). To identify fertile periods, the clutch completion date for each female's nests must be identified. Therefore, females whose nest contents survived either from egg-laying to incubation, incubation to hatching, or nestling to fledging were included within the synchrony analysis because these nests could be back-dated to a clutch completion date by subtracting the field's mean incubation period and/or nestling rearing period from the observed dates. To determine the effect of haying on the synchrony of subsequent re-nesting, we used the first post-harvest re-nests of females on the harvested field. If females' first post-harvest re-nest failed (due to predation), we ignored further re-nests by these individuals, as their inclusion in synchrony analyses was confounded by the joint effects of predation and haying.

Paternity analysis was performed with four hypervariable microsatellite loci: *Psa12*, *Passerculus sandwichensis* (Freeman-Gallant *et al.* 2005); *Escu6*, *Emberiza schoeniclus* (Hanotte *et al.* 1994); *Mme1* and *Mme8*, *Melospiza melodia* (Jeffery *et al.* 2001). All molecular and paternity assignment methods followed Freeman-Gallant *et al.* (2005). We sampled a total of 107 broods ($N = 351$ nestlings), including 24 pre-harvest ($N = 87$ nestlings) and 42 post-harvest ($N = 125$

nestlings) broods on the harvested field, and 41 broods ($N = 139$ nestlings) on the unharvested field.

The opportunity for sexual selection (I_s) on harvested and unharvested fields was calculated as the standardized variance in male fertilization success following Webster *et al.* (1995). Since a male's total fertilization success (T) is the sum of his within-pair (W) and extra-pair (E) fertilization success, variance in W and E both contribute to I_s , along with the degree to which W and E covary: $\text{var}(T) = \text{var}(W) + \text{var}(E) + 2\text{cov}(W,E)$. We further parsed W and E into components describing a male's mating success (number of social or extra-pair mates, M), female quality (number of young per mate, N), and female fidelity (proportion of young sired, P). This allowed us to examine the contribution of variance in each fitness component to the overall opportunity for sexual selection using information for all resident birds. Variance estimates were standardized as the variance/mean².

Invertebrates were sampled in 2004–2005 on the harvested and unharvested fields. Insects were collected both pre- and post-harvest with 10 sweep net samples at 10 randomly selected locations throughout the field. In 2004, pre- and post-harvest sampling occurred on 27 May–4 June and 10–14 June, respectively. In 2005, pre- and post-harvest sampling occurred on 20 May and 3–7 June, respectively. Length-mass regression equations were constructed to convert invertebrate length into estimates of dry biomass for 12 taxonomic groups. To construct the equations, we measured the lengths (to the nearest 0.01 mm) of selected invertebrates obtained from sweep net samples. In 2004, all invertebrates > 3 mm in length that were captured were identified into one of 12 prey categories and counted in the field. In 2005, invertebrates were collected and put in a forced-air drying oven at 100 °C for 24 h and later weighed on an electronic balance (precision ± 0.01 mg). For both years, mass was regressed vs. length using a power function of the form: $\text{mass} = a * \text{length}^b$. Although Savannah sparrows preferred certain prey types for feeding nestlings, there was a general correspondence between prey use and availability (Zalik 2007).

Results

Social mating system

Hay harvest decreased the social polygyny rate. On the unharvested field, the social mating system showed a mixed strategy, with 55% of females in polygynous associations and 45% of females in monogamous pairings over all years ($N = 39$ females; Fig. 1). These proportions were stable over the breeding season. On the harvested field, before haying, 33% of females were in polygynous associations and 67% of females were monogamous ($N = 58$ females). The pre-harvest monogamy rate was

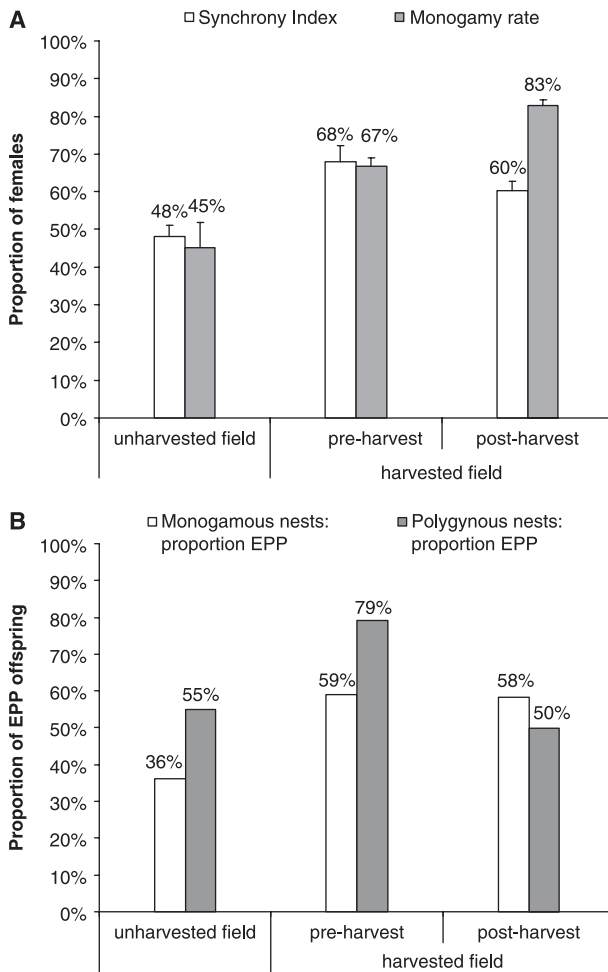


Fig. 1 (A)–(B) The social and genetic mating system post-harvest was significantly different from both the preharvest period and unharvested field. EPP did not differ between preharvest nests and first-brood nests found on the unharvested field before the latest observed harvest date (11 June) ($\chi^2 = 0.26$; d.f. = 1; $P = 0.608$). However, EPP did differ between pre- and post-harvest ($\chi^2 = 12.88$; d.f. = 1; $P < 0.001$); and EPP differed between first broods on the unharvested field and post-harvest renests ($\chi^2 = 7.16$; d.f. = 1; $P = 0.007$). On the unharvested field, 60% of females were in monogamous pairings. Sample sizes indicated; error bars represent standard error values.

likely upwardly biased because the harvested field was cut when polygynous males were beginning to establish social bonds with secondary females. Slight variations in the haying dates (27–28 May; 3, 5 June) provided insight into asynchronous female settlement and pairing patterns, as monogamy and synchrony rates were higher in years with earlier first haying dates. However, the unharvested field was an adequate control because the monogamy rate of the unharvested field's first broods prior to 16 June ($N = 35$ females) was not different from preharvest monogamy rate on the harvested field ($N = 51$ females; $\chi^2 = 0.40$; d.f. = 1;

$P = 0.53$). Harvest caused 99% ($N = 72$) of all first nests to fail simultaneously and females renested immediately (Perlut *et al.* 2006). The monogamy rate increased significantly post-harvest ($\chi^2 = 5.55$; d.f. = 1; $P = 0.02$), where 17% of females were in polygynous associations and 83% of females paired monogamously (Fig. 1A). The monogamy rate on the unharvested field was significantly lower than the monogamy rate on the harvested field after cutting ($\chi^2 = 20.07$; d.f. = 1; $P < 0.001$).

The post-harvest increase in social monogamy was likely a result of changes in mating behaviour rather than immigration or emigration. On the unharvested field, 64% (29 of 45) of all females laid a second clutch; of females whose first attempt failed due to predation, 56% (9 of 16) renested. Females on the harvested field showed similar renesting patterns and site fidelity. Of preharvest breeders, 71% (41 of 58) and 73% (33 of 45) of females and males, respectively, remained on the harvested field and renested post-harvest. Therefore, the preharvest population included males with no social mate; however, post-harvest, females paired with previously unmated males rather than becoming secondary females in polygynous associations. Here, 29% of females switched social mates after haying, and monogamous females were less likely to switch social mates (21%) after harvest than females in polygynous associations (42%).

For first broods on the unharvested field ($N = 17$ monogamous; $N = 22$ polygynous), socially monogamous females were not more synchronous than females in polygynous associations ($F = 0.44$; d.f. = 38; $P = 0.51$). Similarly, on the harvested field, socially monogamous females were not more synchronous than females in polygynous associations either in first broods preharvest ($N = 31$ monogamous; $N = 17$ polygynous) or first renests post-harvest ($N = 41$ monogamous; $N = 10$ polygynous; $F < 0.37$; d.f. = 47,50; $P > 0.55$). Although there were no significant differences, mean synchrony index values were consistently 3–6% higher from monogamous females than those in polygynous associations.

Genetic mating system

Paternity analysis for both fields combined showed high EPP rates, where 72% of broods had at least one extra-pair offspring ($N = 77$ broods). Extra-pair young accounted for a majority of the offspring in each brood (54%, $N = 191$ nestlings); 81% of females produced extra-pair young.

Hay harvest also influenced the genetic mating system. On the unharvested field, the EPP rate was associated with the social mating system, where socially monogamous females had 62% lower EPP rates than socially polygynous females ($N = 41$ females; $\chi^2 = 20.16$; d.f. = 1; $P < 0.001$; Fig. 1B). These rates were consistent among broods across the breeding season ($\chi^2 = 1.68$; d.f. = 3; $P = 0.43$). Again, the unharvested field served as an adequate control, as EPP

Source	Unharvested field	Harvested field post-harvest
	Standardized value	Standardized value
Total variance	0.339	0.773
Total WP variance	0.192	0.249
M_{wp}	0.182	0.201
N_{wp}	0.024	0.050
P_{wp}	0.048	0.028
Total EP variance	0.167	0.174
M_{ep}	0.136	0.133
N_{ep}	0.014	0.024
P_{ep}	0.036	0.049
Total WP and EP covariance	-0.192	-0.079

Table 1 Post-harvest variance in male reproductive success, including both within-pair (WP) and extra-pair (EP) components, increased the opportunity for selection. Both within-pair and extra-pair variance includes the number of mates a male attracts (M), the number of young produced per mate (N), and the percentage of these young he sires (P). Estimates for the unharvested field include only first clutches. Standardized values were computed as the variance/mean²

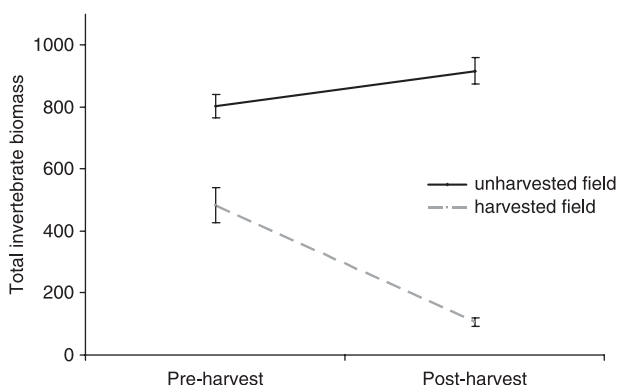


Fig. 2 The total amount of invertebrate biomass and the within-field variance decreased by > 76% after haying. This decrease in distribution of biomass resulted in a change in the social mating system on the harvested field, significantly increasing the monogamy rate. Error bars indicate the standard deviation of these samples.

rates did not differ between preharvest nests and first-brood nests found on the unharvested field before the latest harvest date ($\chi^2 = 0.26$; d.f. = 1; $P = 0.608$). On the harvested field, overall EPP rates decreased significantly ($\chi^2 = 649.81$; d.f. = 1; $P < 0.001$) after the first harvest in both mating systems; proportionally, polygynous females had 29% and monogamous females had 1% fewer extra-pair young than preharvest females (Fig. 1B).

Post-harvest changes in the genetic mating system may result from the effects of changes in social mating system through putative changes in resource distribution. On the harvested field, EPP was also associated with the social mating system ($\chi^2 = 9.80$; d.f. = 1; $P < 0.002$); post-harvest pairings were mainly monogamous, and monogamous nests had less extra-pair paternity. This change in social mating system may have resulted from haying-mediated changes in food resources which decreased the within-field variance (across 10 sample areas) in food biomass by 76%

(Fig. 2). Over the same period, on the unharvested field, the within-field variance in food biomass increased by 15%. Thus, post-harvest, males' inability to monopolize resources may have contributed to their inability to attract multiple social mates.

The effects of hay harvest on synchrony and the genetic mating system were less clear. Synchrony was higher on the harvested field [$SI = 0.68 \pm 0.04$ (s.e.m.), $N = 52$] prior to haying than post-harvest ($SI = 0.60 \pm 0.03$, $N = 57$; $\chi^2 = 2.68$; d.f. = 1; $P = 0.10$), although not statistically different. However, post-harvest nests were significantly more synchronous than nests on the unharvested field ($SI = 0.48 \pm 0.03$, $N = 44$; $\chi^2 = 6.41$; d.f. = 1; $P = 0.01$). On the harvested field, synchrony did not explain EPP rate ($\chi^2 = 2.13$; d.f. = 1; $P = 0.14$); although like the monogamy rate, the preharvest estimate of synchrony on the harvested field is potentially upwardly biased. By contrast, EPP on the unharvested field was associated with synchrony, where more synchronous females had higher EPP rates ($\chi^2 = 18.92$; d.f. = 1; $P < 0.001$). Together, these results support the social mating system, perhaps mediated through changes in food resources and breeding synchrony as the mechanism for decreased EPP rates post-harvest.

Sexual selection

Despite the fact that early haying resulted in increased social and genetic monogamy, harvesting more than doubled the total opportunity for sexual selection, I_s (Table 1). This doubling occurred in two ways. First, relative to the unharvested field, there was a 30% increase in the variance associated with within-pair fertilization success. This effect arose, in part, from a marginal increase in variance associated in within-pair matings (+10%, M_{wp}) and a substantial increase in variance associated with quality (N_{wp} : number of young produced per mate; +110%) of social mates following simultaneous nest failure caused by haying. Second, harvesting ameliorated the strong,

negative covariance between a male's within-pair and extra-pair fertilization success. Operationally, this result suggests that post-harvest, some males were able to both mate guard and seek extra-pair paternity. Overall, fertilizations were distributed less evenly through the population following hay harvest.

Discussion

Because harvesting influenced both the social and genetic mating systems, haying altered the opportunity for sexual selection, thus potentially influencing the evolution of Savannah sparrows in the Champlain Valley. In the unharvested field, high extra-pair paternity occurred at the expense of within-pair fertilizations, greatly constraining the variance in male fertilization success and the overall opportunity for sexual selection. Here, the polygyny rate was high, and polygynous associations had greater EPP rates. On the harvested field, by contrast, some males accumulated both within-pair and extra-pair fertilizations, while others lost within-pair fertilizations.

This result, however, occurred after haying as males were constrained from establishing polygynous associations. Taken together, these results suggest that the strength and target of selection might be affected by haying, to the extent that different fitness components are associated with different phenotypes (Yezerinac & Weatherhead 1997).

In the present study, both the social (M_{wp}) and extra-pair (M_{ep}) mating success of males contributed substantially to the opportunity for sexual selection, together accounting for 43.2% of I_s on the harvested field. In other birds, male traits such as song (Hasselquist *et al.* 1996) and plumage (Johnsen *et al.* 1998) are known to influence the number of social and extra-pair mates a male attracts, suggesting that on harvested fields, the increased opportunity for sexual selection may translate into an increased strength of selection on these traits. Previous work with Savannah sparrows, however, has shown that genetic similarity between females and prospective mates can be a strong predictor of social and extra-pair mating patterns (Freeman-Gallant *et al.* 2003, 2006). Whether a male's fertilization success is influenced more by his phenotype or by his genetic similarity to potential social and extra-pair mates is unknown; however, the results of this study suggest that the strength and perhaps traits may differ pre- and post-haying.

Like selection, the strength of genetic drift is also responsive to changes in I_s . As variation in individual reproductive success increases, the effective population size, N_e , decreases relative to the actual population size (N) (Wright 1931; Nunney 1993; Parker & Waite 1997), fewer males contribute genes to the next generation, and the effects of drift may increase (Nunney 1995). If N_e is reduced substantially,

populations may rapidly lose genetic variation, leaving them vulnerable to changes in environmental conditions. Whether any effect of haying on N_e/N is meaningful depends on the size of Savannah sparrow populations and the geographical extent of haying. In the Champlain Valley, the majority of available hayfield habitat is cut during the breeding season (Perlut *et al.* 2006), and female density is similar in harvested and unharvested fields (see Materials and methods). Thus, a significant proportion of the breeding population is likely subjected to haying, and haying-mediated effects on N_e/N (via increased variance in male fertilization success) are likely to be pervasive. Nonetheless, given the abundance and valley-wide distribution of Savannah sparrows (Shustack 2004), it seems unlikely that the significant but modest effect of haying on I_s is extreme enough for drift to drain variation from populations and/or to counter adaptive evolution.

This study provides a rare experimental test of long-standing mating systems theory that relates the incidence of social polygyny to the spatial and temporal distribution of resources and mates. Consistent with Emlen & Oring's (1977) environmental potential for polygyny model, haying seems to have decreased the incidence of polygyny in managed fields by decreasing the abundance and variability of food resources, a pattern similar to that observed by Weatherhead (1979) where the brevity of the tundra breeding season limited Savannah sparrows to social monogamy. The influence of breeding synchrony is less clear, especially with respect to the occurrence of extra-pair paternity. For the population on the unharvested field with high rates of social polygyny, increased synchrony was associated with increased EPP, as predicted by Stutchbury & Morton (1995). Likewise, in the harvested field, females were relatively asynchronous following haying and EPP rates were low. However, there was no relationship between synchrony and EPP on the harvested field after haying, suggesting that any effect of synchrony on extra-pair paternity may depend on the social mating system, with a stronger relationship occurring in predominantly polygynous than in predominantly monogamous populations.

When viewed from the landscape perspective in which up to 40% of available habitat is harvested by early June (Perlut *et al.* 2006), these data indicate a strong evolutionary pressure applied by agriculture. Hay harvest offset the resource distribution and to a lesser degree, breeding synchrony that enabled social polygyny, causing the population to become more socially and genetically monogamous. These changes doubled the strength of sexual selection, and as a consequence, potentially altered evolutionary processes of the population. We know of no other vertebrate studies that have identified both ecological and evolutionary effects linked to human influenced agricultural management.

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Noah Perlut is a post-doctoral fellow in the Rubenstein School of Environment and Natural Resources, University of Vermont. He is interested in the joint ecological and evolutionary influences of managed ecosystems on terrestrial wildlife. His main research focuses on how hayfield and pasture management affects grassland songbirds' life-histories. Corey Freernan-Gallant is an associate professor of biology at Skidmore College. His research interests include sexual selection and epigamic signaling in birds as well as genetic compatibility mechanisms of female choice. Allan Strong is an assistant professor in the Rubenstein School of Environment and Natural Resources. He teaches classes in ornithology, conservation biology, and wildlife management. His research has focused on the effects of human land use changes on habitat quality for birds across temperate, tropical, and montane ecosystems. Therese Donovan is the Assistant Unit Leader of the Vermont Cooperative Fish and Wildlife Research Unit. Therese's research focuses on wildlife population dynamics and modeling. She has also developed several pedagogical tools for teaching quantitative methods in ecology and evolution (<http://www.uvm.edu/envnr/vtcfwru/spreadsheets/>). C. William (Bill) Kilpatrick is the Howard Professor of Zoology and Natural History in the Department of Biology. His research interest ranges from systematics to molecular ecology and conservation genetics. Nathan Zalik recently received his master's degree from the Rubenstein School of Environment and Natural Resources. His research interests center on factors that limit bird population growth.
