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ORIGINAL PAPER

Positive association between social and extra-pair mating in a polygynous songbird, the dickcissel (*Spiza americana*)

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Abstract In polygynous species, males appear to gain additional offspring by pairing with multiple females simultaneously. However, this may not be true if some females copulate outside of the social pair bond. Polygynous males could experience lower paternity because of trade-offs among gaining multiple social mates, guarding fertility with these mates, and pursuing extra-pair matings. Alternatively, polygynous males could simultaneously gain extra social mates and have high paternity, either because of female preferences or because of male competitive attributes. We tested four predictions stemming from these hypotheses in a facultatively polygynous songbird, the dickcissel (*Spiza americana*). Unlike most previous studies, we found that males with higher social mating success (harem size) also tended to have higher within-pair paternity and that the number of extra-pair young a male sired increased significantly with his social mating success. Females that paired with mated males were not more likely to produce extra-pair young. In contrast, extra-pair paternity was significantly lower in the nests of females whose nesting activity overlapped that of another female on the same territory. This pattern of mating was robust to differences in breeding density. Indeed, breeding density had no effect on either extra-pair mating or on the association between polygyny and paternity. Finally, nest survival increased with harem size. This result, combined with the positive association between polygyny and paternity, contributed to significantly higher realized reproductive success by polygynous male dickcissels.

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Introduction

In polygynous species, some males pair with multiple females simultaneously (Ligon 1999), and it would appear these males have higher reproductive success as a result (e.g., Orians 1969; Payne 1979; Alatalo and Lundberg 1984; Hasselquist 1998; Fiumera et al. 2002; Heckel and Von Helversen 2003; Moon et al. 2006; Vedder et al. 2011). An increase in reproductive success with an increase in number of mates is a fundamental assumption of sexual selection theory (Trivers 1972; Borgia 1979; Arnold and Wade 1984) and was first established by Bateman (1948). However, in a variety of organisms, social breeding relationships may not necessarily reflect mating relationships. Females can copulate with other males, and extra-pair paternity (EPP) is widespread, especially in birds (Jennions and Petrie 2000; Griffith et al. 2002). Extra-pair paternity may alter the nature of the relationship between social mating and reproductive success.

EPP could have either of two effects on the relationship between social mating success and reproductive success. One possibility is that it decreases or eliminates the expected positive relationship (e.g., Dunn and Robertson 1993). One explanation for this is that males may be faced with trade-offs between attracting social mates and maximizing paternity (Arak 1984; Westneat et al. 1990; Hasselquist and Sherman 2001). The pursuit of additional social or extra-pair mates might reduce the amount of time males may spend in other activities, such as guarding existing mates (Hasselquist and Bensch 1991; Westneat 1994; Smith 1995; Pilastro et al. 2002). A handful of studies have found evidence supporting such trade-offs (reviewed in Vedder et al.

2011). In red-winged blackbirds (*Agelaius phoeniceus*), for instance, females whose fertile periods coincided with the settlement of a new female on the same territory were more likely to have extra-pair offspring than other polygynously mated females (Westneat 1993). This result suggests that males were unable to simultaneously attract new mates and maximize paternity with existing mates. Similarly, polygynously mated male tree swallows (*Tachycineta bicolor*) were twice as likely to be cuckolded as monogamous swallows (Dunn and Robertson 1993).

The alternative pattern is for extra-pair paternity to enhance the disparity in reproductive success between polygynous and monogamous males. Meta-analysis of interspecific variation in EPP rates lends indirect support to this idea, since polygynous species generally exhibit lower rates of EPP than monogamous ones (Hasselquist and Sherman 2001). A positive effect of EPP on the relationship between number of mates and reproductive success could arise through female mate preferences. For example, polygynous male blue tits (*Cyanistes* [formerly *Parus*] *caeruleus*) spent less time guarding their mates than monogamous males, but still achieved a similar level of paternity. Even after experimental removal of polygynous males, copulation attempts by neighboring males largely failed due to lack of female cooperation (Kempenaers et al. 1995), suggesting that female preferences favor paternity by polygynous males. Alternatively, males that achieve polygyny may be inherently better at attracting and guarding mates (Kempenaers et al. 1995). Superior fighting ability could make such males successful at defending attractive territories, guarding paternity in their own nests, and gaining paternity in other males' nests. For example, larger male red-winged blackbirds were more successful in gaining both social and extra-pair mates (Weatherhead and Boag 1995), but female red-winged blackbirds were not able to mate with higher quality males through extra-pair behavior, nor was female involvement in EPC repeatable among years (Weatherhead 1999). These results suggest that male competitiveness, not female choice, is driving patterns of mating in the Ontario population of red-winged blackbirds studied by Weatherhead and colleagues.

Whether polygyny typically trades off with EPP or covaries positively with it is uncertain. The studies to date contain a mix of predominately monogamous birds that occasionally show polygyny (in which trade-offs appear more likely, Vedder et al. 2011) and species showing regular polygyny in which within-pair paternity is usually unaffected by polygyny but EPP gained tends to increase with number of social mates (e.g., Bollinger and Gavin 1991; Westneat 1993; Weatherhead and Boag 1995).

It is possible that other factors may influence the interplay between polygyny and EPP. Breeding density, for example, could also influence the association between social and extra-pair mating. Increased breeding density should increase encounter rates between females and males (Birkhead 1978). One would then expect that mate guarding would become more difficult as density increases (Moller and Birkhead 1993). Thus, increased breeding density could exaggerate trade-offs between social and extra-pair mating. High breeding densities could also exaggerate the effects of female choice and male competitiveness on social and extra-pair mating patterns. If female behavior drives extra-pair mating, then increased proximity to potential extra-pair mates could facilitate extra-pair mating for females seeking such opportunities (i.e., monogamous females). If male competitiveness drives extra-pair mating, then increased proximity could also facilitate a competitive male's attempts to gain extra-pair copulations with his neighbor's females.

Predation could also affect whether polygynous males achieve greater realized reproductive success than monogamous males, particularly in species with high nest predation. Males of many species act as anti-predator sentinels and actively defend nests from predators (e.g., Yasukawa et al. 1992). Vigilance and nest defense may compete with other activities used to attract or guard mates. If so, then nest survival may decline with increasing social mating success. In red-winged blackbirds, nest survival declined with increased harem size (Weatherhead and Robertson 1977; Lenington 1980). Polygynous male great reed warblers (*Acrocephalus arundinaceus*) defended their nests less vigorously than monogamous males (Trnka and Prokop 2010). Nevertheless, the latter result could be a consequence of decreased predation pressure on the territories of polygynous males (Hansson et al. 2000). A male's ability to gain and defend a high-quality territory may increase both his social mating success and the survival of nests on his territory. Female choice should also favor males that defend territories with low predation pressure, leading to a positive association between male social mating success and nest survival.

We investigated the relationship between polygyny and EPP in a population of dickcissels (*Spiza americana*) breeding in northeastern Kansas. Dickcissels exhibit resource defense polygyny, with males defending territories that contain both nesting and foraging areas (Zimmerman 1966; Fretwell 1986). Social mating in this species includes simultaneous nesting of multiple females, partial overlap of nesting activity, sequential monogamy, and true monogamy. About half of all male dickcissels mate polygynously, with harem sizes varying from two to five females (Zimmerman 1971, 1982). Unlike most male songbirds, male dickcissels do not normally feed their offspring, although they do provide paternal care in the form of nest and fledgling defense (Temple 2002). Lack of male parental care suggests that males devote much of their time to attracting mates, either through polygyny or pursuing extra-pair copulations.

Although no data are available on extra-pair copulations or EPP in this species, even monogamous males provide little care, making it likely that many males pursue extra-pair copulations. The prevalence of polygyny and variation in harem size in dickcissels provided a good setting to test the predictions of the two alternative hypotheses for a link between polygyny and EPP. Specifically, we predicted that if polygyny traded-off with EPP that: (1) monogamous male dickcissels would have higher paternity than polygynous ones, (2) among polygynous males, paternity would decrease as the overlap in fertile periods within a harem increased, and (3) monogamous males would be more successful at siring extra-pair young. If polygyny and EPP are driven by male competitiveness (or by female preference for more competitive males as extra-pair partners), we predicted that: (1) monogamous males would have lower paternity than polygynous males, (2) paternity would not be affected by overlap in female fertile periods within harems, and (3) polygynous males would be more successful at siring extra-pair young than monogamous males. In addition, if polygynous males are indeed more attractive or more competitive for social mates, we expected the probability of new females settling on a territory to be higher for already mated males than for unmated males. We tested the possibility that breeding density would exacerbate any trade-offs between polygyny and EPP or facilitate the positive effects of female choice or male competitiveness. Finally, we tested for an association between polygyny and nest predation.

Materials and methods

Field site and general methods

We studied dickcissels at the Konza Prairie Biological Station (KPBS) located in Riley and Geary Counties, KS (approximately 39°05'N and 96°35'W) in 2006 and 2007. The KPBS is a 3,487-ha area of native tallgrass prairie managed by periodic burning. In 2006, we followed birds inhabiting an unburned watershed (KPBS designation: R20A, 26.3 ha) in the southwestern corner of KPBS. In 2007, the adjacent, biennially burned watershed (KPBS designation: 2A, 28.0 ha) was added to the study area. Burning did not occur on either site during this study.

We captured males on their territories using mist nets combined with song playback and, occasionally, a male model. We banded all birds with a U.S. Geological Survey aluminum band and also banded adults with a unique combination of three plastic color bands. We located nests primarily by observing female behavior. We then checked nests every 3 days until the nests either fledged or failed. We assumed a nest had been depredated if it was empty before chicks were old enough to fledge (~8–9 days old). We assumed nestlings had fledged based on the behavior of the parents, since female dickcissels continue to feed fledglings and both parents actively defend them in the vicinity of the nest for an extended period of time (Gross 1921; Temple 2002). Females were trapped at the nest during the nestling phase using a cylindrical nest trap (Sousa and Stewart 2011). Nestlings were banded when at least 3 days old. Social fathers were assigned to nests based on a combination of active nest defense, pairing behavior with female, and/or location of the nest within a male's territory (determined from GPS coordinates).

We censused the study area weekly to determine the arrival and departure dates of each male. We assumed that males were present on the site until the day before the census after they were last seen. The length of each male's territory tenure was calculated as the number of weeks a male was present on the study site. The mating status of each male at the beginning of each week was determined retrospectively using the first egg dates of nests occurring within the male's territory.

We calculated the first egg date for each nest in the study site, assuming one egg laid per day. For nests that were found after the clutch had been completed and survived to the nestling phase, we calculated first egg date from nestling age, assuming a 12-day incubation period. For nests found after the clutch was completed, but depredated before hatching, the first egg date was calculated by assuming that the nest was 6 days old at the midpoint date of nest checks. We also assumed that the female's fertilizable period began 5 days prior to the day the first egg was laid and continued until the day the penultimate egg was laid (Westneat 1993).

Density estimate

The locations of each male were recorded during censuses and focal watches with a Garmin GPSmap 76 or 60Cx handheld unit. Territorial boundaries were determined by recording the GPS coordinates of perches used during 1-h focal watches and by flushing males after the watch. One to three focal watches were conducted per male, depending on the length of a male's tenure on the study site. GPS points were imported into ArcGIS 9.3 for analysis. Minimum convex polygons (MCP; Mohr 1947) were constructed for each male from nest, focal, and census points using the Geospatial Modeling Environment (GME, Beyer 2010). Only nests assigned to males using behavioral data were used when constructing MCPs. The central point of each male's territory was calculated as its center of gravity (weighted by density of points). Territory size and center points were calculated using the GME. We then calculated an observation area curve relating the number of GPS points collected to territory size to determine whether sufficient points were collected to accurately determine territory size

(Odum and Kuenzler 1955). This curve failed to reach an asymptote, indicating that an insufficient number of points had been collected to accurately measure territory size. We therefore used the center points instead of territorial boundaries to calculate distances to neighbors and other density measures.

We calculated breeding density for each nest as the number of territorial center points within 150 m of the nest. A distance of 150 m was chosen because it is approximately twice the average distance between a nest and the territorial center point of its nearest neighbor (BF Sousa, unpublished data). We estimated the breeding density for a given nest in the week in which the nest was initiated. Census data were used to determine which males were present in a given week.

Apparent reproductive success

Social mating success in polygynous species can be estimated in a number of ways. One of the most common methods is to measure harem size, which is the maximum number of females simultaneously nesting within a particular male's territory. Because this measure misses some of the variation in male mating success, we also measured the average number of nests per week for each male. These two values were strongly positively associated (Pearson $r=0.83$, $p<0.0001$, $N=80$). We therefore estimated each male's social mating success using harem size, since this measure is less likely to be confounded by predation and other stochastic events.

The apparent reproductive success of males with different harem sizes was assessed in two steps. First, we determined the number of nestlings for which a male was the social father then tallied the subset of these nestlings that were genetically sampled. This measure was used to compare apparent and genetic reproductive success. Second, we used the total number of fledglings a male produced on his territory as the best measure of his apparent reproductive success.

Paternity analysis

We defined paternity as the proportion of a social father's sampled young that he sired. Small blood samples (~50 uL) were collected from all adults and nestlings and stored in Queen's Lysis Buffer (Seutin et al. 1991). Eggs that failed to hatch were collected and examined for contents. No living embryos were found, but partially developed embryos were sometimes present. Dead nestlings were also found at some active and abandoned nests. These nestlings and inviable embryos were collected and stored in 95 % ethanol.

DNA was extracted from blood and tissue samples using a 5-M NaCl extraction solution (Laird et al. 1991). A phenol–chloroform solution was used to extract DNA from samples with yields less than 5 ng/μL (Chomczynski and Sacchi 2006). Ten to twenty nanograms of the extracted samples were amplified in a total reaction volume of 10 μL consisting of 0.2 mM each dNTP, 0.2 μM fluorescently labeled forward primer, 0.2 μM reverse primer, 1X Taq buffer (1.5 mM MgCl, 10 mM Tris–HCl, 50 mM KCl), and 0.35 units *Taq* polymerase. Amplification was performed in a thermal cycler with the following cycling regime: 94 °C for 4 min followed by 35 cycles of 94 °C for 30 s, T_A (Table 1) for 30 s, 72 °C for 45 s and a final cycle of 72 °C for 10 min. Amplification for locus Lsw 5 was carried out with the following slight modifications to this procedure: 0.2 μMM13-tagged forward primer, 0.6 μM reverse primer, and the addition of 0.2 μM of fluorescently labeled M13(−21); cycling was carried out as

Table 1 Characteristics of microsatellite loci used in analysis of dickcissel paternity

Locus	k[a]	T_A[b]	Number[c]	H_O[d]	H_E[e]	P_1[f]	P_2[g]	Source
Dp 16	14	55	215	0.69	0.71	0.32	0.51	Dawson et al. 1997
Mcy 4	18	43	214	0.86	0.86	0.55	0.71	Double et al. 1997
Lei 160	10	51	214	0.81	0.84	0.50	0.67	Gibbs et al. 1997
Emb 112	25	55	214	0.87	0.088	0.61	0.76	Mayer et al. 2008
Lsw 5	10	55	208	0.69	0.69	0.29	0.47	Gibbs et al. 1999
Hofi 5	23	55	197	0.92	0.93	0.75	0.85	Polakova et al. 2007
VeCr 2	5	55	146	0.67	0.68	0.24	0.39	Stenzler et al. 2004
Total						0.992	0.9995	

[a] Number of alleles

[b] Annealing temperature (degrees Celsius)

[c] Number of adults genotyped

[d] Observed heterozygosity

[e] Expected heterozygosity

[f] Exclusion probability of first parent

[g] Exclusion probability of second parent

in Schuelke (2000). After amplification, 1 μL of PCR product was mixed with 8.8 μL of formamide and 0.2 μL GeneScan LIZ 500 size standard and genotyped in an ABI 3730 capillary sequencer. Genotypes were visualized and scored using GeneMapper 4.0. A small number of samples were genotyped using untagged primers and silver staining (as in Stewart et al. 2010). Genotypes obtained from silver staining were compared to those obtained using the capillary sequencer to ensure comparable results. Exclusion of genotypes obtained from silver staining did not change the results of paternity analysis.

Individuals were genotyped at six or seven microsatellite loci originally developed in other bird species (Table 1). Because variability was low at locus VeCr 2, it was not used for all 2007 samples. Cervus 3.0 was used to test for null alleles, deviations from Hardy–Weinberg equilibrium, and to assign paternity to extra-pair young (Kalinowski et al. 2007). There was no evidence of null alleles among any of the loci used, nor were there any significant deviations from Hardy–Weinberg equilibrium. Nestlings were considered extra pair if their genotypes did not match their presumed father's genotype at two or more of the loci typed, since single locus mismatches could be due to mutation.

To minimize erroneous paternity assignments, multiple criteria were used to assign sires to extra-pair chicks. A male was determined to be the sire of an extra-pair chick if he was assigned by Cervus with 95 % confidence, had a positive trio LOD score (indicating he was more likely to be the sire than a male randomly drawn from the same population), mismatched the chick's genotype at no more than one locus, and was present at the research site in the week the nest was initiated. We conducted the paternity analysis in three nested stages. First, the pool of candidate sires for each nest was restricted to the males defending territories directly adjacent to the territorial male. If no sire was assigned at 95 % confidence in the first stage, we added all males within 150 m of the focal nest to the pool of candidate sires. If this did not identify a sire, the pool of potential sires was then extended to all males present on the field site during the female's fertilizable period.

Nest survival analysis

Predictions regarding variation in nest survival were tested by examining support for a set of candidate nest survival models. First, preliminary models were constructed in Program MARK (White and Burnham 1999) to determine whether nest age (age of nest at each nest check), time in season (Julian date of first egg), nesting stage (egg or nestling), or year affected nesting success. Model fit was assessed using the Akaike Information Criterion adjusted for finite sample sizes (AICc, Hurvich and Tsai 1989). The terms of the best preliminary model were included in all subsequent models testing the effects of variables related to polygyny on nest survival. A likelihood ratio test was conducted to determine whether these variables contributed significantly to daily nest survival rates.

Statistical analyses

For analyses of male reproductive success, all nests within a male's territory were pooled to obtain overall measures of social and extra-pair mating success. Because some males occurred on the study site in both years of the study, male identity was included as a random factor in analyses of reproductive success and patterns of paternity. When these analyses were conducted on binomial variables (e.g., paternity), a generalized linear mixed model (GLMM, Proc GLIMMIX) with a logit link was used. Harem size was not normally distributed (Kolmogorov–Smirnov (KS) test=0.22, $p<0.0001$), but did fit a Poisson distribution (KS=0.02, $p=1.00$). We therefore used a Poisson distribution and log link (GLMM, Proc GLIMMIX) when analyzing harem size. The number of young a male sired through EPC, apparent success (number of young fledged on a male's territory), and realized reproductive success (number of related young fledged) did not fit either a normal or Poisson distribution (Kolmogorov–Smirnov test, $p<0.0001$), primarily due to the excessive number of zero counts in these variables. We therefore used a zero inflated Poisson model (ZIP, Proc GENMOD) to analyze these variables (Lambert 1992). The number of nests built in a male's territory was used to model the zero inflation portion of the ZIP model for apparent and realized reproductive success. The intercept only model of zero inflation was used to analyze extra-pair siring success.

Patterns of parentage among nests were also analyzed using a GLMM. Since the probability of extra-pair paternity is unlikely to be constant across broods, variance in EPP is likely to be overdispersed in a manner similar to the structure of variance in brood sex ratios (e.g., Krackow and Tkadlec 2001). Therefore, the default restriction of $\phi=1$ was lifted, and a residual variance parameter was estimated for events by trials tests of extra-pair paternity. Male identity was included as a random factor to control for possible non-independence of EPP among broods of the same male, both within and between years. The effects of year and site on the incidence of extra-pair paternity were assessed using a mixed model that included the random effect of social male identity. Site effects were only assessed for 2007 since only one site was studied in 2006.

Means are reported ± standard deviation and effect sizes are reported ± standard error. All analyses were conducted in SAS 9.2, and tests were considered significant at $\alpha=0.05$.

Results

In total, 96 male, 74 female, 175 nestling, and three fledgling dickcissels were banded in the course of this study. In 2006, 45 males defended territories on the study site, 38 of which were captured and banded. In 2007, 62 males defended territories in the study area, 48 of which were banded. Of the banded males in 2007, 16 had been marked the previous year (42 % return rate).

Polygyny and apparent success

Polygyny was common in both years of the study. Thirty-seven percent of territorial males were polygynous, and harem size peaked at five females with an average of 1.28±1.03 females. Harem size did not differ between 2006 and 2007 (GLMM: effect=0.28±0.20, $F_{1,78}=1.93$, $p=0.17$). There was also no significant difference in harem size between the two study sites in 2007 (GLMM: effect=−0.27±0.25, $F_{1,41}=1.11$, $p=0.30$).

Harem size was positively associated with territory tenure (GLMM: effect=0.11±0.03, $F_{1.78}=11.47$, $p=0.001$); however, male identity could not be included as a random factor in this analysis because the variance components were estimated to be zero. Thus, this test violated the assumption that observations were independent. We therefore repeated the analysis with only one record per male (chosen at random) and obtained similar results (GLMM: effect=0.09±0.03, $F_{1,68}=7.48$, $p=0.008$).

The total number of fledglings each male produced on his territory was highly correlated with harem size and was not different between seasons (ZIP: harem size, 0.36±0.08, $X^2_{1,75}=19.76$, $p<0.0001$; year, 0.38±0.22, $X^2_{1,75}=3.03$, $p=0.08$).

Female settlement

In order to determine whether females settled preferentially with mated males, we calculated the proportion of nests initiated in the territories of already mated males versus unmated males each week of 2006 (9 weeks) and 2007 (12 weeks). For each week, we first calculated the fraction of males present on the study site that were already paired. We then calculated the expected number of polygynous nests started each week as the product of this proportion and the number of nests initiated in that week. Because sample sizes were small, we used a G-test to compare the observed and expected numbers of polygynous nest starts. There was no evidence that females settled non-randomly with respect to male mating status (2006: $G^2=1.29$, $p=0.999$, df=9; 2007: $G^2=5.20$, $p=0.95$, df=12).

Paternity analysis

At least one extra-pair offspring occurred in 48 of 92 broods (52 %), accounting for 84 of 218 chicks (39 %). This excludes a single nestling in 2007 that amplified at fewer than four loci and two fledglings in 2006 whose social father could not be reliably determined. It includes 48 nestlings for which the female was not sampled but were typed at a sufficient number of loci to assess paternity. Extra-pair sires were assigned to 57 chicks (68 %). Over a third of extra-pair young (38 %) were assigned to a male from a bordering territory. Of the 27 unassigned offspring, 20 came from nests where a male in a neighboring territory was not sampled, and all had at least one unsampled male within two territories. The distance between a nest containing an extra-pair chick and the territory of its sire ranged from 35.5 to 760.1 m (median=153.2, first quartile=95.4, third quartile=196.9 m).

In 22 broods, all of the chicks were sired by an extra-pair male. This included nine nests containing a single nestling, and eight with two nestlings. These broods were re-examined to determine whether there had been a mistake when assigning the social male. In all 22 cases, the nests were located within the assigned social male's territory and blood sample labels matched the field notes taken at the time of capture. Erroneous assignment of a chick as extra-pair can also result if the social male was replaced after a previous observation. However, during two years of study, only two cases of mate switching were observed. Both occurred between males on adjacent territories where the nest was located near the territory border. In both cases, a switch occurred when one male took over part of the territory of an adjacent male that contained the nest. In one case, blood samples were collected from the brood, and the DNA analysis showed that the new social mate did not sire any of the chicks, and the original mate shared paternity with a third, unidentified male.

In four broods, the extra-pair chicks were sired by more than one male, as indicated by three paternal alleles at multiple loci. One of these broods occurred in 2006 and was likely the result of the transitory tenure of several immigrating males. Rapid territorial changeover in the area made it impossible to assign a social mate with any confidence; however, none of the three potential social mates matched any of the three offspring of this nest, nor were there any unsampled males on adjacent territories. Four of the seven loci typed produced three paternal alleles per brood, indicating that at least two males likely contributed paternity. Each chick was assigned to a different banded male from neighboring territories. In 2007, three cases of multiple extra-pair paternity were observed. In two cases, the social father shared paternity with two extra-pair males. In the remaining brood, the social male sired none of the brood, an adjacent male sired two chicks, and the remaining chick could not be assigned a sire.

Neither year nor site had a significant effect on the proportion of a brood that was sired by a female's social mate (GLMM: year, $F_{1,88}=0.24$, $p=0.62$; site, $F_{1,20.2}=2.67$, $p=0.12$; Fig. 1). The proportion of nests containing no extra-pair chicks was not different between years (GLMM: $F_{1,88}=0.67$, $p=0.42$). The effect of site on the proportion of nests containing no extra-pair young could not be estimated when social male identity was included in the model (variance for this parameter was estimated as zero). Therefore, this term was removed from the model, and a logistic regression showed that the proportion of nests without extra-pair young was significantly higher in watershed R20a than in 2a (Wald $X^2=6.53$, $p=0.01$).

Polygyny and paternity

Paternity (the proportion of a social father's sampled young that he sired) tended to be higher among males with larger harem sizes (GLMM: effect=0.34±0.18, $F_{1,17.8}=3.58$, $p=0.07$). There was no evidence that polygynous males lost paternity when two or more of the females on his territory had overlapping fertile periods (GLMM: effect=0.20±0.42, $F_{1,59}=0.22$, $p=0.64$). Females that paired with unmated males did not produce broods with higher within-pair paternity than females that settled with already mated males (GLMM: effect=0.02±0.46, $F_{1,73.2}<0.01$, $p=0.96$). In contrast, a male achieved higher paternity in the nests of females that experienced overlapping nesting activity (i.e., when a female was polygynously mated at any point in her nesting cycle; GLMM: effect=0.84±0.35, $F_{1,24.8}=4.36$, $p=0.05$).

The number of offspring a male gained through extra-pair mating was positively associated with his harem size when using the full dataset (Fig. 2; ZIP: effect=0.36±0.15, $X^2_{1,77}=5.94$, $p=0.01$). However, extra-pair mating success may be underestimated for males defending territories on the border of the study site. To account for differences in sampling, we defined a male's opportunity to sire extra-pair offspring as the number of genotyped nestlings within 150 m of the center of each male's territory center (excluding nests within the male's own territory). This excluded any nestlings sired before or after a male was resident on the study site. We then tallied the proportion of these chicks sired by the focal male. This measure was also significantly positively associated with harem size (GLMM: effect=0.52±0.24, $F_{1,72.9}=4.62$, $p=0.03$). This association appears to be driven by males with no social mates, who were also unsuccessful at gaining EPP. When unmated males are removed from the analysis, extra-pair siring success does not significantly increase with harem size (GLMM: effect=0.24±0.26, $F_{1,43.8}=0.87$, $p=0.36$).

A male's total realized reproductive success (total number of fledglings including both within pair and extra-pair young) also increased with his harem size (Fig. 3; ZIP: effect=0.39±0.08, $X^2_{1,76}=22.04$, $p<0.0001$). This remained significant when males with no social mating success were excluded from the analysis. Males gained 0.74±0.15 fledglings per additional female (GLMM: $F_{1,40.4}=24.82$, $p<0.001$). Polygynous males were also more likely to fledge at least one related chick than monogamous males (GLMM: effect=1.20±0.56, $F_{1,61}=4.59$, $p=0.04$).

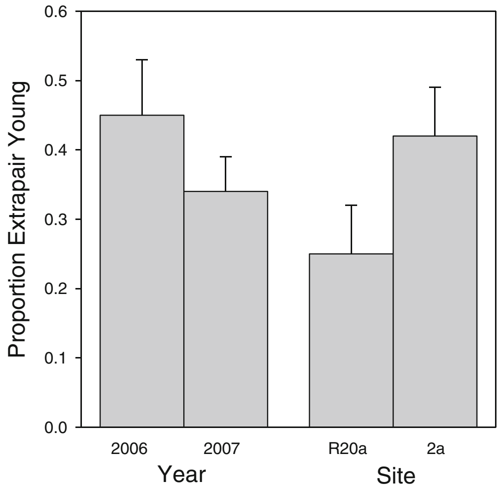

Fig. 1 Variation across years and sites in the proportion of extra-pair young occurring in dickcissel broods. Means are plotted ± standard error. Means for site are calculated for 2007 only. Statistical analysis revealed no differences once random effects were used to adjust degrees of freedom

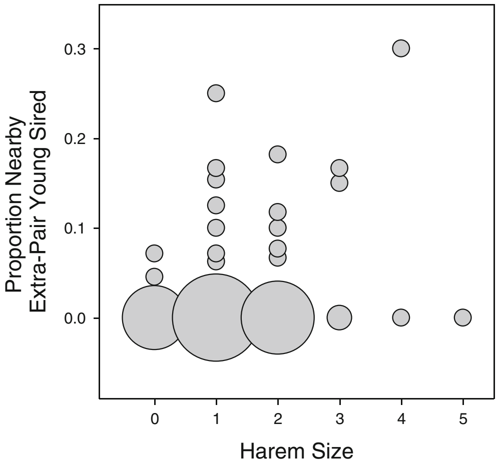

Fig. 2 Scatter plot of the proportion of nearby dickcissel chicks sired through extra-pair copulations by males with different harem sizes. From the smallest to the largest dot, the sample size is 1, 2, 13, 17, 24

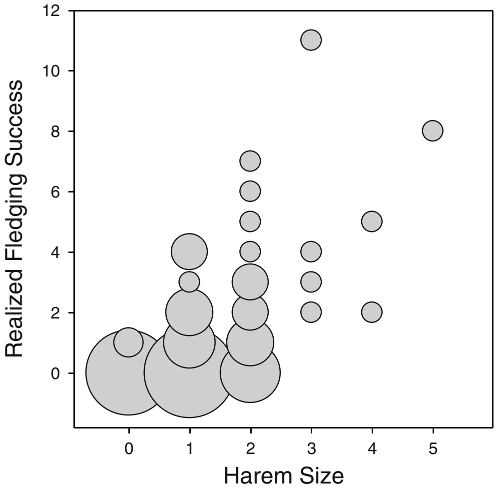

Fig. 3 The total number of related dickcissel fledglings (both within-pair and extra-pair) sired by males with different harem sizes. Point size indicates number of coincident values. From the smallest to the largest dot, the sample size is 1, 2, 3, 5, 6, 8, 16, 18

Density and polygyny

Breeding density did not significantly influence paternity. The proportion of within pair young in a nest was not influenced by the number of males within 150 m of the nest in the week of nest initiation (GLMM: effect=−0.05±0.07, $F_{1,77.5}$=0.45, p=0.51). This remained true when nests within 150 m of the border of the study site were excluded from the analysis (GLMM: effect=−0.08±0.09, $F_{1,59.6}$=0.74, p=0.39).

Breeding density could enhance the association between paternity and social mating success. We tested this idea using a model relating paternity in each nest to breeding density, the number of other females on the territory with nesting activity concurrent with the focal nest, and the interaction of the two. There was no main effect of breeding density on within-pair paternity (GLMM: effect=−0.004±0.09, $F_{1,78.9}$=0.00, p=0.97). Likewise, the proportion of WPY in a brood was not influenced by the interaction term (effect=−0.09±0.11, $F_{1,80.4}$=0.73, p=0.40). This did not change when nests within 150 m of the border of the study site were excluded from the analysis (density effect=−0.005±0.11, $F_{1,54.9}$=0.00, p=0.96; interaction effect=−0.16±0.14, $F_{1,60.5}$=1.31, p=0.26).

Polygyny and nest survival

Nest abandonment was rare in both years of the study (eight of 218 nests). However, nest depredation rates were generally high and stable across years and sites at around 64 %. In 2006, 23 % of nests fledged at least one chick, while 31 % of nests fledged in 2007. Since depredation rates were stable across years, higher fledging rates in 2007 were due to a decrease in the number of nest failures resulting from severe weather, poor construction, or abandonment. The best fitting base model of nest survival included age, age^2, stage and year, but not time of season (Table 2). This model was substantially better at explaining variation in daily nest survival rate (DSR) than the null model of constant DSR (ΔAIC=28.28). The addition of a female's pairing status (monogamous vs. polygynous) on the day of clutch initiation did not improve the fit of the nest survival model. Similarly, whether a female's nesting attempt temporally overlapped that of one or more of the other females on the territory did not improve the model's fit. In contrast, the addition of the male's peak harem size did significantly improve the model, with harem size having a positive effect on nest survival (X^2=5.17, p=0.02).

Table 2 Comparison of models explaining nest survival in dickcissels, with null model first, base model second, followed by three models adding measures of the number and timing of within-territory female nesting

Model	K[a]	AICc	ΔAIC	w_i[b]	β[c]	SE
Constant DSR	1	469.93	31.43	0.00		
B_0 + age + age^2 + stage + year	5	441.65	3.15	0.13		
B_0 + age + age^2 + stage + year + harem[d]	6	438.50	0.00	0.62	0.26	0.12
B_0 + age + age^2 + stage + year + pair[e]	6	441.67	3.17	0.13	0.32	0.23
B_0 + age + age^2 + stage + year + overlap[f]	6	441.72	3.22	0.13	0.30	0.22

The number of parameters, AICc, delta AIC, and Akaike's weight are reported for each model. Effect size and standard error are reported for polygyny variables

AICc Akaike Information Criterion

[a] Number of parameters

[b] Akaike's weight

[c] Effect size

[d] Maximum number of simultaneously nesting females

[e] Monogamous or polygynous on day clutch was initiated

[f] Whether nesting activity overlapped that of any other female on the territory

Discussion

Our results concerning the relationships between social and genetic mating in dickcissels generally indicate a positive covariance between polygyny and paternity, although the fit of the data to the predictions was not always strong. First, a male's within pair siring success tended to increase, albeit nonsignificantly, with harem size. Second, there was no evidence of trade-offs affecting mate guarding (e.g., Westneat 1993) since paternity was similar whether a polygynous male's mates had overlapping fertile periods or not. Instead, paternity was higher in nests where at least a portion of nesting activity overlapped that of another female on the same territory. Additionally, females that settled with mated males produced broods with similar paternity as females that settled either monogamously or as primary females. Third, extra-pair siring success increased with harem size, although one possible concern is that biased sampling contributed to this result. Polygynous males defended territories longer than other males. Simply by being on the study site longer, polygynous males increase the number of opportunities they have to sire extra-pair young (more nearby nest starts) and the probability that at least one of these offspring will survive to sampling. Nonetheless, the positive association between extra-pair and within-pair mating success remained significant when this sampling bias was accounted for. Fourth, there was no evidence that male mating status influenced female settlement decisions. Such evidence, taken as a whole, lends some support to the idea that polygynous males are successful in both mating contexts and apparently experience few trade-offs between them.

The apparent lack of trade-offs in dickcissels is fairly atypical. In a review of 21 studies, Vedder and colleagues (2011) found that polygynous males suffered higher frequencies of EPP than monogamous males in seven studies. They found only a single study demonstrating the opposite pattern, although nonsignificant positive associations were found in red-winged blackbirds and great reed warblers (Westneat 1993; Weatherhead and Boag 1995; Hasselquist 1998). Some of the studies uncovering evidence of trade-offs were on species in which either polygyny (e.g., Dunn and Robertson 1993) or EPP (e.g., Freeland et al. 1995) are rare. In species where both polygyny and extra-pair paternity are common and adaptation to their co-occurrence is more likely, more complex relationships exist. For example, in red-winged blackbirds, polygynous males lose paternity when a female's fertile period overlaps the arrival of a new female, yet polygynous males tend to have higher paternity overall (e.g., Westneat 1993), suggesting that processes that trade-off and that produce positive covariance exist simultaneously. In dickcissels, trade-offs appear even less important, although because of statistical power it is unclear whether they differ from red-winged blackbirds in this regard. In addition, most studies have focused on the relationship between polygyny and within-pair paternity, but in those studies that have been able to assess success at siring extra-pair young, our results join a growing body of evidence that suggests males who attract more social mates also gain more extra-pair paternity (e.g., Bollinger and Gavin 1991; Westneat 1993; Kempenaers et al. 1995; Weatherhead and Boag 1997; Freeman-Gallant et al. 2005).

There are several mechanisms that could produce these patterns of mating success in dickcissels. One possibility is that certain males are more competitive and thus better able to obtain and defend a high-quality territory. The ability to hold a high-quality territory could enhance both social and extra-pair mating success. For example, being able to defend a territory with abundant food could increase the number of social mates a male attracts (Verner and Willson 1966), decrease the number of extraterritorial forays those mates need to make (Vaclav et al. 2003), and could even attract neighboring females to the territory for foraging bouts and thereby increase opportunities for EPCs (Gray 1998). Previous studies provide mixed support for this idea in dickcissels. Harmeson (1974) found significantly more arthropods in the territories of polygynous versus monogamous male dickcissels, but this was true in only one of three sampling periods. Finck (1983) and Zimmerman (1966) found no differences in arthropod densities between monogamous and bigamous dickcissel territories. Nevertheless, these results do not entirely rule out the possibility that food availability is an important factor in male mating success. Finck (1983) found that males supplemented with food increased the amount of time they spent in activities related to female attraction (e.g., singing). Furthermore, conditions on the tallgrass prairie can vary substantially across years (Knapp et al. 1998), and arthropod abundance may be more important in some years than in others. It is also possible that some other aspect of territory quality is an important factor in male mating success. For instance, vegetation height, density, and composition have repeatedly been linked to both nest site selection and nest survival in this species (Hughes et al. 1999; Dechant et al. 2003; Berkeley et al. 2007; Frey et al. 2008). While it is not clear how these factors could influence extra-pair mating success, there is some support for their positive effect on social mating success (Zimmerman 1966; Finck 1983).

Another possibility is that, rather than attracting females to the territory itself, male behaviors that favor the acquisition of attractive territories also contribute to obtaining EPCs off the territory. For example, territorial disputes between neighboring dickcissels can involve chases and direct fighting. Males that excel in such contests could also be more successful in chasing extra-pair females and eluding or fighting their mates. Male dominance has been associated with male mating success, but this is often attributed to female preference for dominant males rather than male competitive ability (Otter et al. 1998; Woodcock et al. 2005). Experience could also be an important factor in both social and extra-pair mating success. Indeed, a number of studies have found that older, more experienced birds have higher reproductive success (e.g., Nol and Smith 1987; Weatherhead and Boag 1995; Poesel et al. 2006). The effects of age on male mating success have not been examined in dickcissels, and low return rates between years make the effects of experience difficult to assess in this species.

If females control mating, then female choice could result in the same males being successful in all mating contexts (Weatherhead and Robertson 1979; Hasselquist and Sherman 2001). Females will seek to pair socially with preferred males and resist copulation attempts by other males. When females are unable to settle with their preferred mate, they may still pursue extra-pair copulations with that male. In dickcissels, there is little evidence that females prefer particular male traits. Neither body size, bib size, nor the amount of time males spend singing led to higher social mating success (Finck 1983, 1984), but their impact on extra-pair success, either in increasing within pair paternity or affecting extra-pair siring success, has not been assessed in this species. Bright colors and song traits have frequently been implicated as targets of female choice in other species (reviewed in Hill 2006; Catchpole and Slater 2008), and male dickcissels have a bright yellow breast and use a simple song in mate attraction and territory defense. The effect of these traits on mating success has not been examined in dickcissels. So while evidence for female choice of male traits is lacking, it is possible females are attending to traits that have not yet been assessed in dickcissels. Thus, female choice for male plumage and song traits could be an important factor in shaping mating patterns.

We found no evidence that the proximity or number of conspecifics affected patterns of male mating success by increasing encounter rates between potential extra-pair mates. Moreover, we found that paternity was not influenced by the interaction between social mating success and breeding density. This result is not consistent with the trade-off hypothesis, but is consistent with the predictions of the choice/competiveness hypothesis. When females seek copulations only with preferred males, the number of other males in the immediate area could affect the range of choice, but might not affect the frequency of EPP (Lifjeld et al. 1994). Alternatively, especially competitive males may establish their dominance early in the season, leading to fewer attempts by neighbors to cuckold such males regardless of proximity.

We did find evidence that patterns of predation negatively correlate with male mating success, indicating potential compensating effects of polygyny in this species (Searcy and Yasukawa 1989). Polygynous male dickcissels maintained high realized reproductive success in the face of high nest depredation rates, and peak harem size was the only variable to successfully predict nest success. However, the presence of other nesting females on the territory at the same time as the focal nest and mating status of the female at clutch initiation did not significantly affect nest survival. This suggests that nest survival may be more influenced by the male or his territory, not by the benefits of nesting near other females.

The Kansas dickcissels exhibited a high rate of EPP, with more than half of the broods sampled containing at least one extra-pair offspring and 39 % of all chicks the result of extra-pair fertilizations. This level of EPP appears unusual since polygynous species typically have lower rates of EPP (11 %) than monogamous species (23 % EPP, Hasselquist and Sherman 2001; Griffith et al. 2002), although three other polygynous species exhibit similar levels of EPP (Freeman-Gallant 1997; Pilastro et al. 2002; Forstmeier 2003). Density, a factor sometimes associated with high rates of EPP in other species (Birkhead 1979; Westneat et al. 1990; Stutchbury and Morton 1995; Griffith et al. 2002; Stewart et al. 2010), did not contribute to EPP rates in dickcissels. Several other possible reasons for the high rate of EPP in dickcissels exist. First, the lack of male provisioning means that males are released from this time constraint on their pursuit of EPP (Werren et al. 1980; Westneat et al. 1990; Gowaty 1996; Wright 1998). It also means that males cannot further decrease provisioning in response to female infidelity, freeing females from this cost of extra-pair mating (Westneat and Sherman 1993; Mulder et al. 1994; Gowaty 1996; Arnold and Owens 2002; Griffith et al. 2002). Second, female dickcissels are known to foray off territory to forage (Zimmerman 1966). Such forays would increase the likelihood that females will encounter extra-pair males. Further study is needed to determine whether females actively seek extra-pair copulations when foraying off territory and to determine whether males also engage in extra-pair copulation attempts off territory.

Higher than average rates of extra-pair paternity, combined with a positive association between social and extra-pair mating suggest that sexual selection plays an active and important role in shaping mating patterns in this species. None of the three possible explanations above (territory quality, male competitiveness, and female choice) are mutually exclusive. It is possible that all three contribute to creating a positive association among polygyny, paternity, and extra-pair siring success. For example, females could prefer male traits that confer an advantage in territorial acquisition and defense. While the results of this study cannot distinguish among these mechanisms, there is some evidence that all three occur and may interact to produce the patterns observed. Data on the characteristics of successful males, as well as the ecological factors contributing to patterns of EPP are needed to elucidate the causes of high levels of EPP in a polygynous population with high variance in male matting success.

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Ethical standards The authors declare that all experiments comply with current US laws.

Conflict of interest The authors declare that they have no conflict of interest.

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