Active formation of mixed-species grouse leks: a role for predation in lek evolution?

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Behavioural ecologists have interpreted avian leks as products of sexual selection, in which males display socially to increase their opportunities to mate. However, without invoking reproductive queuing or kin selection, this paradigm does not necessarily explain why many males that fail to mate participate in leks. An alternative solution, that males also aggregate to reduce predation, has previously lacked compelling support. We show that mixed-species leks, comprising two congeneric grouse, form when single males or small groups of one species, the greater prairie chicken *Tympanuchus cupido*, join leks of another, the sharp-tailed grouse *T. phasianellus*. We documented the process by observing lek dynamics and comparing group sizes between mixed- and single-species leks. Joining implies that prairie chickens benefit from displaying with sharp-tailed grouse. The numbers of females of each species attending a lek increased with the number of conspecific, but not heterospecific, males. This suggests that the joining of heterospecifics is unlikely to increase mating opportunities, and leaves lowered predation risk as the most likely benefit of associating with heterospecifics. Active formation of mixed-species leks therefore suggests that predation may be sufficient to drive lek formation. The benefits of participation in mixed leks may be asymmetrical because prairie chickens display more and are less vigilant than sharp-tailed grouse.

Keywords: lek mating; mixed-species groups; *Tympanuchus*

1. INTRODUCTION

For the past 20 years, behavioural ecologists have interpreted the spectacular social displays of lek-breeding birds as a product of sexual selection in which males aggregate to increase their opportunities to mate (Höglund & Alatalo 1995). However, despite evidence that grouping can increase male access to females by multiple mechanisms (Alatalo *et al.* 1992; Gibson 1992; Lank & Smith 1992; Westcott 1997; Widemo & Owens 1995), this approach faces the unresolved paradox that many males participating in leks apparently fail to mate (Kokko 1997). Queuing, or kin selection, might resolve this difficulty (McDonald & Potts 1994; Kokko & Lindström 1996; Kokko *et al.* 1998; Petrie *et al.* 1999). Alternatively, like many foraging animals (Pulliam & Caraco 1984), lekking males might aggregate to reduce predation (Lack 1968; Wiley 1974). Grouping reduces individual predation risk in some dipteran swarms and anuran choruses (Höglund & Alatalo 1995). Predators are also observed regularly at avian leks, but their role has been difficult to test because predation is rarely seen (Höglund & Alatalo 1995).

Mixed-species groups provide an opportunity to analyse the economics of sociality in a context that is potentially uncomplicated by either kin selection or benefits based on access to conspecific sexual partners (Terborgh 1983). Thus, in a mixed-species mating aggregation, the main factors invoked to explain lek display are unlikely to apply, leaving reduced predation risk as the most probable benefit for associating with heterospecifics. Mating benefits might still be relevant to mixed groups involving closely related species if vestigial sensory biases predispose

females to visit groups of displaying heterospecific males (Phelps *et al.* 2001), even though the same females prefer conspecific males when choosing within a mixed-species group. Alternatively, if displaying with heterospecifics provides no benefits, mixed-species mating aggregations might form passively through common use of preferred habitat patches (Kimsey 1980), landmarks (Alcock 1984; Beani & Turillazzi 1990) or interspecific overlap in female traffic hotspots (Westcott 1994). These arguments suggest that reduced predation risk could be implicated as a benefit of lekking by demonstrating that (i) males of at least one species in a mixed-species lek actively join heterospecific males (implying a benefit); and (ii) this behaviour does not increase the opportunities to court conspecific females.

We examine these issues by analysing the formation of mixed-species leks by two congeneric grouse, the greater prairie chicken (*Tympanuchus cupido*) and sharp-tailed grouse (*T. phasianellus*) (henceforth referred to as prairie chickens and sharp-tails, and collectively as prairie grouse). These two North American species are distinct ecologically, morphologically and in the vocal and visual components of their male epigamic displays (Hjorth 1970; Schroeder & Robb 1993; Connelly *et al.* 1998), but nevertheless form mixed-species leks throughout a wide area of sympatry (Johnsgard & Wood 1968; Sparling 1980). Sympatric populations also hybridize at low frequencies (Johnsgard & Wood 1968; Sparling 1980; Ellsworth *et al.* 1994). As assumed by the predation risk hypothesis, prairie grouse are vulnerable to an overlapping set of avian and mammalian predators (Schroeder & Robb 1993; Connelly *et al.* 1998).

Whether a species has an active or passive role in mixed-species lek formation could be revealed both by observation of the process and by comparing group-size
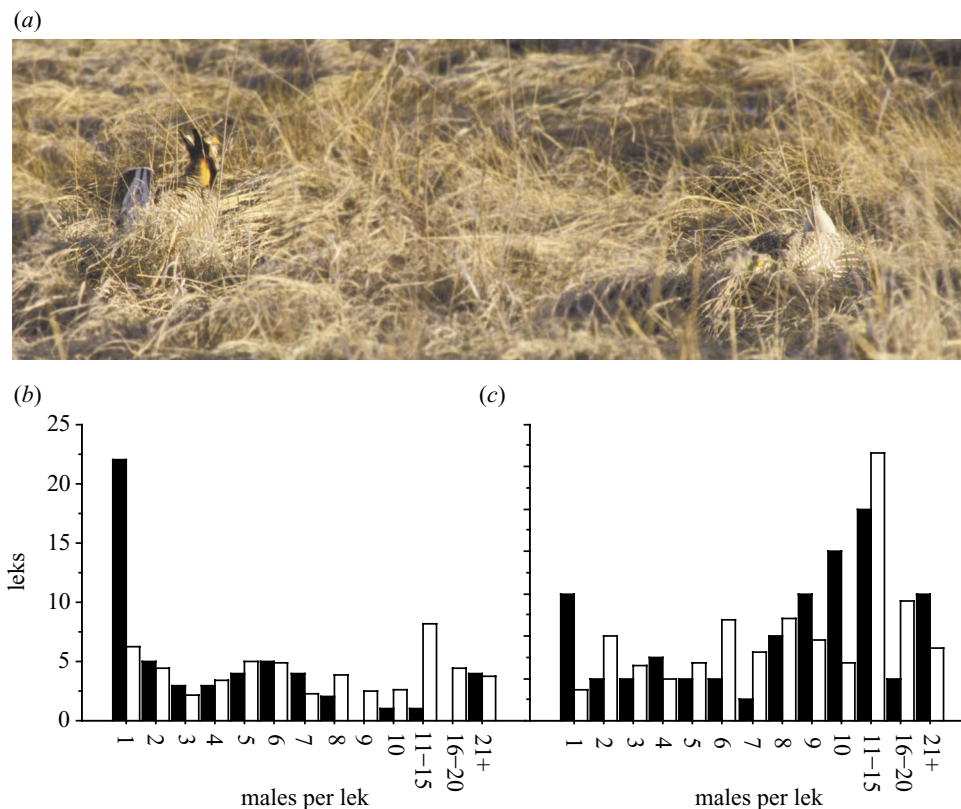
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Figure 1. (*a*) Greater prairie chicken (left) and sharp-tailed grouse (right) displaying at a mixed-species lek in the Valentine National Wildlife Refuge, Nebraska, April 1999. (*b,c*) Distributions of male numbers in 54 mixed leks (filled bars) compared with distributions expected from single species leks counted in the same years (open bars) for (*b*) prairie chickens and (*c*) sharp-tailed grouse. For computation of expected values, see § 2.

distributions between mixed- and single-species leks. Associating with heterospecifics is unlikely to provide the same range of benefits as with conspecifics (see above) and might incur additional costs, such as acoustic masking of advertisement signals (Schwartz 1993). Consequently, males should join a heterospecific lek only if they are unable to find other conspecific males nearby. As a result, a joining species should occur in smaller numbers in mixed- than in single-species leks, while a species that is joined should show no difference between the two contexts. By contrast, if mixed leks formed by passive merging of adjacent leks, the numbers of males of each species in mixed leks should either be similar to single-species leks or higher if larger leks more often merge with a neighbouring heterospecific lek due to their greater area. To examine how mixed prairie grouse leks form we combined short-term observations of lek dynamics with analyses of group-size distributions from long-term census data. We also investigated possible reproductive benefits of joining mixed leks by measuring visitation rates by females of each species to leks of varying size and species composition. Because of their relevance to the predation theory, we also summarize observations of male time budgets.

2. MATERIAL AND METHODS

We studied the formation of mixed-species leks at the Valentine National Wildlife Refuge, a 294 km² area of sand hills prairie grassland and wetlands in north-central Nebraska, USA. Leks of both species are widely distributed throughout the area, with prairie chickens concentrated in the wetter valley bottoms

and sharp-tails on drier upland sites (Aspbury 2002), reflecting the divergent habitat preferences of nesting females (Sisson 1976; L. L. McDaniel, unpublished data). Despite these differences, lek site characteristics overlap and the two species frequently display in close proximity (Aspbury 2002). Spacing patterns and their ecological correlates will be reported elsewhere.

To characterize short-term lek dynamics, the relationship between female lek attendance and lek composition, and male time-budgets, we watched nine leks of widely varying size and species composition (table 1) from first light until the end of the morning display period on 83 lek-mornings (more than 200 observation hours) between 19 March and 30 April 1999 using previously described methods (Gibson 1996). We estimated daily attendance during peak female attendance of both species by observing a rotating set of three leks per day on each of four days between 11 and 27 April. Daily peak values from counts at 10 minute intervals were used to measure the numbers of individuals of each sex and species attending the lek. Activities of all males were also recorded at 10 minute intervals. Activities were later grouped into four major classes (sexual advertisement, agonistic behaviour, inactivity and foraging) that included more than 90% of all activity in both species. Because inactive birds adopt more vigilant postures, we interpret inactivity as potentially vigilant behaviour. To compare species' time-budgets we used a single value for each species per lek: the daily mean proportion of males engaged in each activity from first light until one hour after sunrise.

To test propositions about the mechanisms of mixed-species lek formation we also analysed data on size and species composition of 1021 leks counted during annual population surveys

Table 1. Lek attendance (mean ± s.d.) by species and sex at nine focal leks in 1999.

lek	prairie chicken		sharp-tailed grouse		
	males	females	males	females	hybrid males
Cambell Lake	21.0 ± 1.0	7.0 ± 2.7	0	0	0
West Long Lake	11.8 ± 1.3	6.0 ± 4.2	0	0	0
North Cow Lake	6.8 ± 0.5	1.0 ± 0	1.8 ± 0.5	0	0
Little Hay 1	2.8 ± 1.3	1.3 ± 1.5	11.0 ± 1.6	5.3 ± 1.3	0
Little Hay 2	0.5 ± 0.6[a]	0[a]	8.3 ± 0.5	5.3 ± 1.9	0
West Round Lake	0	0	3.0 ± 1.7	1.3 ± 1.5	0
Ballard 2	0	0.3 ± 0.5	7.0 ± 0	1.0 ± 1.2	0
Ballard 1	0[b]	0[b]	11.0 ± 0.8	2.8 ± 2.9	2.0 ± 0
West Twin Lake	0[c]	0	27.8 ± 1.7	7.0 ± 7.6	0

[a] A male prairie chicken joined during the sample period and a female visited afterwards.
[b] One to four male prairie chickens attended on 5 days and one to two females on 4 days before the sample period.
[c] One to two male prairie chickens attended on 2 days before the sample period.

over 17 years (1983–1999). Each year, in the second and third weeks of April, one of us (L.M.) surveyed the study area for leks of both species during the first three hours of daylight and recorded the composition of each lek. Most leks were visited twice each year and the higher count was recorded. Observers recorded pairs of prairie chicken and sharp-tail leks as mixed if males of the two species were interacting socially, or were located within 50 m of each other. This classification was made without prior knowledge of theories about mixed lek formation.

We undertook two analyses of group size. First, for each species, we compared mean lek sizes between mixed- and single-species leks within 14 years in which mixed-species leks occurred. We tested the effect of lek type on group size by fitting a repeated measures ANOVA that included an autoregressive term to remove any serial dependence in mean lek size values between successive years (Littell *et al.* 1996). Second, to characterize more precisely how lek size distributions differ between mixed- and single-species leks, for each species we compared the pooled distribution of male numbers in mixed leks with an expected distribution generated by computing the relative frequencies of male numbers in single-species leks in each year, multiplying by the number of mixed leks observed in the same year and then summing across years. We compared observed and expected distributions using Kolmogorov–Smirnov one-sample tests.

Unless specified otherwise, summary statistics are reported as mean ± s.e.

3. RESULTS

(a) *Mechanisms of mixed lek formation*

We recorded several examples of male prairie chickens visiting and/or becoming established at focal sharp-tail leks observed in 1999 (table 1). Male prairie chickens visited two sharp-tail leks in late March before peak female attendance. In one case, a male displayed and fought at the lek periphery for two days but failed to establish a territory. A male prairie chicken joined a third sharp-tail lek in mid-April and was present on each sample day until the study ended. A female prairie chicken visited the lek and mated with him nine days after his first appearance. Two other mixed-species leks were visited by floater males of both species. We did not observe male sharp-tailed grouse visiting the two prairie chicken leks.

Between 1983 and 1999, 30.7 ± 2.5 prairie chicken, 23.0 ± 1.2 sharp-tail and 3.2 ± 0.7 mixed leks were counted annually. Mixed leks contained fewer male prairie chickens than prairie chicken leks counted in the same year (5.4 ± 1.0 versus 9.3 ± 0.4 males, $F_{1,13} = 13.07$, $p = 0.003$), whereas mean numbers of sharp-tails in mixed and sharp-tail leks were similar (9.1 ± 0.9 versus 9.6 ± 0.5 males, $F_{1,13} = 0.27$, $p > 0.6$). This is the pattern predicted if mixed leks are generated by prairie chickens joining sharp-tailed grouse. Relative to prairie chicken leks, mixed leks contained a large excess of singletons (figure 1*b*; Kolmogorov–Smirnov one-sample test: $D = 0.323$, $n = 54$ leks, $p < 0.001$), suggesting that single prairie chickens were more likely to initiate mixed lek formation than larger groups, that this combination was more stable, or both. Single male sharp-tails also occurred in mixed leks more often than expected (figure 1*b*), but the overall distribution did not differ significantly from that for sharp-tail leks ($D = 0.084$, $p > 0.5$).

(b) *Female lek attendance*

Females of both species visited leks in proportion to the numbers of conspecific males present. In multiple regressions, numbers of females of each species increased with numbers of conspecific, but not heterospecific males (data in table 1: prairie chicken females—model: adjusted $r^2 = 0.876$, $p < 0.001$; intercept = 0.034, $p > 0.9$; prairie chicken males: $b = 0.358$, $p < 0.001$; sharp-tail males: $b = -0.001$, $p > 0.9$; sharp-tail females—model: adjusted $r^2 = 0.683$, $p < 0.02$; intercept = 0.811, $p > 0.4$; sharp-tail males: $b = 0.247$, $p < 0.02$; prairie chicken males: $b = -0.046$, $p > 0.6$). This suggests that heterospecific males do not attract females of either species. The only possible exceptions involved female prairie chickens visiting, but not mating at, two focal sharp-tailed grouse leks (table 1). Although this raises the interesting possibility that prairie chickens might join sharp-tails partly to exploit such occasional 'mistakes', this conclusion is not supported by the multiple-regression analysis. Moreover, at one of the two leks, visits by female prairie chickens coincided with and closely followed transient display by prairie chicken males (described in § 3a) and thus do not necessarily indicate that females were attracted to sharp-tail displays.

(c) Male time-budgets

The two species allocated time differently among four main activity classes during the first 2 h of daylight (MANOVA: $F_{4,7} = 40.28$, $p < 0.0001$). Prairie chickens spent more time in sexual advertisement than sharp-tails (66.1 ± 11.0 versus $29.2 \pm 9.5\%$, $p < 0.0001$) and less time inactive (8.2 ± 5.0 versus $23.2 \pm 9.5\%$, $p < 0.01$). Prairie chickens also tended to spend less time in agonistic interactions (10 ± 9.8 versus $24.9 \pm 13.5\%$; $p = 0.06$), but foraging time did not differ (7.5 ± 10.3 versus $13.7 \pm 13.8\%$, $p > 0.4$). In short, prairie chickens allocated more time to display and less to potentially vigilant inactivity.

(d) Discussion

To the best of our knowledge, our analyses provide the first demonstration that mixed-species leks can form by one species actively joining another. We observed prairie chickens visiting and joining sharp-tailed grouse leks and the species-specific differences in group size between mixed- and single-species leks predicted by this process were robustly confirmed in a large population dataset. This conclusion does not preclude the possibility that additional processes may operate at frequencies too low to be robustly detected by our analyses.

As argued in § 1, active joining suggests that male prairie chickens benefit from joining sharp-tail leks. This interpretation assumes that joining males are not committing errors in species recognition as a result of misdirected social imprinting. The latter suggestion seems improbable since it would require interspecific egg dumping and/or brood mixing, neither of which has been documented between these species. We also found no compelling evidence that joining heterospecifics provides a mating advantage. Despite occasional visits by female prairie chickens to sharp-tailed grouse leks, exposure to conspecific females did not increase with numbers of heterospecific companions as would be expected if female prairie chickens were attracted by sharp-tail as well as by conspecific advertisement signals. It is also unlikely that participation in mixed leks provides opportunities for fertile matings with heterospecific females. The two species occasionally hybridize (see § 1; table 1) and both female hybrids and backcrosses are fertile (Sparling 1980). However, in mixed leks females of both species prefer conspecific to heterospecific mates (Sparling 1981), making it unlikely that this is the context in which hybrids are generated.

The inference that male prairie chickens benefit from joining sharp-tails, the apparent absence of any reproductive benefits and vulnerability to a common set of predators suggests that mixed-species lek formation is likely to reduced predation risk (see § 1). Further studies should investigate how social display may reduce predation-imposed costs. Foraging birds and mammals form mixed-species groups partly in response to increased predation risk (Szekeley *et al.* 1989; Noe & Bshary 1997) and shared vigilance is among the best-supported consequences of these associations (Sullivan 1984; Metcalf 1989; Dolby & Grubb 1998). Prairie chickens might benefit more from shared vigilance because they allocate less time to vigilant behaviour, potentially explaining why they take an active role in mixed lek formation. Differential

costs of mixed lek membership could also be involved. For example, in a mixed lek sharp-tail acoustic displays might be masked by prairie chickens due to their shorter duty cycle (Hjorth 1970) and because prairie chickens display more.

Although participating in mixed leks is unlikely to provide a mating advantage, the dynamics of mating competition may explain the preponderance of mixed leks containing a single prairie chicken. Because females visiting mixed leks mate with conspecific males (Sparling 1981), a single member of one species in a lek of heterospecifics does not face intrasexual competition within the lek, an advantage that disappears with the addition of conspecific males. This suggests that mixed leks with a single prairie chicken (or sharp-tail) should be more stable than other combinations.

Predation has moulded both the courtship and grouping behaviour of many animal species (Andersson 1994; Pulliam & Caraco 1984). Our results suggest that lekking birds are no exception to these generalizations. This conclusion may apply to other lekking taxa, many of which are exposed to predation while displaying (Höglund & Alatalo 1995; but see Wikelski *et al.* 1996). Exploration of the ways in which lekking animals of both sexes adjust their behaviour in response to the trade-off between mating opportunity and predation risk could lead to fundamental reinterpretations of these conceptually important mating systems.

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