ORIGINAL ARTICLE

Mobbing for matings: dynamics, plumage correlates, and fitness impacts of conspicuous group extra-pair behaviors in the lark bunting

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Abstract

The widespread occurrence of extra-pair paternity (EPP) in birds adds rich complexity to our understanding of sexual selection and mating system evolution. Extra-pair matings are typically cryptic so for most species, we lack the detailed behavioral observations needed to fully determine whether both sexes benefit from EPP and when trait correlations with EPP are found, whether they reflect female choice or male intrasexual competition. Here we examine behavioral and morphological correlates of EPP in the lark bunting (*Calamospiza melanocorys*), a grassland songbird where EPP-seeking behaviors of males are unusually overt and conspicuous. Males sought EPP by closely following receptive pairs, often in groups. Virtually all observed extra-pair copulation attempts involved male aggression, were resisted by females, and larger females had a lower rate of extra-pair paternity in their nests. Male plumage traits predicted both male effort in seeking EPP (number of mating groups joined) and fitness gained through EPP; these same male traits have previously been linked to male-male competition but were not linked to consistent mate choice in lark buntings. There was no trade-off between investment in seeking EPP and fitness at a male's own nest, indicating that fitness from EPP is likely a potent driver of sexual selection in lark buntings, one that may not entirely be driven by female fitness interests.

Keywords Extra-pair copulation · Forced copulation · Mating system · Lark bunting · Sexual selection

Significance statement

Extra-pair matings and paternity are common in many birds that are otherwise socially monogamous, yet many behavioral and evolutionary questions remain unclear, in part because extra-pair matings are typically hard to observe. In the lark bunting, a prairie songbird, extra-pair mating behaviors are common, conspicuous, and easily studied, enabling an unusually in-depth study to determine which traits and behaviors predict success at obtaining extra-pair matings. Males sought extra-pair matings by shadowing pairs during the female's receptive period, often in small groups. Most extra-pair copulation attempts were aggressive and appeared forced. Male plumage traits correlate with the effort a male invested in obtaining extra-pair copulations, and paternity gained from EPP, but not with the male's ability to fend off extra-pair males at his own nest. That these same male traits correlate generally with male-male competition but not female mate choice bolsters the suggestion that males rather than females may drive the occurrence of extra-pair matings.

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Introduction

Animal mating systems have long been classified and studied, by patterns of social pair-bonds (Lack 1968; Orians 1969; Emlen and Oring 1977). Avian mating systems are particularly diverse and played an outsized role in the

development of mating system theory. This rich body of theory assumed that the patterns of social pairing we observe in a species reflect the actual genetic mating patterns (Verner and Wilson 1966; Pitelka et al. 1974; Wiley 1974; Emlen and Oring 1977; Wittenberger 1979). However, modern genetic methods now reveal that social and genetic mating systems are often uncoupled, sometimes spectacularly so, because males and females often mate outside the pair-bond (Birkhead and Møller 1992; Arnold and Owens 2002; Westneat et al. 1990; Kempanaers and Schlicht 2010; Brouwer and Griffiths 2019). The widespread occurrence of this extra-pair paternity (EPP) not only challenges our understanding of mating system evolution but also has important implications for sexual selection. EPP can increase variance in male mating success and therefore the potential for sexual selection, potentially explaining the occurrence of extreme sexual differences seen in many socially monogamous species (Birkhead and Møller 1992; Webster et al. 1995; Westneat et al. 1990; Schlicht and Kempanaers 2011).

A major gap in our understanding of EPP is that for most species, we lack information on the behaviors that occur during the attempted and successful copulations that lead to EPP (although not all copulations lead to paternity). However, such observations are critical in resolving some of the most contentious questions in studies of EPP—genetic methods can reveal the occurrence of EPP but cannot tell us how or why EPP occurs. Because extra-pair copulations are typically cryptic and difficult to observe, for the vast majority of species, we lack observations of the behavioral aspects of extra-pair mating needed to make full sense of why EPP occurs, despite decades of research focus (Dickinson 2001; Westneat and Stewart 2003). For example, which sex engages in forays to seek extra-pair matings—females, males, or both? Once the sexes encounter each other, are copulations solicited by the female, as would be expected if females gain fitness benefits from EPP (Jennions and Petrie 2000; Griffith et al. 2002; Pryke et al. 2010), or are extra-pair mating attempts aggressive, violent, and avoided by females, as would be expected if males benefit from EPP but females do not (McKinney et al. 1983; Westneat and Stewart 2003)? Finally, correlations between EPP and both male traits and male fitness indicate that EPP can drive sexual selection (Hasselquist et al. 1996; Dunn and Cockburn 1999; Thusisus et al. 2001; Webster et al. 2007). However, without observations of the behavioral interactions that underlie these trait correlations, we cannot know the mechanism of sexual selection involved: female mate choice, intrasexual male competition, or both (Westneat and Stewart 2003). Indeed, despite calls for added focus on these questions nearly two decades ago, the challenges of observing and measuring extra-pair behavior in the wild have limited our understanding of the drivers of extra-pair mating.

Perhaps the most important and contentious issue about EPP is whose fitness interests drive extra-pair matings (Westneat and Stewart 2003; Chaine et al. 2015). Males should always benefit from any chicks they sire that are raised in somebody else's nest (Bateman 1948; Trivers 1972), so the critical issue is whether and how females benefit from extra-pair copulations. Several potential female benefits have been proposed: direct benefits like male provisioning of chicks, indirect genetic benefits through high-quality offspring, increased genetic diversity of offspring, or insurance against infertility (Birkhead and Møller 1992; Jennions and Petrie 2000; Griffith et al. 2002). Most previous work has implicitly assumed that females benefit from EPP (Westneat and Stewart 2003), but only a few studies provide convincing evidence that females do benefit from EPP.

Tests of the female benefit hypothesis involve both behavioral and fitness studies. Convincing indirect behavioral evidence that females likely benefit from EPP comes from the dozen behavioral or tracking studies showing that females leave their territories to actively seek copulations from their extra-pair partners (summarized in Westneat and Stewart 2003). Some genetic studies have shown that EPP chicks are superior to within-pair chicks in some attributes relevant to fitness (Hasselquist et al. 1996). However, in some cases the superior performance of EPP offspring could simply arise from their non-random positions in the hatching order (Magrath et al. 2009; Ferree et al. 2010) rather than differences in the genetic quality of EP offspring, making any female benefit from extra-pair matings less clear. In addition, theory and a meta-analysis suggest that indirect genetic benefits to females are unlikely to favor EPP because the costs of lost male parental care likely outweigh these benefits (Arnqvist and Kirkpatrick 2005). However, this conclusion is contentious (Griffith 2007; Eliassen and Kokko 2008) and potential flaws to the theoretical analyses have recently been identified (Fry 2022).

For many studies, the indirect evidence for female benefit is equally compatible with male benefits alone driving the occurrence of EPP (Westneat and Stewart 2003), underscoring the need for behavioral information. In fact, a few such behavioral studies do provide fairly convincing evidence that many instances of EPP may be driven solely by the interests of the males seeking EPP. In these species, extra-pair matings appear forced and are actively and strongly resisted by females (McKinney et al. 1983; Townsend et al. 2010; Brekke et al. 2013). Forced EPP is particularly widespread in the waterfowl (McKinney et al. 1983), one of five avian taxonomic groups that have an intromittent organ (Briskie and Montgomerie 1997). Gowaty and Buschhaus (1998) proposed that forced copulations cannot be successful in birds that lack an intromittent organ, including songbirds. However, findings from one songbird study challenge this assumption by showing

that what appears to be forced copulations do correlate with male fitness (Townsend 2009; Townsend et al. 2010). Additional tests of this assumption are needed. More generally, whether forced copulations are rare or more common than initially assumed requires more direct observations of extra-pair behavior (Westneat and Stewart 2003).

The lack of consensus on a single unifying explanation for EPP may reflect the fact that there is not one. In the small sample of studies with indirect behavioral evidence, in some species EPP appears to involve the EP males' interests only (females vigorously resist male efforts), while females appear to benefit in other species (females actively seek out EPP), indicating that the explanation for EPP likely varies among species. Such variation would be expected if the occurrence of EPP depends on variable social and ecological conditions that affect the costs and benefits of extra-pair matings and EPP for the three participants involved—the paired male and female and the extra-pair male (Westneat and Stewart 2003; Chaine et al. 2015). Davies (1989) suggested that differences in the resolution of sexual conflict could account for the variation we see in avian mating systems generally, and this view may extend to the EPP component of mating systems as well. However, the small number of studies with convincing behavioral evidence for male- versus female-driven EPP makes it difficult to evaluate this idea. In addition, it is also important to keep in mind that behavioral observations provide only indirect evidence for which sex benefits from EPP; fitness data are needed for direct evidence (Westneat and Stewart 2003).

Here, we examine the behavioral and fitness correlates of extra-pair copulation-seeking behaviors in a songbird where these behaviors are unusually overt and conspicuous. Lark buntings (*Calospiza melanocorys*) breed on the shortgrass prairies of western North America and provided an early classic test of the polygyny threshold model (Pleszczynska 1978; Pleszczynska and Hansell 1980). However, the mating system of this species turns out to be more complex than previous characterizations—as we report here, many males invest heavily in seeking extra-pair copulations. Lark buntings are aggressively territorial until they attract a social mate, at which point they cease territorial defense or display. The birds move widely across the habitat and their movement is not restricted by territories or nest sites. Thus, mated pairs often roam far from the male's former display territory and, prior to clutch completion, many mated pairs are often closely followed by small groups of males seeking extra-pair copulations (Fig. 1). These male flocks are conspicuous and easily observed. Our ability to observe known individually marked males in the pursuit of EPP allowed us to characterize the behavioral, morphological, and fitness correlates of EPP-seeking behaviors in unprecedented detail and consequently to address several key unsettled questions about

EPP: (1) Behaviorally, how do successful and attempted extra-pair copulations occur? Do females solicit copulations from specific males or are copulations forced? (2) Do males vary in their investment in seeking EPP and, if so, does this variation correlate with male traits? (3) Do male traits correlate with EPP, and if so, why? And (4) Are there tradeoffs for males between seeking fitness from EPP and fitness from the male's own nest?

Methods

Study animal and area

Lark buntings breed on the short-grass prairies of western North America and are unusual among the sparrows for being highly sexually dichromatic (Shane 2020). We observed individually color-marked lark buntings on the Pawnee National Grassland, CO, USA, (40°38'26.7"N, 104°29'15.7"W) during the breeding season (May–July) on a 50-ha study site (1999–2001) that was expanded to 80 ha (2002–2003). The conspicuous black and white males are visible from long distances on the treeless shortgrass prairie habitat and pairs and groups were easily found and followed. Polygyny has been reported in some populations (Pleszczynska 1978); most lark buntings are socially monogamous at our site but modest levels of sequential polygyny occur, almost entirely through polyterritoriality (BEL and ASC, unpubl. data). Males defend territories upon arrival on the breeding grounds but then cease defending their territories when they obtain a mate (Chaine and Lyon 2008b). For a temperate zone passerine bird, male parental care is particularly well developed in lark buntings—in addition to feeding the nestlings and fledglings, typical of many songbirds, male lark buntings also assist with incubating the eggs (Barna 2004). This high level of male parental care occurs despite the high levels of extra-pair paternity (Chaine and Lyon 2008b).

Trapping and banding

In all facets of the study, it was not possible to record data blind to the identity of the birds because our study involved focal animals in the field. We trapped birds in Potter traps away from their territories at baited feeding stations throughout the season, and all individuals were measured and marked with unique color band combinations for field identification of individuals (Chaine and Lyon 2008b). Most males observed in the male flocks that follow mated pairs were banded, individually-identifiable birds because philopatry of banded birds is high across years and also because were able to quickly capture and band most new unbanded birds early in each breeding season since the birds forage broadly across

Fig. 1 Mobbing in lark buntings. **A** Illustration of a pair of buntings being mobbed by two males that follow the pair closely, seeking extra-pair copulations. **B** Photograph of a female fleeing from a forced copulation attempt by mobbing males. **C** Distribution of the number of different pairs mobbed by each male, during a given breeding season. Only mated males ($N = 233$ males) are included, and males observed in more than one breeding season are included for each season they were observed. Painting by Christopher Schmidt, photo by Bruce Lyon
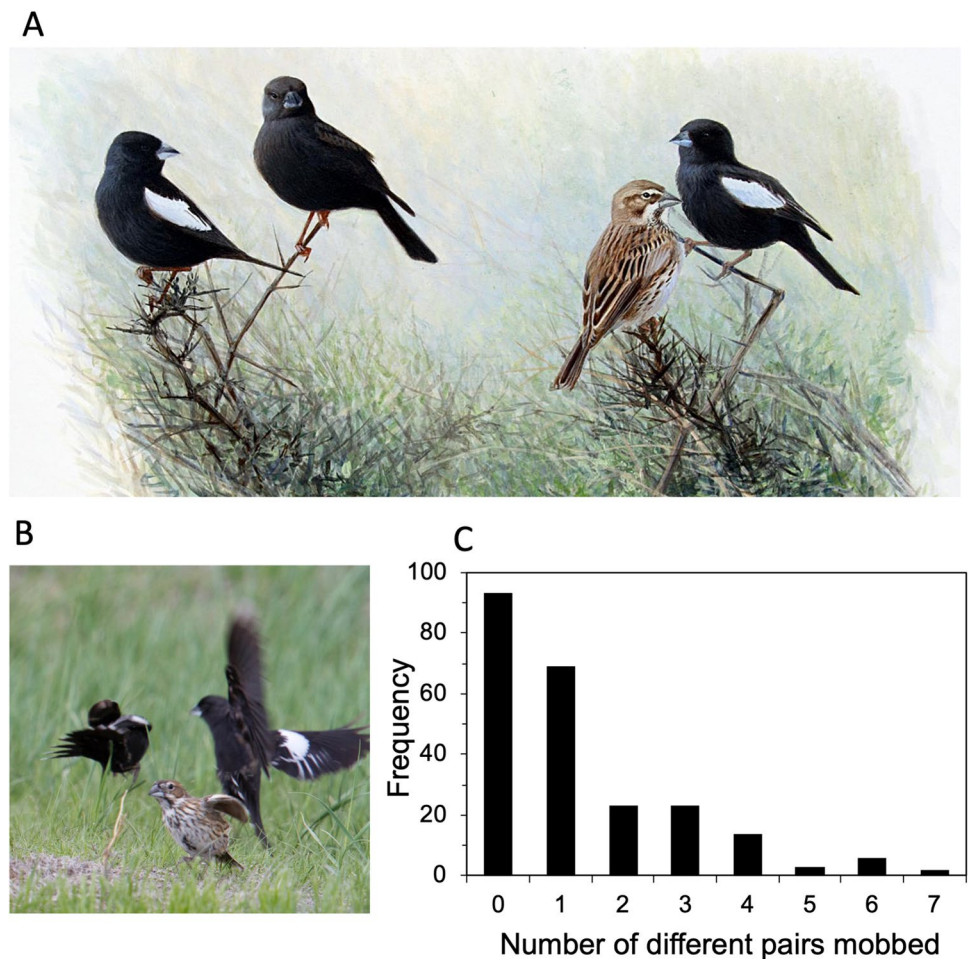
the study area and can be trapped at regular feeding stations we established (Chaine and Lyon 2008b). Most females and some males were trapped at their nests. We collected blood samples (~ 20 µl) for paternity analyses from all trapped individuals and from nestlings just prior to fledging and stored them in Queen's lysis buffer (Seutin et al. 1991). At capture, we measured several morphological traits, including both body size measures and plumage traits (see below).

Measuring morphological and plumage traits

We measured body mass and length of four traits for each adult: exposed culmen, beak from tip to nares, tarsus, and wing chord. As in previous work (Chaine and Lyon 2015), we reduced these measurements to two orthogonal measures with principal components analysis (PCA, accounting for 67% of the variation in these traits) signifying beak size (exposed culmen loading = 0.87; beak to nares length loading = 0.86; tarsus loading = 0.07; wing chord loading = − 0.01) and body size (tarsus loading = 0.76; and wing chord loading = 0.78; exposed culmen loading = − 0.01; beak length loading = 0.08) after VARIMAX

rotation. We calculated residual mass as the residual of mass regressed on the body size principal component. The problems of using residuals instead of multiple regression are well known (Freckleton 2002). However, here we use residual mass as an index of condition, not as an alternative to multiple regression. Moreover, the use of residuals is problematic when variables are too strongly correlated (Freckleton 2002), but male traits in lark buntings are only weakly correlated (Chaine and Lyon 2015).

Males molt from their dull winter plumage into their conspicuous alternate (breeding) plumage during migration. Males are mostly black while females are brown, and males have white wing patches that are both larger and brighter than those of females. We measured five male plumage traits that vary considerably among individuals following methods described in Chaine (2006) and Chaine and Lyon (2015). "Wing patch size" was assessed either as a rectangle by length and width (1999–2000) or as precise area extracted from digital photographs (2001–2003). As such, wing patch size was centered and standardized for each method separately (Chaine and Lyon 2008b).

To obtain the measure "body color," we scored the color of black body feathers into four rank categories of

black coloration, based on reference photographs, for four different body regions (head, nape, back, rump) and then combined the measures into a single color measure using PCA (loadings: head $= 0.63$, nape $= 0.73$, back $= 0.82$, rump $= 0.82$): the PCA score accounted for 66% of the trait variation on a single axis. These rank estimates of color are highly correlated with spectrometer measures of black coloration taken for the same individuals from 2001 to 2003 (Pearson's $r = 0.6$, $n = 337$; Chaine 2006). Finally, we determined two other measures of plumage color: "% rump black" was the proportion of black feathers versus brown feathers on the rump, while the "% body black" was the proportion of black feathers for the rest of the body excluding wings and tail (i.e., head, nape, back, and belly combined). We examined these two body regions separately because they are morphologically distinct and our behavioral observations also indicate that they are used in somewhat different behavioral contexts. All measures were significantly repeatable (Lessells and Boag 1987) within a year, based on measurements of males captured two or more times in the same year (repeatability $= 0.63–0.92$, Chaine 2006; Chaine and Lyon 2015).

Determining the pairing status of males

To determine male residency status, territory location, pairing status, and the outcome of aggressive social interactions, we observed each resident male at least every other day for 10 to 30 min from when they first established their display territories to when their females completed laying their clutch of eggs. We monitored nests daily to determine the number of chicks each pair successfully fledged. Some males were only seen once after banding and may have been transients and were excluded from analyses. We also distinguish between known mated males and unmated males that were never seen with a female or associated with a nest. Unmated males could include transients, males that established territories but failed to attract a female, or males that had a mate and nest away from our study site but that visited our study area to mob pairs. More than half of the unmated males were observed defending territories on the study site and therefore were confirmed residents, not transients (57%, $N = 145$ unmated males).

Male social mating status (mated, unmated) was determined either by male association with a nest or using behavioral indices (Chaine and Lyon 2008b). Most of the males designated as mated (207/233 mated males) were confirmed as paired by identifying them when they were flushed from their nest, either during incubation or when seen feeding chicks, but in most cases, they had previously been identified as a paired male based on behavioral criteria outlined below. In no case did more than one male incubate or feed at a single nest. In some cases, males were considered paired with a female if three or more of the following criteria were met: (1) they were seen closely associating with a female alone on several consecutive days, (2) the pair conducted characteristic behaviors when alone (unforced copulations, male post-copulatory display, mate-guarding behavior), (3) the male no longer displayed on his former territory and in some cases, (4) the male was seen clearly defending a female during neighbor harassment. Many males that fit these criteria were also subsequently associated with a nest, thereby validating our method of assessing pair status from behavioral data.

Behavioral observations of male mating flocks

To facilitate description of our observations, we refer to the small groups of males that follow mated pairs as "mating flocks " and the activity of following pairs to seek extra-pair copulations as "mobbing," since the behavior of groups following target individuals superficially resembles flocks of birds that follow and mob predators. To quantify the occurrence of mobbing behavior, we conducted focal observations of all known pairs of birds that were either not yet nesting or were in the egg-laying stage. We assumed that focal pairs at these breeding stages were potential recipients of extra-pair copulation-seeking males (e.g., females were fertile and male copulations could result in paternity). Once such focal pairs were found, we conducted standard 30-min observations (< 30 min if we lost sight of the pair), recording the identities of all banded males that mobbed the pair and noting all attempted copulations. In addition to these scheduled observations, we made opportunistic observations of any mating flocks we happened upon. The latter observations inflate the estimate of the overall rate at which mobbing occurs. However, our interest was not in the overall mobbing rate but in determining which males participated in mating flocks, which pairs were followed by these flocks, and identifying correlates of mobbing; inclusion of fortuitous encounters of mobbing events should not bias the identities of recipient and mobbing males but instead increases overall sample size. Our study plot was long and narrow and surrounded by suitable habitat with nesting buntings. As a result, many resident banded males on the study grid would likely have mobbed additional unbanded males adjacent to the study grid. We did not follow mating flocks where the recipient focal male was unbanded, so our sample of the total number of focal pairs mobbed may be incomplete for some males but our sample should be random with respect to traits of mobbers or the recipients of mobbing.

Paternity analysis

We conducted paternity analyses to measure male fitness, including within-pair and extra-pair success (details in Chaine and Lyon 2008b). We genotyped 492 progeny, 324 potential sires, and 154 nesting females using 6 hyper-variable microsatellite loci (Mme10, Mme12, Mme8, Mme2: *S8*, FhU2: *S9*, Gf06). Fragments were amplified using standard PCR techniques with fluorescently labeled primers, analyzed on an ABI3100 sequencer with ROX500 size standard (Applied Biosystems, Foster City, CA), and all peaks were scored manually by ASC. We used Cervus software (Marshall et al. 1998) to exclude social mates as sires in each brood and assign paternity of extra-pair offspring with 98% exclusion probability given that the female was known on nest (88% exclusion probability if neither parent had been known). The mothers at all nests were known based on female associations with the nest (incubation, chick feeding) and these females were never excluded as parents by the analysis using Cervus. Paternity was assigned if the male could not be excluded at a $P < 0.15$ level on the basis of 100,000 run simulations that used actual allele frequency data, the capture rate of males (90% from field observations), and a 1% genotyping error rate (Marshall et al. 1998). Allelic identities were identical for 68 samples that were typed twice (from the various loci we used). When the social mate was excluded as the sire, we searched for extra-pair fathers in a sequential procedure, first including neighbors, and then more distant males where required, using the same criteria (LOD score; likelihood of the odds) as for nesting males (Richardson et al. 2001; Berg 2005). Significance tests by simulation require an estimate of the number of potential sires, but since neighborhood sizes varied for each male and for the level of analysis (neighbors vs. whole population), simulations were run separately for each year and each neighborhood size. In cases where more than one extra-pair male could have feasibly been a sire based on the LOD score from Cervus, we used differences in LOD score and number of mismatched alleles to assign paternity to the more likely male. With this approach, we were able to assign a sire to 96% of all nestlings (485/503) including 88% of all extra-pair nestlings at the $P < 0.15$ confidence level. In our previous parentage study, we assigned paternity at the more stringent level $P < 0.05$ (Chaine and Lyon 2008b). Results presented here are similar to this more stringent criterion but the $P < 0.15$ cutoff increases our sample of EP sires (55 more chicks assigned a sire, most at the $P < 0.1$ criteria).

Repeatability of mobbing

We used the rptR package (R version 4.0.2: Developmental Core Team (2020), Stoffel et al. 2021) to assess the repeatability of mobbing behavior for males. We assess two aspects of mobbing behavior: the total number of mating flocks a male was observed in for a given year and the total number of pairs he mobbed in a given year. In total, our dataset included 378 males with 69 that were present in multiple years.

Correlates of mobbing and extra-pair paternity

We determined the timing of mobbing with respect to the recipient female's timing in the nesting cycle for two years of the study, 2001 and 2003. The timing of a female's nesting cycle was categorized relative to egg laying and the contents of her nest: prior to and during egg laying, during incubation, chicks at the early and mid-nestling stage, older nestlings about to fledge or in the process of fledging, and after the chicks fledged or the nest was depredated (females renest after nest predation and several females had second broods after fledging chicks from their first nest). Prior to and during egg laying or after a successful or failed nest are periods when the female is likely fertile, while she would be expected to be much less fertile, if at all, during incubation and most of the nesting period. There were a couple of cases of mobbing on the day prior to fledging or on the day of fledging; this may be a time when females are already preparing to begin a second brood and may be fertile.

We conducted three different analyses using GLMM with the appropriate distribution in the lme4 package (R version 4.0.2, Bates et al. 2015). All models included fixed effects and both year and male ID as random effects, but because some models did not converge, we conducted a model reduction procedure on random effects (Zuur et al. 2009). We compared models with and without each random effect and retained the model with the lowest AIC which in all cases was > 2 lower than the next lowest model. In contrast, we retained all fixed effects and did not conduct model reduction as those were our variables of interest. We first assessed which male size and plumage traits correlate with fitness from EPP using a Poisson distribution, with a number of extra-pair chicks sired in a given year as the dependent variable and several size and plumage traits as fixed effects, and individual male identity was retained as a random effect in the best model. We next assessed which male size and plumage traits correlate with mobbing effort using a Poisson distribution, with a number of different pairs mobbed in a given year (effort) as the dependent variable and several size and plumage traits as fixed effects, and both individual male identity and year were retained as random effects. Finally, we assessed which male size and plumage traits correlate with fitness from EPP using a Poisson distribution as above but while also controlling for mobbing effort on fitness. The model included the number of extra-pair chicks sired in a given year as the dependent variable and size and plumage
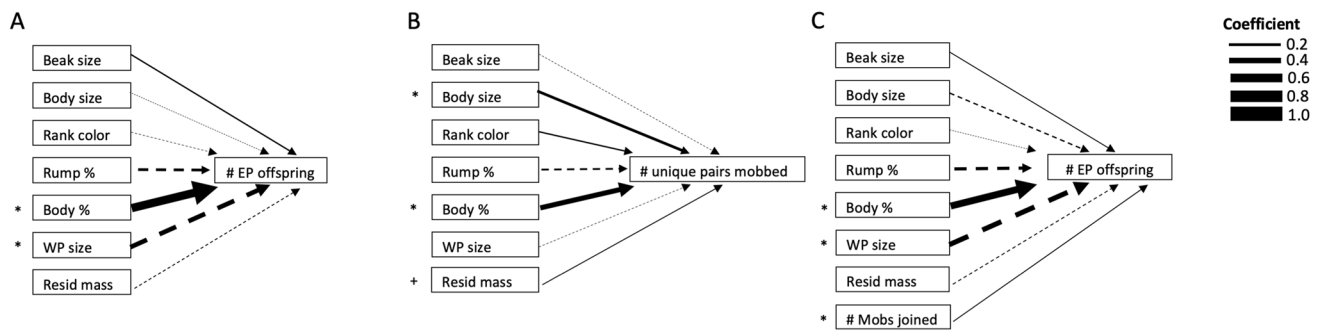
Fig. 2 Association between male traits and either mobbing-related behaviors or extra-pair fitness. **A** Male traits and number of extrapair offspring sired. **B** Male traits and number of pairs mobbed. **C** Male traits and number extrapair offspring sired, with number of mating flocks joined as a covariate. Full model and estimates for each trait are from a GLMM with appropriate error structure. Arrows between traits and mobbing effort as fixed effects, and only individual male identity was retained as a random effect.

traits and male behavior/fitness traits represent the estimated coefficient from the model. Weight of the arrow indicates the value of the partial correlation coefficient and solid arrows indicate a positive relationship whereas dashed arrows represent a negative relationship. WP size is wing patch size. $N = 373$ for all analyses. Significance of each factor in the original GLMM is designated as $*P < 0.05; +P < 0.1$

Fitness trade-offs between mobbing and paternity lost in the home nest

To assess whether mobbing behaviors come at a cost of either loss of paternity or decreased fitness in the male's own nest, we constructed two GLMMs using the appropriate distribution in the lme4 package (R version 4.0.2: 2020). As above, we simplified random effects using an AIC approach. The first model assessed whether the proportion of extra-pair chicks in a focal male's own nest was influenced by the number of times he was observed mobbing other pairs, using a binomial distribution. We used the cbind function between the number of extra-pair young and the total number of young in the nest to generate a proportion EPP. The best model did not include any random effects. Second, we assessed if the number of within-pair young that successfully fledged from a male's own nest was associated with the number of times he was seen mobbing other pairs as a fixed effect, and only male ID was retained as a random effect in a model with a Poisson distribution.

Correlates of mobbing and extra-pair paternity of the recipients of mobbing

To assess whether plumage and size traits predict a pair's vulnerability to mobbing, we constructed two GLMMs using the appropriate distribution in the lme4 package (R version 4.0.2). As above, we simplified random effects using an AIC approach. The first model assessed whether male traits correlate with the number of mobbers a male was mobbed by in a given year using a Poisson distribution, with a number of mobbers as the dependent variable and size and plumage

traits as fixed effects, and the best model did not include random effects. The second model assessed whether male traits correlate with fitness lost to EPP by in a given year using a Poisson distribution, with proportion of EP chicks in a male's nest in a given year as the dependent variable (using the cbind function again) and size and plumage traits as fixed effects, and only individual male identity retained as a random effect. We repeated these same two analyses for the female in each pair, although for females, we have morphological data but no plumage data. Both the model examining the number of males that mobbed a female and the proportion of extra-pair young in her nest included female ID only as random effects.

Results

### Rate and correlates of extra-pair paternity

Extra-pair paternity was common in our population and an important component of male fitness: 27.4% of all offspring were extra-pair ($n = 492$ offspring) and 49.7% of nests ($n = 148$ broods) contained at least one extra-pair chick. Fitness gained from EPP correlated with several male traits. Of the seven male traits included in the model, the percentage of black plumage on the body (excluding rump) was positively correlated with the number EP chicks sired (Fig. 2A, ESM Table S1). The size of the white wing patch, in contrast, was negatively correlated with number EPP chicks sired. Different mechanisms could account for the relation between these male traits and fitness from EPP: EPP could be driven by female choice of extra-pair partners with these particular traits or reflect male dominance and the ability to coerce or force extra-pair matings related to male traits (Chaine and Lyon 2008a). To distinguish between these explanations,

we examined the behavior and social aspects of behaviors involved in the occurrence of extra-pair matings.

The high frequency of extra-pair paternity is in part the result of overt EPP-seeking behavior that we refer to as mobbing—mated pairs are frequently followed by one or more males clearly seeking extra-pair copulations (Fig. 1A). Mobbing males closely follow the mated pair, often so closely (1–2 m) that in some mating flocks, it would have been difficult to distinguish the social mate based on proximity to the female alone. Oddly, the mated male of the pair often tolerates the mobbers and overt aggression towards mobbers was quite rare. Copulations were also quite rare and in most observations of mating flocks, males simply shadowed the mated pair. For the attempted or successful copulations that did occur (see below), we could not determine any particular behavior or factors that triggered the attempts—one or more males seemed to suddenly fly to the female and attempt to copulate.

Several factors lead us to conclude that the groups of males that shadowed pairs were seeking extra-pair copulations and that the groups did not serve some other social function like foraging or reduced risk of predation. First, females should also benefit from any such group foraging or predator defense benefits of flocking but females never joined these flocks, other than the female of the pair being followed. Second, the mobbing males do not feed but instead perch on bushes and are quite exposed and visible (Fig. 1). Third, the effort that males invest in mobbing correlates with their fitness from EPP (see below). Finally, the temporal occurrence of mobbing matches remarkably closely to a female's fertile period (Fig. 3). Most mobbing occurs before incubation begins up to clutch completion, is virtually absent during incubation and the nestling period, and then shows an uptick around fledging or after a nest suffers depredation (Fig. 3). Several females began second broods after successfully fledging their first brood and would have been fertile after fledging, and most females renested if they lost a nest to predation early enough in the season. In addition to the timing of mobbing, the timing of attempted and observed extra-pair copulations also closely matches the time in the females' nesting cycles when the female would have been fertilizable.

Roughly, half of all banded males were seen in at least one mating flock (51.1%, $n = 378$ males) both before and after starting their own nest if they eventually got a mate. Males that attracted a mate were more likely to be seen in at least one mating flock (60.0% of mated males, $n = 233$ males, Fig. 1C) compared to males that were never seen with a social mate but were seen in at least one mating flock (36.6% of males that did not get a mate, $n = 145$ males, Fisher's exact $P < 0.0001$). This pattern held when we excluded non-resident transients so it may occur because unmated males differ in traits that affect success with mobbing or because these birds remained for less time at the study site.

| Attempt cops | 9 | 2 | 0 | 0 | 6 |
| Copulations | 3 | 0 | 0 | 0 | 1 |
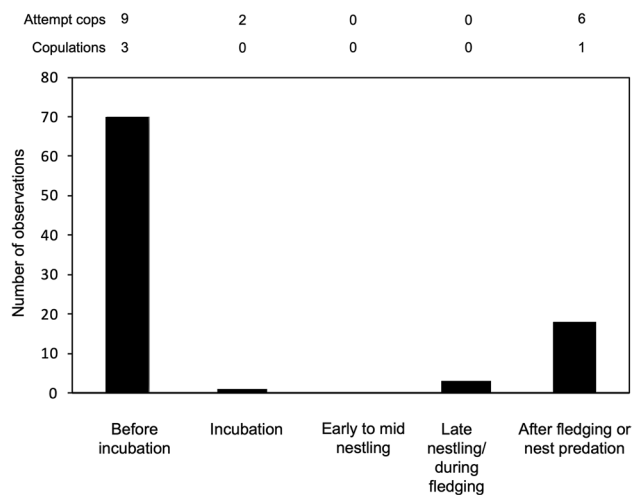
Fig. 3 Timing in the nesting cycle when focal pairs were observed being mobbed by mating flocks of males and when attempted or successful extra-pair copulations were observed. For pairs mobbed on more than 1 day, each day is included. $N = 92$ total pair-days for 44 unique pairs (a few males paired with more than one female and each pair was counted). Numbers of attempted and successful extra-pair copulations observed in each phase of the focal females' nesting cycles are shown above the graph. Observations of timing of mobbing are from 2 years (2001, 2003); observations of attempted and successful copulations are from the entire study

A map of representative males from 1 year of study illustrates the spatial nature of mobbing. Males typically mobbed nearby neighboring males but occasionally traveled further distances to join mating flocks (Fig. 4). It was also not uncommon to observe reciprocal mobbing, where two males mobbed each other when the other female was receptive (double arrows in Fig. 4).

Switching focus to the recipients of mobbing; virtually, all pairs were followed by mobbing males (Fig. 5): 69 of 71 pairs (97%) were mobbed by at least one male; this sample was limited to pairs that were observed for at least 30 total minutes. Mobbing is typically social in that mating flocks more often than not contain at least two males. The total number of different males seen mobbing a given focal pair across all observations ranged from 1 to 9 males (median 3) (Fig. 5A). The maximum number of males seen in a mating flock on a given day for each focal pair ranged from 1 to 6 males (median 3) (Fig. 5B).

## Evidence that most attempted extra-pair copulations are forced

Copulations between mated pairs differed in important ways from extra-pair copulations. We observed 489 copulations involving mated pairs in 201 h of observations of mated pairs. We also saw many attempted within-pair copulations where the male approached the female and clearly seemed interested in copulation but she prevented the
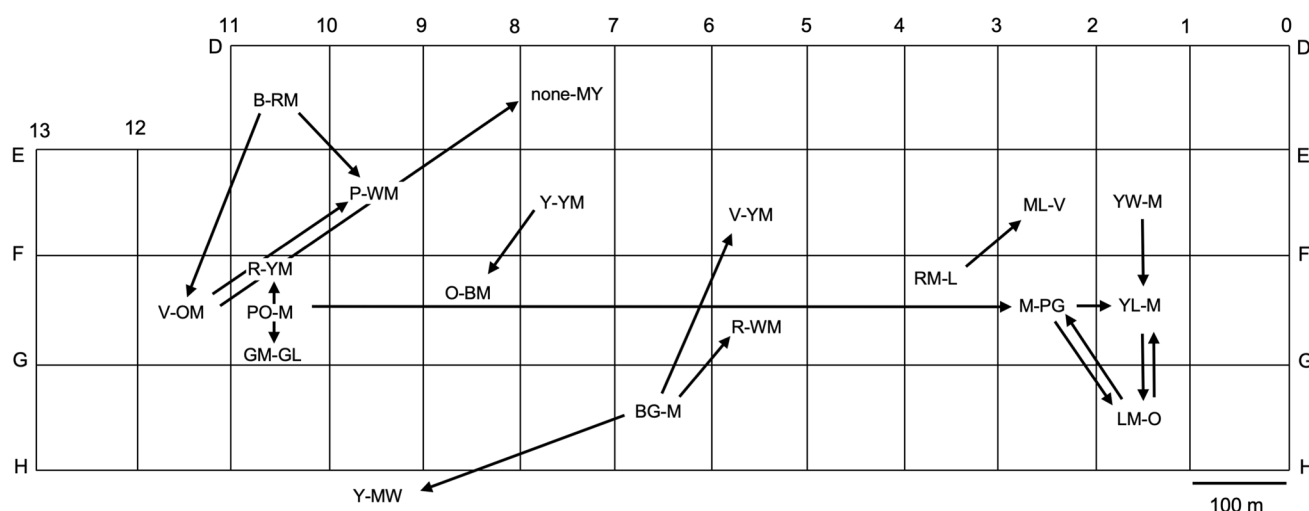
Fig. 4 Map of the 50-ha study plot showing the spatial relationships between mobbing males and the pairs they mobbed in 2001. Each grid square is 1 ha. The locations of male display territories are indicated by the letters for a male's unique color band combination.

Arrows extend from a mobbing male to the pairs he mobbed. Not all nesting males or mobbing males are included but for each mobbing male included, all pairs that were mobbed by the male are shown
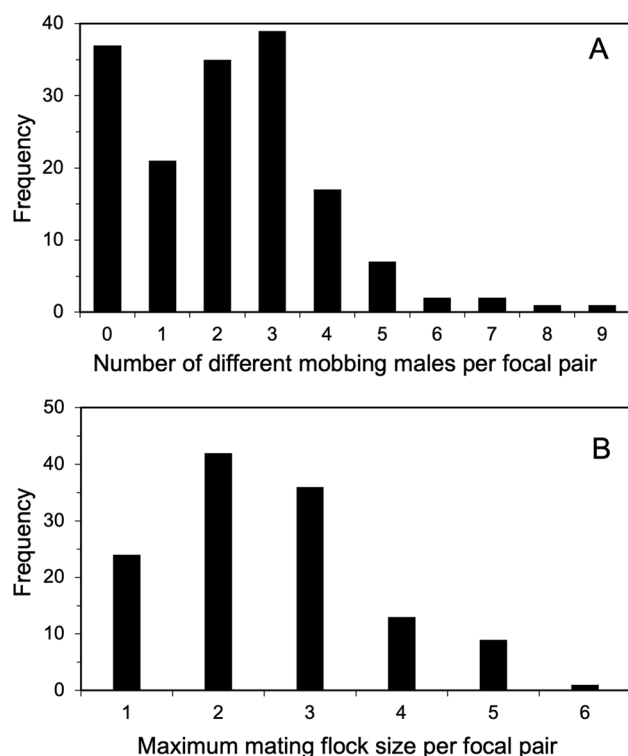
Fig. 5 The number of males that mobbed focal mated pairs. **A** Total number of different individual males observed across all observations for a focal pair (N = 378 focal pairs). **B** Maximum mating flock size observed for each pair that was observed being mobbed at least once

solicited the copulation with stereotypical songbird behavior: they crouched low and cocked their tails high. These copulations were also long and calm enough that we could determine if they were successful, as assessed by observing cloacal contact. Although not all female solicitations result in successful copulations, most do and, when successful copulations did occur, the female appeared to be in control. We only once saw successful within-pair copulations that appeared to be aggressive enough to be considered forced.

The nature of most attempted and successful extra-pair copulations differed strikingly from within-pair copulations. We observed 46 attempted extra-pair copulations during observations of mating flocks. We categorized these as attempted rather than successful copulations because they were rapid and chaotic, and it was impossible to tell if cloacal contact occurred, in contrast to the more slow-moving and subdued within-pair copulations. However, it is possible that some or many of these were successful. The extra-pair copulation attempts typically occurred when one or more males suddenly lunged at the female and attempted to pin her down. In some cases, males were observed pulling the female's tail in what appeared to be a maneuver to expose her cloaca. During these forced copulations, the social mate of the female sometimes also joined the fray, presumably in an attempt to get his sperm into the mix. For 22 of the 46 attempted copulations, we recorded enough information to determine whether they were forced, passive, or solicited. In all 22 cases, the copulations appeared forced—with the males lunging at the females and the females resisting the attempt by fleeing or challenging the males (e.g., Fig. 1B). The female resistance and evasive tactics suggest that females were trying to prevent the copulation.

copulation simply by moving away a very short distance when he got close and the male did not further pursue the attempt. In all cases of successful copulations, females

We observed eight extra-pair copulations that we felt we could accurately conclude were successful copulations. Two of the copulations were solicited, where a lone female flew up to a male and solicited copulation. In both cases, we did not know if the female was paired with another male. Three other successful copulations were deemed forced based on the aggressive behavior of the males and for the remaining three, we did not comment in our observation notes on whether the copulations were forced.

Correlates of mobbing effort and EPP gained from mobbing

Males varied in how often they were observed in mating flocks—some males never joined flocks while some others were seen in over 20 mating flocks (median number of flocks joined = 1; median number including only males that mobbed at least once = 2 mating flocks). Males also varied in how many different pairs they mobbed (Fig. 1C). The number of pairs a male mobbed was also highly correlated with the total number of mating flocks he was observed in (Spearman rank $rho = 0.98$ $P < 0.0001$). The correlation remains significant if males that never mobbed are excluded (Spearman rank $rho = 0.78$, $P < 0.0001$). There was also a seasonal pattern to mobbing: the earlier a male nested, the more mating flocks he was observed in (Spearman rank $rho = -0.29$, $P < 0.0001$). Many individual males were observed for two or more years so we could estimate the repeatability of mobbing behavior. The total number of mating flocks a male was observed in was repeatable across years ($R = 0.29 \pm 0.16$ SE, $P = 0.0030$) as was the total number of different pairs a male mobbed ($R = 0.26 \pm 0.15$ SE, $P = 0.0059$).

Importantly, mobbing effort also correlated with fitness: the number of extra-pair chicks a male sired was correlated with the number of pairs he mobbed (Spearman rank $rho = 0.25$, $P < 0.0001$). Notably, many of the specific males that sired EP chicks in nests were also observed mobbing the pair whose nest contained his EP chick(s). For pairs with EP chicks and those which were well-observed (≥ 90 min of observations during the female's fertile period), 50% of the sires of EP chicks had been observed specifically mobbing that pair ($N = 14$ sires at 12 nests). Expanding the sample to include focal pairs observed for ≥ 30 min, 38% of the EPP chicks could be matched to males that had mobbed the focal pair ($N = 28$ sires in 23 nests).

We determined whether several traits known to correlate with other aspects of sexual selection in lark buntings (Chaine and Lyon 2008a, b) correlate with a male's mobbing effort. Of the six male traits included in the model, body size and percent body black feathers (excluding rump) were significantly positively correlated with the total number of different pairs that a male mobbed in a given year (Fig. 2B, ESM Table S2). An identical pattern holds for an analysis of

correlates of total mating flocks joined rather than a number of different mated pairs mobbed.

Male traits correlate both with fitness from EPP (Fig. 2A) and effort invested in mobbing (Fig. 2B). Some of the trait correlations with EPP fitness could simply reflect the fact that the traits correlate with effort, and increased effort yields increased fitness [(e.g., % black on body correlates with both fitness (Fig. 2A) and mobbing effort (Fig. 2B)]. To determine whether male traits directly affect EPP fitness independent of mobbing effort, we repeated the analysis of extra-pair fitness in relation to traits but also included a number of mating flocks a male joined as a factor. The number of mating flocks a male was observed in does predict his fitness from EPP (Fig. 2C, ESM Table S3). However, even with mobbing effort taken into consideration, two male traits still correlate with EPP fitness: wing patch size and the amount of black feathering on the plumage excluding the rump (Fig. 2C, ESM Table S3).

We found no evidence that investment in obtaining EPP comes at the expense of a male's fitness in his own nest, either through increased risk of EPP chicks in his own nest or a reduction in the total number of his own chicks he fledged from his nest. The number of mating flocks a male joined was not associated with the proportion of chicks in his own nest that were EP chicks ($N = 158$, estimate = -0.031, $P = 0.36$), nor was it correlated with the number of chicks he sired in his own nest ($N = 158$, estimate = 0.022, $P = 0.13$).

Recipient's perspective: male and female traits, vulnerability to mobbing, and fitness lost through EPP

Of the seven male traits included in the model, males with more brown plumage on their rump were mobbed by more males in a given year (Fig. 6A, ESM Table S4). However, none of the seven male traits was correlated with the proportion of EP chicks in a male's nest (Fig. 6B, ESM Table S5). For females, none of the three morphological variables included in the model was correlated with the number of males that mobbed the pair (Fig. 6C, ESM Table S6). However, smaller females (body size PC) had a higher rate of EPP in their nests than larger females (Fig. 6D, ESM Table S7).

Discussion

Male lark buntings are social and conspicuous when seeking extra-pair copulations, making possible our detailed study into the behavioral and evolutionary dynamics of extra-pair matings and EPP. Specifically, we could integrate behavioral observations with trait and fitness measures to try to understand how the behavioral interactions between the sexes
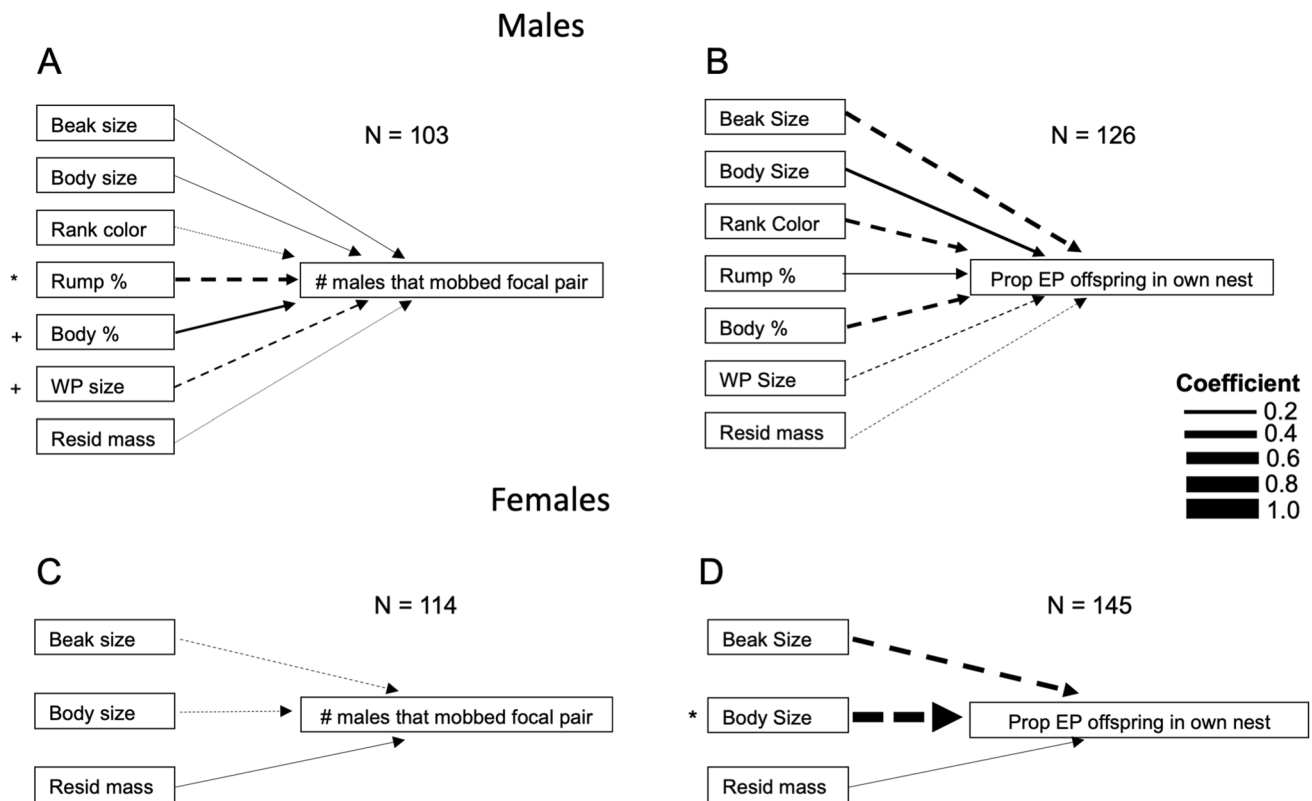
Fig. 6 Association between male and female traits and either vulnerability to mobbing or proportion of extra-pair offspring in the nest of the focal male or female. **A** Male traits and the total number of males a male was mobbed by. **B** Male traits and the proportion of chicks in his nest sired by other males. **C** Female traits and the total number of males a female was mobbed by. **D** Female traits and the proportion of chicks in a female's nest sired by extra-pair males. Full model and estimates for traits are from GLMM with appropriate error structure and the sample size is given below each diagram. Arrows between traits and behavior/fitness traits represent the estimated coefficient from the model. The weight of the arrow indicates the value of the partial correlation coefficient and solid arrows indicate a positive relationship whereas dashed arrows represent a negative relationship. WP size is wing patch size. Significance of each factor in the original GLMM is designated as * $P < 0.05$; + $P < 0.1$

influence the occurrences of extra-pair matings, which male traits correlate with extra-pair mating effort and fitness, and whether this is likely to reflect active female mate choice or simply the behaviors of EP-seeking males. Genetic analysis revealed that EPP is common; half of all nests have at least one EP chick and over a quarter of all offspring in the population are sired by extra-pair males. These are at the high end of reported rates (Arnold and Owens 2002; Griffith et al. 2002)—with a quarter of all male fitness deriving from EP offspring, seeking extra-pair copulations appears to be a profitable alternative male reproductive tactic in lark buntings. This fitness, however, is not randomly allocated among males; instead, males with more black feathers in their plumage and smaller white wing patches were more likely to sire extra-pair offspring. Our behavioral observations show why these traits correlate with EPP—males with these traits invest more in mobbing and also gain higher paternity for a given mobbing effort. In contrast, for the recipients of mobbing, few male or female traits predicted the risk of being attended by mating flocks or EPP in their nests. In other words, males with particular traits are successful at gaining extra-pair fitness, but male and female traits were less able to predict vulnerability to mobbing or extra-pair offspring in the home nest.

An unresolved issue in the study of mating systems is whether both sexes benefit from EPP. Since males should always benefit from siring chicks they do not have to care for (Trivers 1972), the critical question becomes whether females also benefit, and in what contexts. The answer likely varies among species as well as within species, depending on the specific female. The question of who benefits is important not only for understanding the evolutionary dynamics of extra-pair matings and paternity but also for making sense of male traits that correlate with EPP—do these trait correlations reflect mate choice for specific extra-pair males or competition among males to obtain EPP? Evidence that females might benefit can be indirect, for example observations of female actively seeking EPP (Neudorf et al. 1997; Double and Cockburn 2000), or direct, based on components of female fitness such as the performance of offspring sired

by extra-pair matings (Hasselquist et al. 1996). Our evidence that much of the EPP in lark buntings is male-driven is based on indirect behavioral evidence rather than a direct assessment of female fitness: extra-pair copulations are aggressive, appear forced, and are strongly resisted by females. Moreover, given that the intense scrambles that occur during these attempted matings often involve several males, there should be little scope for females to directly choose among the several potential EP sires.

We cannot, however, rule out the possibility that some extra-pair matings occur at times of the day when we did not observe the birds and that copulations at such times might have high probabilities of fertilizing an egg—for example, in some species, extra-pair copulations occur primarily before dawn (Double and Cockburn 2000), but we did not conduct observations during this time. Nonetheless, that half of all sires of extra-pair offspring in nests of well-observed pairs were seen mobbing those specific pairs suggests that mobbing accounts for a substantial proportion of EPP in our lark bunting population. Attributing half of the EPP chicks specifically to males that mobbed the focal pair is especially remarkable given that even our most observed pairs were observed for less than 5% (conservatively) of the total time that the females would have been fertile. Our very incomplete sampling means that we would have observed only a small fraction of the mating flocks that mobbed each pair. It could be argued that mobbing serves as a form of courtship, where the males return later (perhaps before dawn) to obtain high-quality copulations in peace, but we never observed the typical courtship flight songs male buntings use to court females ("skylarking," Shane 2020). Instead, we often observed a second multi-male flight display that is used in competitive male encounters ("aggressive song flight," Shane 2020).

Based on similar studies in other species, evidence for a female benefit differs among species, and sometimes even among populations and among individual females within populations (Westneat and Stewart 2003). We now have enough detailed behavioral and fitness information to be confident that females in some species determine the occurrence of EPP by controlling which males they mate with. Our study adds to the fairly small list of species for which there is compelling indirect behavioral evidence that many instances of attempted extra-pair copulations and EP chicks successfully sired are likely driven more by the EP male's interests than the female's (McKinney et al. 1983; Westneat and Stewart 2003).

An unusual aspect of our study was our ability to accurately assess the effort individual males invest seeking EPP, at least in terms of the total number of mating flocks joined or the total number of different pairs mobbed. Males varied considerably in their mobbing effort, and this variation correlated with male traits like body size and plumage color.

We are aware of only one other study that assessed conspicuous male effort in obtaining EPP. Low (2005) studied extra-pair-seeking behaviors in the male stitchbirds (*Notiomystis cincta*) of New Zealand that, like lark buntings, use forced copulations to obtain EPP, and often do so in groups. However, in contrast to our findings, Low (2005) did not find any male traits that correlated with the number of forced extra-pair copulation attempts, perhaps indicating that success at extra-pair matings reflects a random scramble for these matings.

In lark buntings, the same male traits predict effort invested in seeking EPP as well as fitness gained from this effort. This suggests that males strategically invest time and effort in seeking EPP relative to their ability to profit from the investment. Investment in mobbing could carry costs including reduced paternity in a male's own nest or a reduced number of offspring produced if he invests less parental care in his own nest (Magrath and Elgar 1997; Whittingham and Dunn 2005; Schlicht and Kempenaers 2011). However, no such trade-offs were observed in the lark bunting: EPP fitness was not correlated with fitness in the male's own nest in terms of proportion of paternity or the number of own chicks fledged. Open habitat and the highly conspicuous mating flocks could allow nesting males to reduce the costs of seeking extra-pair behavior as they could easily join mating flocks for short periods of time rather than dedicating considerable effort and time to seeking extra-pair opportunities. Males may also strategically invest in mobbing at times in their own nesting cycle where their care is less important.

Several previous studies also report correlations between male traits and EPP (Kempenaers et al. 1997; Akcay and Roughgarden 2007; Wells et al. 2016), but interpretation can be ambiguous without additional behavioral information. In many such studies, these trait correlations are assumed to reflect female mate choice but could equally result from male-competition driving EPP without female choice (Dickinson 2001; Westneat and Stewart 2003). Our behavioral observations suggest that the extra-pair copulations in lark buntings that occur during mobbings are driven by male but not female interests. Females solicit most copulations from their social mates but only rarely do so for extra-pair males and most attempted copulations from extra-pair males were resisted vigorously. Moreover, the male traits that correlate with mobbing effort and fitness—larger body size, greater percent black body feathers and smaller white wing patches—were all shown in a previous study to correlate with social dominance (Chaine and Lyon 2008a). In contrast, although some of these same male traits did correlate with mate choice in particular years, female preference for male traits changed from year to year and none of these traits consistently correlated with mate choice across all years (Chaine and Lyon 2008b). We do not know the specific behavioral

mechanisms that link these male traits to EPP, but a role for dominance seems likely. Extra-pair copulations are relatively rare and most mating flocks consist of groups of males closely shadowing a pair without actually attempting copulations—more dominant birds may be able to follow the mated pair more closely and be better poised to capitalize on rare and unpredictable forced copulation opportunities when they suddenly arise. Regardless, the fact that these male traits consistently correlate with EPP but not mate choice suggests that fitness from EPP could be an important driver of male sexual traits in lark buntings, as has been suggested for other species (Westneat and Stewart 2003; Webster et al. 2007; Schlicht and Kempanaers 2011).

From the recipient pairs' perspective, few male or female traits predicted vulnerability to mobbing or the proportion of EPP in the pairs' nests. Virtually all pairs were mobbed at least once so we assessed vulnerability to mobbing in terms of the total number of different males that mobbed each pair. Of the seven male traits we measured, only the amount of brown on a male's rump predicted the vulnerability of the male (and his mate) to being mobbed and this same trait is associated with being subordinate in male dominance interactions generally (Chaine and Lyon 2008a). However, this plumage correlated with mobbing vulnerability did not extend to fitness loss through EPP for the male. One explanation for why few male social traits predict vulnerability to mobbing is that there may be little that males can do to fully protect themselves from being followed by groups of males, nor from preventing occasional forced copulations by these groups. It appears that traits of extra-pair males rather than those of the males that are attended by mating flocks drive the dynamics of extra-pair paternity in lark buntings. Interestingly, female traits did not correlate with the number of males that mobbed the pair. However, larger females had a lower proportion of EP chicks in their nests which is consistent with the notion that females do resist forced extra-pair copulations, and that larger females are better at resisting and as a result have fewer EP chicks in their nest.

Conspicuous social EPP-seeking behavior like we observed in lark bunting is rare in birds and it is unclear what particular ecological and social factors explain its occurrence in lark buntings. Buntings live in extremely open habitats where the birds—particularly the black and white males—are unusually conspicuous. This may make it easy for males to find pairs, and even monitor information that could reveal a female's stage of nesting and likely fertility, such as observing nest building or within-pair copulations. The possibility that males can accurately determine a female's stage of nesting is supported by the remarkable overlap of the timing of mobbing with when individual females would have been fertile in their nesting cycles, including an uptick in male interest after fledging or nest predation.

The open prairie habitat might also contribute to the ability of the buntings to seek extra-pair copulations in groups since the males are conspicuous from a distance and mobbing males could attract additional males. Seeking extra-pair copulations in groups may have two consequences. First, the groups could explain why recipient males rarely try to chase off the mobbing males but instead opt to closely guard their females. If a male were to chase an intruding male, his undefended female might then be more vulnerable to being jumped by the other males. Indeed, we observed a number of instances where the focal male chased a sole EP-seeking male away only to return rapidly as a second EP-seeking male approached the unguarded female. Second, groups of males may be more successful in physically restraining the female and successfully obtaining forcing copulations. These possibilities lead to the interesting idea that males in a mating group may need to cooperate to gain extra-pair copulations despite then being in competition for fertilizing an egg.

Open habitat, however, is not essential for group extra-pair seeking behaviors generally because groups of EPP-seeking males have been reported in two other species, neither of which live in open habitat. Groups of male bearded reedlings (*Panurus biarmicus*) pursue females, seeking extra-pair copulations (Hoi 1997). These birds breed in dense reedbeds, which should make it harder for males to find females. However, females initiate the chases with displays and appear to benefit from the extra-pair copulations (EPC) so the dynamics differ greatly from what we observed in lark buntings. Furthermore, female resistance to EPC attempts does not occur (Hoi 1997). In the forest-dwelling stitchbird, EPCs also involve groups of males chasing females but, as with lark buntings, these EPCs appear forced (Castro et al. 1996; Low 2005; Brekke et al. 2013). As we observed with lark buntings, males appear to hold females down and hold their tails in a position that exposes the female's cloaca in a manner that facilitates forced copulation. Remarkably, this species is unique among birds with its face-to-face copulations, speculated to reflect a forced copulation behavior by males. In both lark buntings and stitchbirds, mobbing and aggressive behaviors to expose the female's cloaca provide key evidence that many EPCs are male-driven. More broadly, there has been considerable debate over whether successfully forced copulations are even possible in birds without an intromittent organ (Briskie and Montgomerie 1997; Gowaty and Buschhaus 1998; Westneat and Stewart 2003; Low 2005; Townsend 2009). Our findings add to an increasing list of studies showing that forced copulations can in fact lead to extra-pair fitness in birds without an intromittent organ (Low 2005; Townsend 2009).

The frequency of EPP varies dramatically among bird species but explanations for this variation remain elusive. Ecological factors like habitat, nesting synchrony, and density have all been suggested as drivers of variation

in the frequency of EPP but support for them has been inconsistent and varies among comparative studies (Sherman and Morton 1988; Birkhead and Møller 1992; Westneat and Sherman 1997; Stutchbury 1998; Westneat et al. 1990; Westneat and Stewart 2003; Biagolini et al. 2017; Brouwer and Griffith 2019). Difficulty in distinguishing between female-driven and male-driven EPP could, in part, explain the difficulty in finding ecological correlates for EPP because the two forms may differ in the way that ecological factors are expected to facilitate or constrain the occurrence of EPP. For example, when EPP is driven, in part, by the female's interests and behaviors, females should readily be able to find potential EPP partners because male song and displays make males conspicuous and relatively easy to find, irrespective of habitat, density, or breeding synchrony. In contrast, in species where EPP is primarily male-driven, the ability of males to find receptive females and obtain forced copulations is more likely to be affected by population density and habitat, as we have suggested for lark buntings. With open habitat and high population densities, females may be less able to hide from males seeking extra-pair copulations. This contrast between male- and female-driven EPP is nicely illustrated by the similar mobbing behaviors shown by two species that live in very different habitats and that show very different extra-pair dynamics—lark buntings and bearded reedlings. Extra-pair copulations are forced in lark buntings but solicited in reedlings. More generally, a clearer idea of whether EPP is female- or male-driven in a broad variety of species may be essential for understanding how ecological factors shape the evolution, occurrence, and behavioral dynamics of EPP in birds. In addition, the increasing evidence that forced copulations can be successful in birds without intromittent organs suggests that the prospects for male-driven EPP may be more widespread than previously believed.

Declarations

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