Limited indirect fitness benefits of male group membership in a lekking species.

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Abstract

In group living species, individuals may gain the indirect fitness benefits characterising kin selection when groups contain close relatives. However, tests of kin selection have primarily focused on cooperatively breeding and eusocial species, whereas its importance in other forms of group living remains to be fully understood. Lekking is a form of grouping where males display on small aggregated territories, which females then visit to mate. As females prefer larger aggregations, territorial males might gain indirect fitness benefits if their presence increases the fitness of close relatives. Previous studies have tested specific predictions of kin selection models by using measures such as group-level relatedness. However, a full understanding of the contribution of kin selection in the evolution of group living requires estimating individuals' indirect fitness benefits across multiple sites and years. Using behavioural and genetic data from the black grouse (*Tetrao tetrix*), we show that the indirect fitness benefits of group membership were limited because newcomers joined leks containing few close relatives who had limited mating success. Males' indirect fitness benefits were higher in yearlings during increasing population density but overall remained small and only marginally changed the variation in male fitness. Kin selection acting through increasing group size has a limited influence on male fitness and is therefore unlikely to contribute substantially to the evolution and maintenance of lekking in this black grouse population.

Introduction

Group living is widespread in animals and may take many different forms, with individuals associating with conspecifics in a range of temporal (short-term to life-long) and spatial associations (Krause & Ruxton 2002). Irrespective of the degree of spatial and temporal proximity, group living is often associated with substantial fitness benefits such as reduced predation risks, enhanced foraging efficiency, alloparental care or cooperation (Emlen 1995; Krause & Ruxton 2002; Clutton-Brock 2002). But in addition to these direct fitness benefits, individuals may also gain indirect fitness benefits from living in groups when closely related individuals live together (Kokko et al. 2001; Clutton-Brock et al. 2002; Hatchwell 2010) meaning that kin selection might be involved in the evolution of group living (Hamilton 1964; Griffin & West 2002; Grafen 2006). However, most studies aiming at determining the role of kin selection in shaping specific behaviours in species other than eusocial insect have focused on testing predictions of kin selection models using measures such as group level relatedness (Reeve et al. 1990; McDonald & Potts 1994; Peters et al. 1999) or the modulation of behaviours according to the relatedness of the interacting individuals (Ligon & Ligon 1978; Emlen & Wrege 1988; Komdeur 1994; Russell & Hatchwell 2001). Therefore, actual quantifications of the indirect fitness benefits associated with individuals' action are still scarce (e.g. Creel & Waser 1994; Krakauer 2005; Gorrell et al. 2010; Hatchwell et al. 2014), despite them being necessary to compare individual's direct and indirect fitness benefits and hence better understand the relative contribution of kin selection to the evolution of the wide range of forms of group living observed in nature.

Lekking is a taxonomically widespread form of grouping in which males aggregate on specific locations during the breeding season to acquire and defend a small territory (Höglund & Alatalo 1995). Females visit the leks for the sole purpose of mating and male mating success is highly skewed (Bradbury 1981; Kokko *et al.* 1999).

Leks have become a model for the benefits of group living driven by sexual selection (Höglund & Alatalo 1995) and four non-mutually exclusive hypotheses have been proposed to explain their evolution through increased male direct fitness: (i) increased likelihood of encountering females by displaying where female density is high (Bradbury *et al.* 1986); (ii) increased likelihood of encountering females by displaying close to an attractive male (Beehler & Foster 1988); (iii) increased mating success through female preference for large aggregations (Bradbury 1981); (iv) reduced predation risk in larger aggregations (e.g. Boyko *et al.* 2005). However, males may also gain indirect fitness benefits of group membership. This is because female preference for larger aggregations (Isvaran & Ponkshe 2013) means that males joining a lek with close relatives may increase the fitness of close relatives (Kokko & Lindström 1996). Since the vast majority of males have zero mating success (Kokko *et al.* 1999a; Höglund & Lundberg 1987; Partecke *et al.* 2002), our understanding of the evolution and maintenance of lek-display based upon the extreme male mating skew might be biased if unsuccessful males gain substantial indirect fitness benefits.

Several studies have attempted to determine whether kin selection contributes to the evolution of leks by measuring relatedness across lekking males (Supporting Table S1) with the underlying assumption that males' indirect fitness benefits are low if the average relatedness across lekking males is null. However, mean relatedness at the lek-level is a valid proxy of male indirect fitness benefits only in species where individuals can switch between groups throughout their lives. This is not the case of many lekking species since the choice of group membership occurs only once as males are faithful to their group (Kokko & Lindström 1996). Hence the relatedness of males territorial for the first time (newcomers) to the other group members should be considered to avoid mixing individuals with fundamentally different motivations and fitness pay-offs. Moreover, the distribution of relatedness across lekking males is often bimodal with many unrelated

96 males and a few closely related individuals (e.g. Shorey *et al.* 2000). Therefore, although
97 the mean relatedness across lekking males is not significantly different from zero,
98 newcomers may gain substantial indirect fitness benefits if they are closely related to the
99 dominant male(s) of the lek. Furthermore, individuals' indirect fitness benefits are often
100 context-dependence (Rodrigues & Gardner 2012) as many ecological and individual
101 factors shape individuals' dispersal decision (Emlen 1982; Hatchwell & Komdeur 2000)
102 and hence the likelihood of encountering close relatives (see e.g. Piertney *et al.* 2008;
103 Koenig *et al.* 2011). Therefore, there might be considerable intra- and interspecific
104 variation in the mean relatedness across lekking males (Supporting Table S1) which
105 directly influences the magnitude of kin selection. Finally, lekking is a form of grouping
106 that is primarily driven by sexual selection (Höglund & Alatalo 1995) and the interaction
107 of group members may influence their fitness via increased mating success (Kokko &
108 Linström 1996). Therefore, better understanding the role of kin selection in the evolution
109 of lekking requires quantifying the relative contribution of individuals' direct and indirect
110 fitness benefits to the overall variation in mating success which quantifies the magnitude
111 of sexual selection. Hence, despite considerable previous efforts, previous studies have
112 only implied that kin selection on leks might occur (Petrie *et al.* 1999; Höglund *et al.*
113 1999; Shorey *et al.* 2000) but there is a clear need for studies that quantify the indirect
114 fitness benefits of male display, identify the factors underpinning the magnitude of
115 individuals' indirect fitness benefits, and compare the relative contributions of direct and
116 indirect components of sexual selection.
117 We used long-term data collected in a population of black grouse (*Tetrao tetrix*)
118 in Central Finland to quantify the indirect fitness benefits of group membership. The
119 black grouse is a classical lekking species in which male-male competition is direct
120 (Hämäläinen *et al.* 2012) and males are faithful to their lek site (Kokko *et al.* 1999b).
121 Previous studies have shown that black grouse males maximize their direct fitness

benefit by choosing a lek site according to their competitive ability (Alatalo *et al.* 1992), and gain future direct benefits (Kokko *et al.* 1999b). However, the role of kin selection in the formation of leks in this species is unclear because kin structures have not been consistently found (Höglund *et al.* 1999; Lebigre *et al.* 2008). Genetic and detailed behavioural observations over multiple consecutive years enabled us to identify newcomers and measure their relatedness to the other lekking males. Here, we first show how newcomers' indirect fitness benefits can be quantified as the product of (i) the relatedness of the newcomers to the other lekking males with (ii) the effect of the newcomers' presence on the mating success of the other lekking males (i.e. the difference between the mating success of the other lekking males measured in the presence and absence of the focal newcomers). We then test the hypothesis that such indirect fitness benefits are context-dependent by measuring the effect of population density, newcomers' age and lek site on the newcomers' indirect fitness benefits. Finally, we quantify the contributions of the direct and indirect mating success to the variance in newcomers' mating success to determine the contribution of kin selection acting through increasing group size to the variance in newcomers' fitness.

Materials and Methods

Study population and field methods

Individual black grouse were captured near Petäjävesi (Central Finland) at five study sites during 2001-2007 (Kummunsuo, Lehtosuo, Saarisuo, Teerijärvensuo, and Valkeissuo). Birds were captured using walk-in traps baited with oat seeds. All captured birds were aged as yearling or older according to plumage characteristics and marked with an aluminum ring and a unique combination of colour rings. Lek observations were carried out from hides every morning throughout the mating season (end of April-early

May). Females mate once with a single male; male mating success was estimated from observed copulations as the sire of the broods nearly always matched behavioural observations (Lebigre *et al.* 2007). Males were defined as territorial when present on leks for at least 30% of the number of observations of the most attending male (Kervinen *et al.* 2012). Newcomers were identified when captured as one year old (yearling) and subsequently becoming territorial for the first-time on the studied leks. When full-siblings joined the same leks simultaneously, one male of each pair was retained in the analyses to avoid pseudoreplication (n = 11).

Estimating newcomers' indirect fitness benefits

The relationship (β) between the total number of copulations observed on any given lek (c_z, z denotes each lek site) and lek size (l_z) can be used to estimate the total number of copulations expected to occur on each lek had a newcomer not joined a specific lek ($c'_z = c_z - \beta$). The mating success of each male on a lek without the newcomer ($m'_{z,j}$, j denotes the focal male) can then be calculated as the product of c'_z by the contribution of individual j to c_z (i.e. $m'_{z,j} = (m_{z,j} / c_z) \times c'_z$). The difference between the mating success of each males' with and without the newcomer ($m_{z,j} - m'_{z,j}$) measures the increase in each male's mating success due to the presence of the newcomer. The indirect fitness benefits of a newcomer "i" on lek "z" ($w_{z,i}$) can therefore be estimated as (Eq. 1):

$$w_{z,i} = \sum_{j}^{N-1} R_{z,ij} \times [m_{z,j} - ((m_{z,j} / c_z) \times c'_z)] \quad (1)$$

where "N" is the size of lek "z", $R_{z,ij}$ the relatedness between the newcomer "i" and the other lekking males "j", and "$m_{z,j} - ((m_{z,j} / c_z) \times c'_z)$" is the increase in the other lekking males' mating success due to the presence of the newcomer. This method may be applied in other contexts to estimate indirect fitness benefits when individuals' fitness

increases with group size (Krause & Ruxton 2002), and genetic data are available to measure the relatedness of group members.

Eq. 1 estimates male indirect fitness benefits in terms of mating success as the increasing group size leads to increasing mating success (Kokko & Lindström 1996). However, male mating success might only be weakly related to their reproductive success (i.e. number of offspring produced) if there is a mismatch between observed mountings and genetic paternity. In black grouse, broods sired by multiple males are very rare (Lebigre et al. 2007), parentage analyses nearly always matched lek observations (Lebigre et al. 2007), and the variation in female clutch size is small (Table 2 in Ludwig et al. 2010). Therefore, mating success is a key fitness component in male black grouse and its variation likely reflects the variation in male reproductive success.

An assumption of Eq. 1 is that the share of the total number of observed copulations does not change with lek size which contradicts the commonly observed increase in mating skew with decreasing leks size (Kokko *et al.* 1999a; Alatalo *et al.* 1992). Accounting for such effect would require reallocating fractions of some males' mating success to others. However, three measures of variation (two measures of skewness and the variance) were not related to lek size (Supporting Table S2). Therefore, correcting for such effect is virtually impossible as it would require accounting for changes in some but not all measures of variation with lek size. Besides, multiple factors underpin the variation in male mating success in black grouse (see e.g. Rintamäki *et al.* 2001; Kervinen *et al.* 2012) and two of these traits are expected to change when a focal newcomer is taken out of a group: male territory positions (Hovi *et al.* 1994) and male-male interactions (Hämäläinen *et al.* 2012). Given the complex nature of the changes in the variation in male mating success with lek size and the lack of biological background upon which we could define accurately the males gaining or

197 losing mating success, we decided not to reallocate mating success among males with
198 the disappearance of a specific individual.
199
200 *Relatedness and kinship estimates*
201 Genomic DNA was extracted from blood samples and all birds were genotyped at 11
202 highly polymorphic microsatellite loci (Lebigre *et al.* 2007). The relatedness among
203 individuals (R_{QG}) was calculated using RELATEDNESS 5.0.8 (Queller & Goodnight
204 1989) as described in Lebigre et al. (2008). There was no significant difference between
205 observed and expected R_{QG} values for full-siblings, half-siblings, and unrelated
206 individuals and parent-offspring relationships were slightly underestimated (Lebigre et al.
207 2010). In addition to R_{QG}, we also used the kinship coefficient (*k*) from the reconstruction
208 of a pedigree (Lebigre *et al.* 2010). The pedigree was reconstructed by first using
209 maximum the likelihood parentage assignments implemented in CERVUS 3.0
210 (Kalinowski *et al.* 2007). This allowed us to identify parent-offspring ($k = 0.5$) and some
211 full- and half-siblings relationships when individuals shared both or one parent ($k = 0.5$
212 and 0.25 respectively). Additional close kinships (full- and half-siblings) were then
213 identified using the group likelihood method implemented in COLONY v2.0 (Wang 2004;
214 Wang & Santure 2009). These additional kinships were accurate for full-siblings and
215 unrelated individuals (Type I error: 0.08 and 0.20 respectively; Type II errors: 0.19 and
216 0.10 respectively; see Lebigre et al. 2010). The error rate was higher for half-siblings
217 (Type I: 0.12; Type II: 0.55). To limit the risks of wrongly identifying unrelated dyads as
218 close relatives, the dyads of full- and half-siblings were therefore kept only if $R_{QG} > 0.2$
219 (Lebigre *et al.* 2010).
220
221 *Statistical analyses*:

We first used lek observations collected during 2001-2011 to quantify the effect of increasing lek size on the total number of copulations. The linear mixed effect model to quantify this effect was implemented in the r-package *nlme* (Pinheiro *et al.* 2013) with lek site identity included as a random variable to account for the non-independence of multiple observations of the same lek. The effect of year explained very little additional variation and was therefore excluded of the final model. The variance structure of the model was modified to account for heteroscedasticity (Pinheiro & Bates 2002).

We tested whether the magnitude of newcomers' indirect fitness benefits was context-dependent by quantifying the effect of population density, the age of the newcomers (yearling or older), and the lek site on newcomers' indirect fitness benefits. These variables were chosen because it has been previously shown that population density influences male lekking behaviour and lek size (Kervinen *et al.* 2012) and might underpin changes in local kin structures due to changes in recruitment rate and adult survival (see e.g. Piertney *et al.* 2008). Population density was estimated using wildlife triangles censuses carried out in the previous autumn (Kervinen *et al.* 2012). During 2001-2007, the population underwent a phase of low density, a rapid increase, and a peak of high density (Kervinen *et al.* 2012). Because of unbalanced sampling of newcomers' age, three levels of population density were defined (low: 2001-2005; increasing: 2006; high: 2007). Newcomers' age was also included as a covariate because yearlings may be more likely to display with their father and hence may gain greater indirect fitness benefits than older newcomers. Finally lek site was set as a covariate in the analyses since some sites have consistently high or low total number of observed copulations. Full models containing all independent variables and the interaction between population density and newcomers' age were subsequently simplified using a backward stepwise procedure. Model selection was based on changes

247 in the models' sum of squares (ANOVA), and deviance (logistic regression, generalised
248 linear model) following the removal of a variable.
249 ANOVAs were fitted to newcomers' indirect fitness benefits measured using R_{QG}
250 and the heteroscedasticity was tested using Fligner's test. Since, the distribution of
251 newcomers' indirect fitness benefits measured using *k* was right skewed and zero-
252 inflated, this variable was modelled in two steps: (i) a logistic regression with the binary
253 dependent variable describing whether newcomers' had zero or non-zero indirect fitness
254 benefits, and (ii) a generalized linear model with a Gamma error distribution (inverse
255 link) across males having non-zero indirect fitness benefits.
256 To quantify the degree to which the indirect fitness benefits associated with male
257 display influenced the variation in male mating success, we first carried out a variance
258 decomposition. As mating success has both direct and indirect (i.e. kin selected)
259 components, and as the variance in any two random X and Y variable can be
260 decomposed as Var(X+Y) = Var(X) + Var(Y) + 2Cov(X,Y), then the variance in male
261 mating success can be decomposed as the sum of the variance in its direct component
262 and the variance in its indirect component and twice the covariance between these two
263 components. These variances were standardised by the squared mean in mating
264 success meaning that these variances were expressed in terms of opportunity for sexual
265 selection (I_{SS}, Shuster & Wade 2003). All analyses were carried out in R version 2.15.0
266 (R Core Team 2012).
267
268 ***Results***
269
270 *Lek size and the total number of copulations*
271 The total number of copulations observed on leks was strongly positively related to lek
272 size in black grouse (linear mixed effects model: β = 1.75 ± 0.25 (SE), t-value = 6.95, P

273 < 0.001, Fig. 1). Therefore, if a specific newcomer would not have joined a lek, the
274 expected total number of copulations observed on any given lek would have decreased
275 on average by 1.75 copulations.
276
277 *Kinship and mating success of the newcomers and the other males*
278 The size of the studied leks varied substantially during 2001-2007, ranging from 3
279 to 37 territorial males (Supporting Table S2). During this period, a total of 104
280 newcomers were identified (range: 0-11), and all of them were either 1 or 2 years old
281 (hereafter “yearling” and “older”, $n_{yearling}$ = 61, n_{older} = 43). Only 16% of the newcomers
282 displayed with their father and 27% with at least one full-sibling meaning that newcomers
283 joined leks comprising mainly unrelated males (84% of the R_{QG} newcomers-lekking
284 males were below 0.2; mean R_{QG} ± SD = 0.009 ± 0.186, N = 1798 pairwise R_{QG} across
285 104 newcomers, Fig. 2A). The close relatives of the newcomers had moderate mating
286 success (across the 173 males closely related to at least one newcomer: median mating
287 success = 1, IQR = 0-2, Proportion of males with zero mating success: 0.63, Fig. 2B). In
288 particular the mating success of the full- and half-siblings of the newcomers was very
289 low (full-siblings: median mating success = 0, IQR = 0-2, proportion with zero mating
290 success = 0.54, n = 37; Half-siblings: median mating success = 1, IQR = 0-2, proportion
291 with zero mating success = 0.51, n = 135), while the fathers of the newcomers had a
292 moderate-high mating success (median mating success = 6, IQR = 1-11.5, proportion
293 with zero mating success = 0.13, n = 15, Fig. 3B). The top males of each lek had low
294 relatedness to the newcomers (mean R_{QG} ± SD = 0.002 ± 0.204, N = 98; five newcomers
295 joined a lek with an unringed top males and one newcomer became the top male of a
296 lek) and only 5 newcomers were sons of the top males of the leks.
297

Indirect fitness benefits: context-dependence and contribution to the variance in male mating success

When Eq. 1 was parameterized using R_{QG} or *k*, the indirect fitness benefits of group membership across newcomers was very low, equivalent to *ca.* 4% of an own copulation (Table 1a, Fig. 3A and B). Newcomers' indirect fitness benefits were influenced by the interaction between newcomers' age and population density when estimated using R_{QG} (Table 2a). This effect was due to the greater indirect fitness benefits of yearling than two year old newcomers during the increasing phase of the population density (Supporting Fig. S1). When indirect fitness benefits were estimated using *k*, all considered factors (population density, study site, and the interaction between newcomers' age and population density) influenced to some extent the likelihood of gaining or not gaining indirect fitness benefits as; none of them could be removed without significantly reducing the model fit (Table 2b). Across all newcomers, mating success was low (Table 1a) with yearling newcomers having a significantly lower direct mating success than older newcomers (Table 1b and 1c, Wilcoxon rank-test, $W = 879.5$, $P < 0.001$, $n = 104$, Fig. 3C). Nevertheless, newcomers direct fitness benefits were substantially greater than their indirect fitness benefits which contributed to *ca.* 1% of the standardized variance in male direct and indirect mating success (Table 3).

Discussion

Fully understanding the fitness consequences of group living requires direct measures of individuals fitness and estimates of the effect of each individual's action on the fitness of their close relatives (leading to indirect fitness benefits). In lekking species, newly established territorial males (newcomers) are usually unsuccessful (Höglund & Alatalo 1995), but they may gain indirect fitness benefits by increasing the mating success of close relatives displaying on the same lek (Kokko & Lindström 1996). Here, we show

that male indirect fitness benefits are very small in the black grouse because newcomers joined leks holding few close relatives and because close relatives to the newcomers generally had low mating success.

The lack of strong kin structures in black grouse and several other lekking bird species (Supporting Table S1) may seem surprising given these species' extreme mating skew (Kokko *et al.* 1999a), which combined with male philopatry in birds (Greenwood 1980) should facilitate the formation of kin structures in males (Hamilton 1964). However, key differences in morphology and life histories (Paradis *et al.* 1998) or landscape structures (e.g. Bélisle *et al.* 2001) may lead to substantial inter- and intraspecific variation in natal dispersal which may dampen the formation of large kin groups. Male natal philopatry has been confirmed in black grouse by radio tracking (Caizergues & Ellison 2002; Warren & Baines 2002) and genetic studies (Höglund *et al.* 1999; Lebigre *et al.* 2008). But, the low genetic differentiation found among males in the same study population (Lebigre *et al.* 2008) suggests that among lek gene flow is substantial and that male may also disperse among leks. The likelihood of kin group formation in lekking species might also be overestimated if there is a mismatch between the observed large variation in male mating success and reproductive success. This might be the case in systems where females mate with multiple males on multiple leks or outside leks (Petrie *et al.* 1992; Lank *et al.* 2002), but it is unlikely in black grouse since polyandry is rare and observations provide reliable estimates of male reproductive success (Alatalo *et al.* 1996; Lebigre *et al.* 2007). Therefore, male dispersal and a low recruitment rate (Ludwig *et al.* 2010) are the most parsimonious explanations for the lack of strong kin structures in this black grouse population.

Key life-history traits such as clutch size or adult longevity are widely expected to shape the evolution of sociality (Hatchwell & Komdeur 2000, Hatchwell 2009) because they underpin the formation of kin groups. In black grouse, the most dominant black

grouse males rarely retain their dominant position and generally have one clear peak of mating success at age 2-4 (Kokko *et al.* 1999b) meaning that sons may join their fathers' lek after their age of peak mating success. A full and half-siblings have often the same age (i.e. the vast majority of them will be hatched the year of their father's peak mating success), they will often have an equally low likelihood of mating due to their limited lek experience. Therefore, even if groups do comprise close relatives, individuals' indirect fitness benefits might be limited if their kin have low reproductive prospects or if their parents have short tenures of dominant positions.

Context-dependence of newcomers' indirect fitness benefits

Male indirect fitness benefits were primarily influenced by population density and newcomers' age. Specifically, the interaction between age and population density was significant when indirect fitness was estimated using R_{QG} and when the likelihood of gaining indirect fitness benefits using *k* was considered. These effects were due to the high indirect fitness benefits of yearling newcomers during the increasing phase of the population density. Therefore, the high recruitment rates and survival probabilities of this cohort during increasing density led to increased likelihood of displaying with a close relative and hence increasing indirect fitness benefits as reported in other systems (Piertney *et al.* 2008, Nussey *et al.* 2005). Previous studies have shown that ecological conditions can lead to changes in individual behaviour (reviewed in Hatchwell 2009; Lehmann & Rousset 2010), and our study shows that demographic changes can in turn influence the magnitude of individuals' indirect fitness benefits. Therefore, the indirect fitness benefits of group membership are context-dependent but in spite of this variation their overall magnitude remains small.

Conclusions

376 Fully understanding the role of kin selection in the evolution of any trait requires
377 quantifying all indirect effects associated with this trait. In this study, we quantified one of
378 these indirect effects and found that in black grouse there was a small positive indirect
379 fitness benefit gained through increasing lek size. These should be discounted by the
380 indirect fitness benefits which would have been gained had the newcomer joined another
381 lek and the indirect costs due to kin competition (Maynard Smith 1964; Griffin & West
382 2003) which are difficult to quantify with our current data. Marked males are very rarely
383 resighted far from the study sites. Therefore, they were unable to join the other leks used
384 in this study (distant of 9-36km) and a detailed observations of the territorial males
385 displaying on leks located in the vicinity of the studied sites is needed to estimate the
386 indirect fitness benefits a specific newcomer would have gained had he joined another
387 lek. Quantifying the magnitude of kin competition requires detailed information of the
388 fitness costs of lekking with close relatives. While the lek display is energetically costly to
389 all males in black grouse (Lebigre *et al.* 2013) and results in substantial fitness costs to
390 yearling newcomers (Siitari *et al.* 2007), these data cannot be used to estimate the
391 fitness costs of lekking with close relatives as unmanipulated black grouse choose
392 where and when they join leks according to their current body condition (Alatalo *et al.*
393 1992; Hovi *et al.* 1994; Kervinen *et al*. 2012) and may modulate their behaviour
394 according to their kinship to minimise these fitness costs (see e.g. Reynolds *et al.* 2012).
395 Therefore, additional analyses are needed to fully quantify the magnitude of the indirect
396 effects associated with group display in lekking species.
397 Sexual selection is clearly the main factor driving the evolution and maintenance
398 of group displays such as the leks (Höglund & Alatalo 1995), but the influence of kin
399 selection on the relationship between group size and mating success has never been
400 previously quantified. This study is the first to unequivocally show that the direct mating
401 success of males joining leks far outweighs the indirect fitness benefits gained through

increasing group size. Therefore, male indirect fitness benefits are solely context-dependent by-products of male group display and kin selection is very unlikely to contribute substantially to the maintenance of male aggregations in this black grouse population.

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Electronic Supplementary Material

Supporting Table S1. Studies testing the potential for kin selection in lekking species. Dashes indicate unknown value. Studies with multiple entries reported both significantly positive and non-significant average relatedness across lekking males.

Supporting Table S2. Spearman rank correlation coefficients between lek size and several measures of variation in male mating success.

Supporting Table S3. Variation in lek size across during 2001-2007. Values in parentheses are the number of newcomers (yearling and older) identified on each lek in each year.

Supporting Figure S1. Influence of population density and male age on the newcomers' indirect fitness benefits. Newcomers' indirect fitness benefits were estimated here using Queller and Goodnight's estimator (R_{QG}). The effect of population density on newcomers' indirect fitness benefits are showed for yearling (black dots, solid lines) and older newcomers (open dots, dashed lines).

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Data accessibility

All pairwise relatedness between newcomers and the other lekking males and the mating success of each male are described in the dryad repository doi:10.5061/dryad.5d81k.

Input file for the relationship between lek size and the total number of copulation can be retrieved in the dryad repository doi:10.5061/dryad.5d81k

Author contributions: CL and RVA derived eq.1, RVA CL and HS collected the data, CL and CDS analysed the data, CL wrote the manuscript and all co-authors contributed substantially to revisions. Authors sequence determines their contribution.

Figure legends:

Figure 1. Relationship between lek size and the total number of copulations observed in any given lek. The line represents the predicted values of the linear mixed effect model.

Figure 2. Distribution of the relatedness between newcomers and the other lekking males (panel A) and the distribution of the mating success the lekking males closely related to at least one newcomer (panel B). Relatedness was estimated using Queller and Goodnights' estimator (R_{QG}). The insert shows the distribution of the mating success of the newcomers' fathers.

Figure 3. Distributions of the newcomers' indirect (panels A and B) and direct mating success (panel C). The indirect fitness benefits were estimating by multiplying the coefficient of kinship (*k*, panel A) or relatedness (R_{QG}, panel B) to the expected mating success of the other lekking males, had the newcomer not been present. White and black bars in panel C represent the direct mating success of yearling and older newcomers respectively.

Table 1. Summary statistics of the indirect and direct mating success of the newcomers to a lek. Statistics are presented across a) all males, b) yearling newcomers (1 year old), and c) older newcomers (> 1yr old). Two measures of relatedness were used: the kinship between individuals and Queller and Goodnight's estimator of relatedness (R_{QG}). Non explicit table entries are: proportion of males with zero mating success (prop. zeroes), median (med.) interquartile range (IQR) and standard deviation (SD).

	Indirect mating success						Direct mating success		
	Kinship			R_{QG}					
	Prop. Zeroes	Med.	IQR	Mean	SD	IQR	Prop. Zeroes	Med.	IQR
a) Overall (N = 104)	0.36	0.04	0.00-0.11	0.02	0.20	-0.12-0.15	0.68	0	0-1
b) Yearling males (n = 61)	0.30	0.04	0.00-0.15	0.04	0.21	-0.09-0.16	0.82	0	0-0
c) Older males (n = 43)	0.44	0.03	0.00-0.08	-0.01	0.18	-0.12-0.11	0.49	1	0-2

632 **Table 2.** Most parsimonious models explaining the variation in newcomers' indirect fitness benefits estimated using two measures of
633 relatedness; kinship coefficient (*k*) and Queller and Goodnight's estimator of relatedness (R_{QG}). Non explicit table entries: sample
634 size (N), degrees of freedom (df), F values for ANOVAs and Residual Deviance for logistic regressions (F / Res. Dev.), P-value (*P*),
635 difference in the degrees of freedom during model selection (df2-df1), F value of the changes in sum of squares (ANOVA) or
636 deviance (Logistic regression, generalised linear model), *P*-value of the stepwise backward selection method.
637

	Indirect mating success	Model type	N	Independent variables	Omitted terms	df	F / Res. Dev.	*P*	df2-df1	F (SS/Deviance)	P_{back}
a)	Relatedness (R_{QG})	ANOVA	104	Density		2	0.87	0.42			
				Age		1	1.66	0.20			
				Age:Density		2	5.07	<0.01			
					Site	-	-	-	-4	0.80 (-0.12)	0.53
b)	Kinship (*k*, binary)	Logistic regression	104	Density		2	129.01	0.04			
				Age		1	125.88	0.08			
				Site		4	117.66	0.08			
				Density:Age		2	110.09	0.02			
c)	Kinship (*k*, only if >0)	Generalised linear model	66		Density				-2	1.98 (-3.82)	0.14
					Age				-1	1.69 (-1.50)	0.19
					Site				-4	1.60 (-4.97)	0.19
					Density:Age				-2	0.40 (-0.63)	0.67

638 **Table 3.** Relative contributions of direct (D) and indirect (I) components to the variance
639 in mating success across newcomers. Both the kinship between individuals (*k*) and
640 Queller and Goodnight's estimator of relatedness (R_{QG}) were used as measures of
641 relatedness. Abbreviations are standardised variance in male mating success (I_T the
642 sum of newcomers' direct and indirect mating success), standardised variances in male
643 direct mating success (I_D), standardised variances in male indirect mating success (I_I),
644 covariance between newcomers' direct and indirect mating success ($covI_{D,I}$). Values in
645 parenthesis indicate the ratio of the standardised (co)variance of each component to I_W.
646

	K	R_{QG}
a) I_T	3.40	3.93
b) I_D	3.45 (1.01)	3.95 (1.01)
b) I_I	0.02 (0.01)	0.05 (0.01)
c) 2*$covI_{D,I}$	-0.06 (-0.02)	-0.08 (-0.02)

647
648

Figure 1.

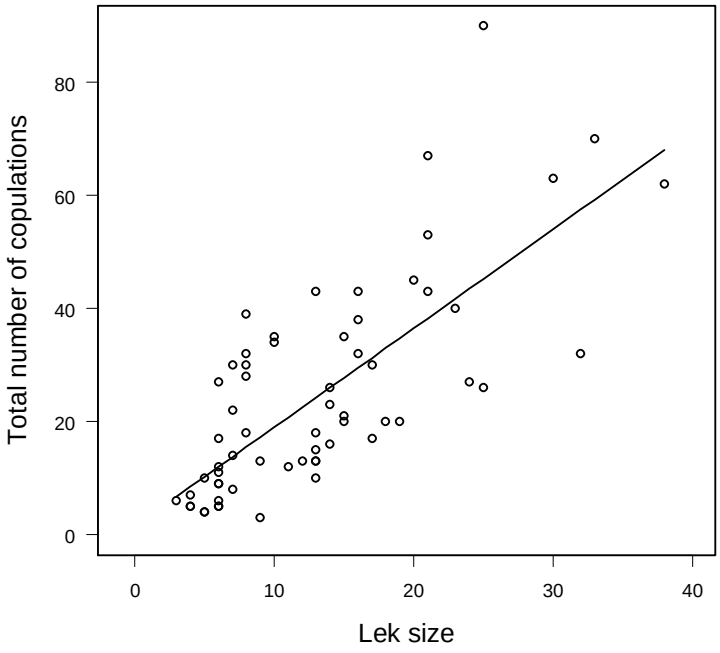


Figure 2.

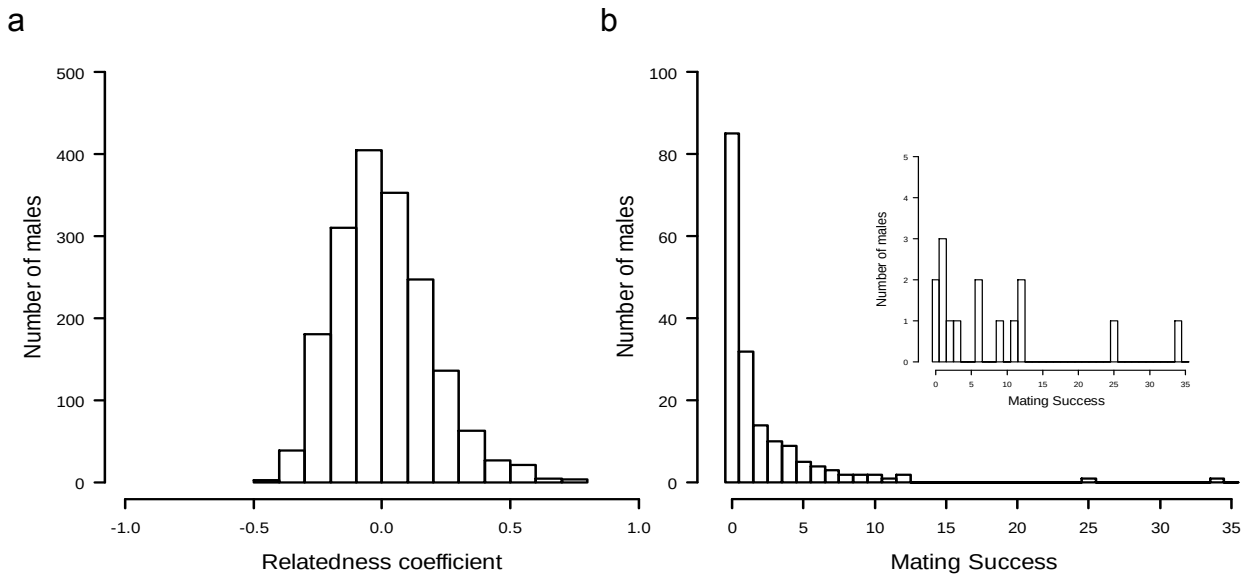
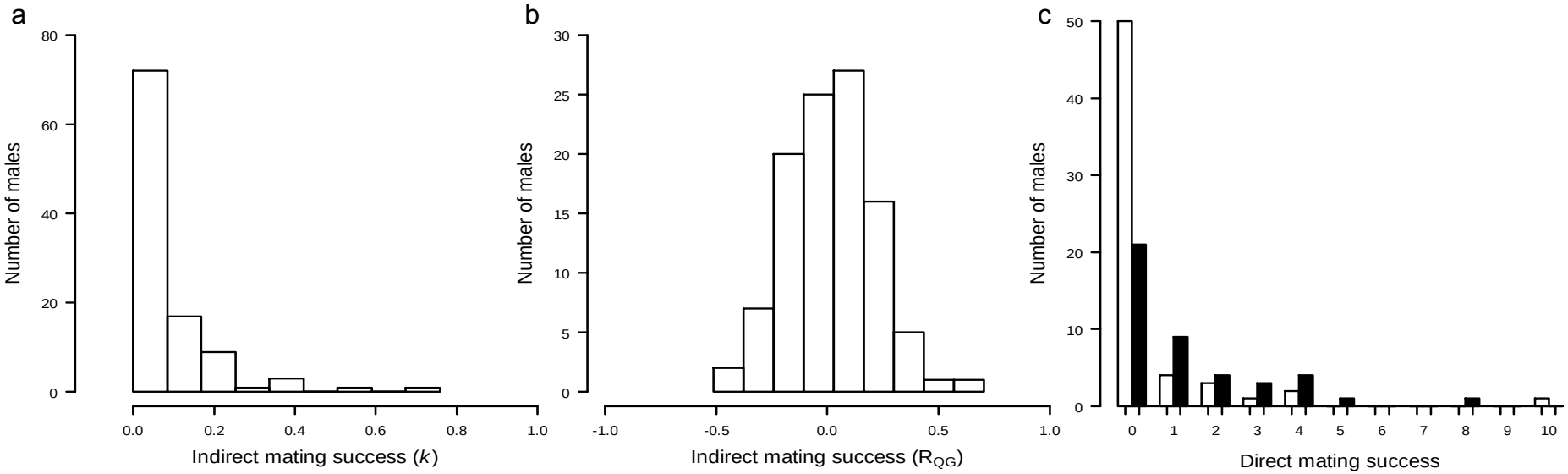

a
b
Number of males
Relatedness coefficient
Mating Success
Number of males
Mating Success

Figure 3.


a
Number of males
Indirect mating success (k)
b
Number of males
Indirect mating success (R_QG)
c
Number of males
Direct mating success