

1 Christophe Lebigre<sup>1</sup>, Catherine Timmermans<sup>2,3,4</sup>, Carl D. Soulsbury<sup>3</sup>

2

3 **NO BEHAVIOURAL RESPONSE TO KIN COMPETITION IN A LEKKING SPECIES**

4

5 <sup>1</sup> Earth and Life Institute, Catholic University of Louvain, Belgium

6

7 <sup>2</sup> Institute of Statistics, Biostatistics and Actuarial Sciences, Catholic University of Louvain,  
8 Belgium

9

10 <sup>3</sup> Joseph Banks Laboratories, School of Life Sciences, University of Lincoln, Lincoln,  
11 Lincolnshire, LN6 7TS, UK.

12

13 <sup>4</sup> Department of Mathematics, University of Liège, Belgium

14

15 Corresponding author:

16 Christophe Lebigre

17 Email: christophe.lebigre@uclouvain.be

18 Phone: +32 10 47 92 28 (office)

19

20 **Acknowledgments:** This paper is dedicated to Prof. Rauno Veli Alatalo who passed away  
21 on November 9<sup>th</sup> 2012. We thank Jefferson Graves, Matti Kervinen and two anonymous  
22 reviewers for their insightful comments on previous versions of this manuscript. We are  
23 grateful to Elina Virtanen, Juho Niva, Anssi Lipponen, Sami Kyröläinen, and Henna Ojaniemi  
24 for help in the lab. This project was founded by the Academy of Finland (Grant nos. 7211271  
25 and 7119165) and a fellowship of the Belgian Fond National pour la Recherche Scientifique  
26 (FNRS). Part of the statistical analysis was conducted within the SMCS (Support en  
27 Méthodologie et Calcul Statistique – Université Catholique de Louvain).

28 **Abstract**

29 The processes of kin selection and competition may occur simultaneously if limited individual  
30 dispersal i.e. population viscosity, is the only cause of the interactions between kin.

31 Therefore, the net indirect benefits of a specific behaviour may largely depend on the  
32 existence of mechanisms dampening the fitness costs of competing with kin. In lekking  
33 species, males may increase the mating success of their close relatives (and hence gain  
34 indirect fitness benefits) because female prefer large leks. At the same time, kin selection  
35 may also lead to the evolution of mechanisms that dampen the costs of kin competition. As  
36 this mechanism has largely been ignored to date, we used detailed behavioural and genetic  
37 data collected in the black grouse *Lyrurus tetrix* to test whether males mitigate the costs of  
38 kin competition through the modulation of their fighting behaviours according to kinship and  
39 the avoidance of close relatives when establishing a lek territory. We found that neighbouring  
40 males' fighting behaviour was unrelated to kinship and males did not avoid settling down with  
41 close relatives on leks. As males' current and future mating success are strongly related to  
42 their behaviour on the lek (including fighting behaviour and territory position), the costs of kin  
43 competition may be negligible relative to the direct benefits of successful male-male  
44 contests. As we previously showed that the indirect fitness benefits of group membership  
45 were very limited in this black grouse population, these behavioural data support the idea  
46 that direct fitness benefits gained by successful male-male encounters likely outbalance any  
47 indirect fitness benefits.

48

49

50 Keywords: dominance, indirect fitness benefits, kin selection, kin competition, territoriality,  
51 sexual selection, sociality

52

53 **Significance statement**

54 Kin selection might be involved in the formation of groups because the fitness benefits of  
55 increasing group size can be accrued when groups hold close relatives. However, the fitness  
56 costs of competing with kin could counter-balance these indirect fitness benefits unless  
57 mechanisms enabling individuals to limit kin competition. Using data collected in the black  
58 grouse (*Lyrurus tetrix*) we show that males do not modulate their fight frequency and  
59 intensity according to their kinship and do not avoid establishing territories with closely  
60 related neighbours. As we previously showed that the indirect fitness benefits of group  
61 display were very small and as this study shows that males do not show any sign of kin  
62 competition avoidance, the indirect effects associated with male group display are likely to be  
63 very small in this system.

64 **Introduction**

65 Kinship among group members influences multiple aspects of animal societies ranging from  
66 individual interactions to group formation. Indeed, individuals can behave in ways favouring  
67 kin (Brown and Brown 1996; Silk 2002), such as increasing their helping rate according to  
68 kinship (Reeve et al. 1990; Komdeur 1994; Russell and Hatchwell 2001), forming mating or  
69 foraging alliances (Russell and Hatchwell 2001; Krützen et al. 2003; Krakauer 2005;  
70 Piertney et al. 2008; Edenbrow and Croft 2012), or showing reduced aggressiveness towards  
71 kin (Silk 2002; Smith et al. 2010; though see West et al. 2001). Individuals may also benefit  
72 kin more indirectly, by avoiding interacting with kin by dispersing (Moore et al. 2006; Bitume  
73 et al. 2013), or through the avoidance of groups holding close relatives (Höner et al. 2007).  
74 As many of these behaviours can co-occur, the adaptive value of a specific behaviour can  
75 only fully be understood when the indirect costs and benefits (defining kin selection and  
76 competition) resulting from these behaviour can be estimated (Hamilton 1964; Griffin and  
77 West 2002; Grafen 2006).

78         In lekking species, males gather on specific areas to display on territories visited by  
79 females for the sole purpose of mating (Höglund and Alatalo 1995). Lekking males are  
80 expected to choose their lek site according to their display abilities (e.g. Alatalo et al. 1992)  
81 and a large number of morphological and behavioural traits has been associated with male  
82 mating success (Höglund and Alatalo 1995; Fiske et al. 1998). By joining large leks, males  
83 might gain both direct fitness benefits (the number of observed copulations increases with lek  
84 size, Isvaran and Ponshe 2013; Lebigre et al. 2014) and indirect fitness benefits when leks  
85 comprise close relatives (males may increase the mating opportunities of their close  
86 relatives; Kokko and Lindström 1996; Höglund 2003; Hatchwell 2010). Several studies have  
87 tested whether leks comprised closely related individuals either by quantifying the mean  
88 relatedness across lekking males (e.g. Bouzat and Johnson 2004) or by measuring the  
89 spatial aggregation of close relatives within (e.g. Shorey et al. 2000; Segelbacher et al. 2007)  
90 and among leks (Höglund et al. 1999). To our knowledge, only one study quantified the

91 indirect fitness benefits resulting from male aggregations and showed that these were very  
92 limited and substantially less than male direct fitness benefits (Lebigre et al. 2014). However,  
93 theory predicts that if population viscosity (i.e. limited dispersal) is the sole driver of the  
94 interaction between kin, the indirect fitness costs associated with individuals' action may  
95 reduce or even cancel out all indirect fitness benefits (e.g. West-Eberhard 1975; Taylor 1992;  
96 Wilson et al. 1992; Van Dyken 2010) and kin selection may only matter in systems where it  
97 has also led to the evolution of mechanisms reducing kin competition (Mitteldorf and Wilson  
98 2000; Alizon and Taylor 2008; Lion and Gandon 2009).

99 Indirect fitness costs are required in order to characterise kin competition. Yet, stable  
100 dominance hierarchies may reduce the costs of aggressive encounters (Berglund et al. 1996;  
101 Hsu et al. 2006) even in lekking species (Magaña et al. 2011). However, such a mitigation  
102 may largely be counter-balanced in lekking species by female preference for male fighting  
103 behaviour *itself* (Höglund et al. 1997; Hämäläinen et al. 2012). Males fighting behaviour  
104 could therefore be an honest indicator of male quality either directly (Briffa and Sneddon  
105 2007) or indirectly through males' ability to maintain intact ornaments during the lekking  
106 season (Kirkpatrick and Ryan 1991; Höglund et al. 1994). Lekking is also energetically very  
107 costly (Vehrencamp et al. 1989; Höglund et al. 1992) and these energetic costs may lead to  
108 fitness costs depending on individuals' age and phenotypic quality (Gosling et al. 1987;  
109 McElligott et al. 2001; 2003; Kervinen et al. 2015; 2016). Therefore, the intense and direct  
110 competition observed in lekking species may lead to indirect fitness costs when males are  
111 displaying with kin either through a reduced attractiveness or a decreased survival likelihood.  
112 Nevertheless, the degree to which kin selection can lead to the evolution of a reduction of kin  
113 competition in lekking species has largely been overlooked. For instance, studies failing to  
114 report strong kin structure (e.g. Gibson et al. 2005; Loiselle et al. 2007; Lebigre et al. 2008)  
115 interpreted their results as indicative of an absence of kin selection, while individuals may  
116 simply avoid competing with close relatives.

117 We used data collected in a classical lekking species, the black grouse (*Lyrurus*  
118 *tetrrix*), to determine whether kin selection can have led to the evolution of two mechanisms  
119 dampening the costs of kin competition: the modulation of aggressive interactions between  
120 close relatives and the avoidance of territories with closely related neighbours. To this end,  
121 we combined behavioural data (territory positions, fighting rate and intensity) with measures  
122 of male kinship and conducted a twofold analysis. In this species, the competition with kin  
123 may lead to fitness costs as it has previously been shown that lekking is energetically costly  
124 (Lebigre et al. 2013), that male fighting behaviour is under direct sexual selection (Höglund et  
125 al. 1997; Hämäläinen et al. 2012; Kervinen et al. 2016) and that male's ability to maintain  
126 high quality ornaments is related to their mating success (Alatalo et al. 1991; Höglund et al.  
127 1994). First we measured the relatedness between neighbouring territorial males and tested  
128 whether males fought less frequently and less intensively with closely related neighbours.  
129 Such type of analysis based is not straightforward as variables such as the fight frequency  
130 and intensity within a group are likely to have a spatial structure. Indeed, the fight frequency  
131 between two males is influenced by and influences their fight frequency with their other  
132 neighbours (i.e. if "A" fights with "B", "B" cannot fight with its neighbour "C") and similarly the  
133 intensity of male fights may be lower with specific neighbours if the dominance hierarchy is  
134 well established. Such dependence structures may result in a spatial correlation which needs  
135 to be explicitly accounted for in a mixed model. Yet, contrary to the usual spatial correlation  
136 models used in e.g. geostatistics, the proximity between individuals should not be measured  
137 in terms of geographical distance *per se* but in terms of neighbourhood. Therefore, we used  
138 the identity of neighbouring males to define a network in which each bird is a node and the  
139 proximity between birds as measured as the number of edges separating them (a measure  
140 named "n-hop distance").

141 Second, we determined whether males avoided settling on territories with closely  
142 related neighbours using a randomisation approach. Like in many other territorial species,  
143 male territory positions are dynamic in the black grouse. Newcomers generally display on the

144 lek periphery and slowly move towards the lek centre as a consequence of shifts of territory  
145 positions and the arrival of other more peripheral males (Kokko et al. 1997, 1999). We  
146 therefore conducted a spatially constrained randomisation test in which a set of potentially  
147 available territories was defined (i.e. the territories of all newly established males and other  
148 very subordinate males). This enabled us to test the hypothesis that new territorial males  
149 (newcomers) established their territory with less closely related neighbours than expected by  
150 chance.

151

## 152 **Material and Methods**

### 153 *Study population*

154 The data used in this study were collected in a black grouse population inhabiting Central  
155 Finland (2003-2005). Upon capture, all males were ringed with an aluminium ring and a  
156 unique combination of colour rings for future identification. Birds were trapped in several sites  
157 but here we will focus on three sites (Kummunsuo, Valkeissuo, Teerijärvensuo) where 95%  
158 of the lekking males were ringed (N = 78 unique individuals for 115 observations; some  
159 males were observed in several years and others had no neighbours, Suppl. Table 1). The  
160 distance between these study sites (range 23.02-36.52 km) exceeds the current recorded  
161 maximum natal dispersal distance in this species (11 km) while the vast majority of the males  
162 remain in their natal area (Caizergues and Ellison 2002; Warren and Baines 2002).  
163 Therefore, the study sites can be considered as separate entities with infrequent movements  
164 between them. A small blood sample was taken from the birds' brachial vein from which DNA  
165 was extracted and all individuals were genotyped at 11 microsatellite loci (detailed  
166 description in Lebigre et al. 2007). We measured individuals' pairwise relatedness using  
167 Queller and Goodnight's estimator ( $R_{QG}$ , Queller and Goodnight 1989; details in Lebigre et al.  
168 2008) and more conservatively identified close relatives as having a value of  $R_{QG}$  over 0.2.

169 This cut-off value was chosen because it enabled us to limit the risks of wrongly identifying  
170 unrelated dyads are close relatives (details in Lebigre et al. 2010, 2014).

### 171 *Lek observations*

172 Male-male interactions were recorded during ca. 10 days at the end of April-early May when  
173 nearly all copulations take place (Lebigre et al. 2007). During the lekking season, males  
174 gather on various open areas such as peat bogs, frozen lakes and forest clear-cuts to defend  
175 a small territory where they display (Hovi et al. 1994; Höglund and Alatalo 1995). Male lek  
176 activity was recorded on behavioural maps every day during the most active lekking days  
177 (ca. 10 days). Maps were drawn every 5 minutes (depending on lek size) from ca. 03:00 to  
178 09:00 with males' exact position and a description of its behaviour categorised as inactive,  
179 rookooing (main vocalisation), hissing (occasional loud scream) and fighting. When fights  
180 occurred, the identities of the two males was recorded as well as the fight intensity (three  
181 levels; Hämäläinen et al. 2012). Male attendance to the lek was calculated as the proportion  
182 of maps drawn on which a specific male is recorded relative to total the number of maps  
183 drawn for the most attending male (Rintamäki et al. 2001). Males were considered territorial  
184 when having an attendance to the lek  $> 0.3$  meaning that their total number of recorded  
185 activity was at least 30% of that of the most attending male of the lek (see Kervinen et al.  
186 2012). The position of the territory of each male was calculated as the median of all x and y  
187 coordinates of the recorded observations and all observations were plotted to delineate  
188 territory boundaries and identify neighbours (Suppl. Fig. 1). This also allowed us to locate  
189 ditches in peat harvested sites which effectively prevent the interaction between  
190 neighbouring males (males were not considered as neighbours if a ditch delineated the  
191 boundary of their territories). The lek centre was defined as the median of all x and y  
192 coordinates across all males. We then calculated the Euclidian distance separating each  
193 male's territory to the lek centre to estimate male's territory centrality. For each unique pair of  
194 neighbours in each year (N = 195 from the 78 unique individuals), we calculated the  
195 proportion of observations in which neighbours were fighting (i.e. the fight frequency) and the



196 median intensity of the fights (i.e. fight intensity). Fights occasionally involving non-  
197 neighbouring males were excluded from the analyses as they occurred when males left their  
198 territories to feed or approach females. This study combines two dataset which were  
199 collected independently. In the field, it was not possible to record data blind because we  
200 used marked birds with colour rings. However, only part of the birds' unique identification  
201 number was used during the genotyping which was carried out with no knowledge of the  
202 lekking behaviour of the males and the location of their lek territories.

### 203 *Statistical analyses*

204 In all analyses we used two measures of relatedness: the direct measures of  $R_{QG}$  (a  
205 continuous and normally distributed measure of genetic distance) and a binary variable  
206 describing whether individuals were close relatives ( $R_{QG} > 0.2$ ) or not (this variable is  
207 denoted  $R_{QG\_binary}$ ). We used  $R_{QG\_binary}$  because if individuals really avoid competing with kin,  
208 these effects will be easier to detect among close relatives. We tested whether the  
209 relatedness between neighbouring males influenced their fight frequency and fight intensity.  
210 Those two cases were considered successively, with slightly different statistical tools.

211 To test the hypothesis that male fight frequency is influenced by their relatedness, we  
212 fitted a linear mixed model explaining the fight frequency between two neighbouring males as  
213 a function of three fixed effects: their relatedness (either  $R_{QG}$  or  $R_{QG\_binary}$ ) their mean  
214 centrality and centrality difference. The two last fixed effects were used to control for the  
215 directionality of male-male interactions as we expected males closer to the lek centre (low  
216 mean centrality) and males having similar distances from the lek centre (low centrality  
217 difference) to be more active. The model also accounts for the fact that the baseline fight  
218 frequency is *a priori* lek-dependent and they are related to lek size by including each lek\*year  
219 combination as a random effect. This implies that we assume that the effects of the pairs'  
220 relatedness, mean centrality, and centrality difference on the variance in fight frequency are

221 not lek-specific. The mixed models are estimated using a simple restricted maximum  
222 likelihood estimator implemented using the R-package *nlme* (Pinheiro et al. 2013).

223 Two adaptations of the models are required to ensure their statistical validity. First,  
224 the fight frequency was log-transformed to produce normally distributed and homogeneous  
225 residuals. Second, we needed to account for the spatial structure resulting from the non-  
226 independence of the interactions between neighbours and its potential cascading effects  
227 across the entire leks. Therefore, we tested whether the residuals of the models were  
228 spatially correlated. As the geographic distance is not the important parameter here, but  
229 rather the neighbourhood, we used the n-hop distance on a graph to describe the spatial  
230 structure instead of the Euclidean distance. The graph was built with birds as nodes, and  
231 undirected edges between each pair if birds were neighbours and the linear model is thus  
232 defined for estimating the fight frequency at each edge. The n-hop distance between two  
233 edges was computed as the number of nodes between them. Hence, a n-hop distance equal  
234 to one between two pairs of neighbours means that one individual is involved in the two  
235 pairs. The n-hop distances were calculated using the r-package using the r-package *spa*  
236 (Culp 2015). As expected, we found that there was a negative correlation in the model  
237 residuals for neighbouring males ( $r = -0.100$ ;  $P = 0.045$ ; Suppl. Table 2) meaning that a male  
238 fighting often with one neighbour fought less often with his other neighbours. To account for  
239 this spatial structure, we re-implemented the mixed effects models including a first order  
240 correlation of the residuals on the graph. P-values of the fixed effects and their confidence  
241 intervals were computed using a student statistics (more details in Suppl. Appendix 1).

242 We replicated these steps to test the hypothesis that fight intensity was influenced by  
243 the relatedness of the males. In all the analyses of male fight intensity, the dependent  
244 variable (median fight intensity) was transformed to a binary variable separating pairs fighting  
245 intensely (median intensity  $\geq 2$ ) from the others. We therefore implemented generalised  
246 linear mixed effects models with a logit link function and a restricted maximum likelihood  
247 estimator. These models included three fixed effects (the pair relatedness measured either

248 as  $R_{QG}$  or as  $R_{QG\_binary}$ , the pair mean centrality, and centrality difference) and the  
249 combination of lek\*year as a random factor. These models were estimated using the R-  
250 package *lme4* (Bates et al. 2015). As there was no significant spatial structure for fight  
251 intensity we directly used the outcome of the generalised linear mixed effects models.

252 To test the hypothesis that lekking males could reduce kin competition by settling  
253 down on territories where they have no relatives, we focussed on newcomers. Newcomers  
254 are males which were captured as yearlings for whom we can therefore ensure that they  
255 defended a lek territory for the first time (newcomers are usually one or two years old; N =  
256 34). We first identified the location and territories boundaries of all newcomers, measured  
257 their  $R_{QG}$  to their neighbours and to the other lekking males. We then used a mixed model to  
258 determine whether males were less related to their neighbours than to the other lekking  
259 males using the mean  $R_{QG}$  as the dependent variable, a binary variable describing whether  
260 the mean was calculated across neighbouring or non-neighbouring males. Male identity was  
261 set as a random factor nested within each year\*lek combination. In addition to these paired  
262 comparisons, we carried out a randomisation test to determine whether males settled down  
263 on a territory with less closely related neighbours than expected by chance. We first  
264 identified potential territories where males could have settled down as those occupied by  
265 other newcomers and peripheral territories. We then calculated the mean  $R_{QG}$  and number of  
266 neighbouring close relatives newcomer would have had if they had occupied one of these  
267 potential territories. We used the software PopTools 3.2 (Hood 2011) to shuffle each  
268 newcomer to each of the potential territories. We ran 500 iterations to generate random  
269 distributions for the mean relatedness between neighbours and the number of closely related  
270 neighbours. The observed mean relatedness to the neighbours and number of close relatives  
271 were then compared to these random distributions and hence determine whether males  
272 settled down with less closely related neighbours than expected by chance.

273

## 274 **Results**

275 Across all leks and years 83% of the neighbouring males were unrelated (mean  $R_{QG} = 0.02 \pm$   
276  $0.18$  (SD),  $N_{Tot} = 195$ , Fig. 1a) and most males had no closely related neighbour (Fig. 1b).  
277 The fight frequency and intensity between neighbouring males were not influenced by their  
278 relatedness whether it was measured  $R_{QG}$  between neighbours nor  $R_{QG\_binary}$  (Table 1). The  
279 only factor which significantly influenced fight frequency and intensity was the difference in  
280 territory centrality as fights were more frequent and more intense at small differences in  
281 territory centrality (Table 1, Fig. 2).

282 Across newcomers, there was no significant difference between the mean  $R_{QG}$  of  
283 neighbours and non-neighbours ( $\beta = -0.023 \pm 0.018$  (SE);  $t = -1.254$ ;  $P = 0.221$ ; Fig. 3). The  
284 spatially constrained randomisation test showed that newcomers were not less related to  
285 their neighbours than expected by chance (mean observed  $R_{QG} = 0.02 \pm 0.11$  (SD),  $N_{Newcomers}$   
286  $= 34$ , mean expected  $R_{QG} = 0.00 \pm 0.02$  (SD),  $P = 0.24$ , Suppl. Fig. 2). Similarly, the  
287 observed mean proportion of close relative neighbours (i.e.  $R_{QG} > 0.2$ ) did not differ from the  
288 random expectation (observed mean proportion neighbouring close relatives = 0.166,  $N = 34$ ;  
289 expected mean proportion neighbouring close relatives =  $0.137 \pm 0.033$  (SD),  $P = 0.19$ ).

290

## 291 **Discussion**

292 As kin selection and competition may occur simultaneously, the overall fitness consequences  
293 of the interactions between close relatives may depend on an adaptive response dampening  
294 the fitness costs of kin competition. We addressed this knowledge gap by testing whether kin  
295 selection could have led to the evolution of the two main behavioural mechanisms through  
296 which males may mitigate kin competition: a decrease in fight frequency/intensity and the  
297 avoidance of closely related neighbours. We found no evidence of these mechanisms in the  
298 studied black grouse leks.

299 As males in lekking species defend clustered territories, one obvious way to  
300 potentially reduce kin competition is to reduce the aggressive interactions with close  
301 relatives. Such a process has been reported in many taxa (e.g. Koprowski 1996;  
302 Pravosudova 2001; Wahaj et al. 2004; Smith et al. 2010), including a lekking species (satin  
303 bowerbirds, *Ptilonorhynchus violaceus*; Reynolds et al. 2008) in which a decrease in  
304 aggression was found between closely related individuals which facilitated the formation of  
305 kin clusters . In our study, the frequency and intensity of fights between neighbours in black  
306 grouse were unrelated to their relatedness. Male black grouse spend a large proportion of  
307 their time fighting (Hämäläinen et al. 2012), whereas in satin bowerbirds, individuals rarely  
308 directly interact and the cooperative behaviours of wild turkeys males is a rare and  
309 remarkable feature for a lekking species (Höglund and Alatalo 1995). Black grouse males  
310 form tightly clustered leks on which females prefer dominant males defending central  
311 territories and expressing a wide variety of behavioural and morphological traits (see  
312 Kervinen et al. 2015, 2016). As male mating success is also strongly related to males' past  
313 lekking performance (Kokko et al. 1997, 1999) and current fighting performance and  
314 frequency (Lebigre et al. 2012; Hämäläinen et al. 2012), the benefits of the modulation of  
315 their behaviour with relatedness may be negligible compared with the direct benefits of  
316 successful male-male contests. Furthermore, there were very few closely related neighbours  
317 meaning that males may actually not even need to modulate their behaviour to reduce the  
318 fitness costs of kin competition. In lekking species where no kin structures have been found  
319 (and hence closely related neighbours are probably rare), relatedness-related changes in  
320 display behaviour are also unlikely but this remains to be tested (e.g. Gibson et al. 2005;  
321 Loiselle et al. 2007). In studies where kin structures have been found, it is critical to  
322 undertake similar analyses to better understand the importance of kin selection as male  
323 philopatry is the main factor explaining the formation of these kin groups and males indirect  
324 fitness benefits may actually be substantially larger if they also reduce their level of  
325 aggression (e.g. Shorey et al. 2000; Segelbacher et al. 2007). Even if in our case the  
326 influence of the spatial structure of the males did not strongly influence males' fight frequency

327 and intensity we stress that applying a similar approach is the most appropriate way to  
328 account for a spatial structure for which the neighbourhood distances are more relevant than  
329 geographical distances *per se*.

330         The lack of closely related neighbours may result from the active avoidance of close  
331 relatives when males establish their lek territories. However, we found no evidence that the  
332 territory location of newcomer males to the leks was not random with respect to the  
333 relatedness of the neighbouring males. This might again be due to the low likelihood of  
334 settling down on a lek holding close relatives in this large continuous population (Lebigre et  
335 al. 2008, 2014) but also be due to the other factors that influence the spatial arrangements of  
336 the territories. Indeed, newcomers may have limited control over the identity of their  
337 neighbours and location of their territory given their lack of prior lek experience in pairwise  
338 conflicts (Templeton et al. 2012) and their lower competitive abilities (Parker and Sutherland  
339 1986; Alatalo et al. 1992). More specifically, information concerning the past territory  
340 positions (Kokko et al. 1999) and the physical strength and ornament expression that  
341 determine male dominance (Kervinen et al. 2012, 2015, 2016) may be far more important for  
342 the current and future dominance status (and hence fitness) of the newcomer males than  
343 their relatedness to the neighbours. Territorial birds may tolerate kin and facilitate their  
344 recruitment in the local populations through the older males' secession of part of their  
345 territories (e.g. Piertney et al. 1999; MacColl et al. 2000; Piertney et al. 2008). In black  
346 grouse, the most successful males defend central territories and therefore are unlikely to  
347 display close to their sons who might only be able to defend peripheral territories (Kokko et  
348 al. 1997). Yet, it might be interesting to examine the temporal changes in both territory  
349 position and neighbours identity to determine the stability of the neighbourhoods and  
350 dominance hierarchies which can strongly influence males' lek performance and their mating  
351 success.

352         When males establish their lek territory, they will have three critical choices to makes:  
353 which lek to join, when to join it, where to establish a territory. We have been able to show

354 that kinship to the other lek member does not contribute substantially to these steps in black  
355 grouse as leks are random subsets of the larger winter flocks (Lebigre et al. 2008), overall  
356 males joining leks have limited indirect fitness benefits (Lebigre et al. 2014), and in this  
357 study, we found that males did not avoid fighting with close relatives and the location of  
358 newcomers' territories was not influenced by its relatedness to its neighbours. Therefore, it is  
359 now important to determine whether such a lack of behavioural response to competitive  
360 interactions with kin are consistent over time and space. We showed that the indirect fitness  
361 benefits gained by the lekking males depend on population density (Lebigre et al. 2014). In a  
362 similar fashion, behavioural adjustments may also be easier to detect when the indirect costs  
363 of competing with kin are high and female visits to the leks are rare (e.g. low population  
364 density years). Moreover, it is now critical to try to quantify both the indirect fitness costs and  
365 benefits and integrate them over individuals' lifespan to fully understand the net indirect  
366 effects associated with male group display to fully quantify males' inclusive fitness and  
367 determine the relative contribution of direct and indirect fitness components. The behavioural  
368 data used in this study therefore imply that the direct fitness benefits gained by successful  
369 male-male aggressive encounters likely outbalance indirect fitness benefits.

370

371

372 **Compliance with Ethical Standards**

373 - Funding: This study was funded by the Academy of Finland (grant numbers 7211271 and  
374 7119165), the Finnish Centre of Excellence in Evolutionary Research (211271), and the  
375 Fond National de la Recherche Scientifique (FNRS A4/5 - MCF/DM).

376

377 - Conflict of Interest: CL declares that he has no conflict of interest. CT declares that she has  
378 no conflict of interest. CDS declares that he has no conflict of interest.

379

380 - Ethical approval: All applicable international, national, and/or institutional guidelines for the  
381 care and use of animals were followed. This work was carried out with the permission of  
382 Central Finland Environmental Centre and the Animal Care Committee of the University of  
383 Jyväskylä (permissions KSU-2003-L-25/254 and KSU-2002-L-4/254). This article does not  
384 contain any studies with human participants performed by any of the authors.

385



386 **References**

- 387 Alatalo RV, Höglund J, Lundberg A, Sutherland WJ (1992) Evolution of black grouse leks:  
388 female preferences benefit males in larger leks. *Behav Ecol* 3:53–59
- 389 Alizon S, Taylor P (2008) Empty sites can promote altruistic behavior. *Evolution* 62:1335–  
390 1344
- 391 Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using  
392 lme4. *J Stat Softw* 67:1–48
- 393 Berglund A, Bisazza A, Pilastro A (1996) Armaments and ornaments: An evolutionary  
394 explanation of traits of dual utility. *Biol J Linn Soc* 58:385–399
- 395 Bitume EV, Bonte D, Ronce O, Bach F, Flaven E, Olivieri I, Nieberding CM (2013) Density  
396 and genetic relatedness increase dispersal distance in a subsocial organism. *Ecol Lett*  
397 16:430–437
- 398 Bouzat JL, Johnson K (2004) Genetic structure among closely spaced leks in a peripheral  
399 population of lesser prairie-chickens. *Mol Ecol* 13:499–505
- 400 Briffa M, Sneddon LU (2007) Physiological constraints on contest behaviour. *Funct Ecol*  
401 21:627–637
- 402 Brown GE, Brown JA (1996) Kin discrimination in salmonids. *Rev Fish Biol Fisher* 6:201–219
- 403 Caizergues A, Ellison LN (2002) Natal dispersal and its consequences in Black Grouse  
404 *Tetrao tetrix*. *Ibis* 144:478–487
- 405 Culp M (2011) spa: a semi-supervised R package for semi-parametric graph-based  
406 estimation. *J Stat Softw* 40:1–29
- 407 Edenbrow M, Croft DP (2012) Kin and familiarity influence association preferences and  
408 aggression in the mangrove killifish *Kryptolebias marmoratus*. *J Fish Biol* 80:503–518
- 409 Fiske P, Rintamäki PT, Karvonen E (1998) Mating success in lekking males: a meta-  
410 analysis. *Behav Ecol* 9:328–338
- 411 Gibson RM, Pirs D, Delaney KS, Wayne RK (2005) Microsatellite DNA analysis shows that  
412 greater sage grouse leks are not kin groups. *Mol Ecol* 14:4453–4459

413 Gosling LM, Petrie M, Rainy ME (1987) Lekking in topi: a high cost, specialist strategy. Anim  
414 Behav 35:616–618

415 Grafen A (2006) Optimization of inclusive fitness. J Theor Biol 238:541–563

416 Griffin AS, West SA (2002) Kin selection: fact and fiction. Trends Ecol Evol 17:15–21

417 Hämäläinen A, Alatalo RV, Lebigre C, Siitari H, Soulsbury CD (2012) Fighting behaviour as a  
418 correlate of male mating success in black grouse *Tetrao tetrix*. Behav Ecol Sociobiol  
419 66:1577–1586

420 Hamilton WD (1964) The genetical evolution of social behaviour I & II. J Theor Biol 7:1–52

421 Hatchwell BJ (2010) Cryptic kin selection: kin structure in vertebrate populations and  
422 opportunities for kin-directed cooperation. Ethology 116:203–216

423 Höglund J (2003) Lek-kin in birds – provoking theory and surprising new results. Ann Zool  
424 Fenn 40:249–253

425 Höglund J, Alatalo RV (1995) Leks. Princeton University Press, Princeton

426 Höglund J, Alatalo RV, Lundberg A, Ratti O (1994) Context-dependent effects of tail-  
427 ornament damage on mating success in black grouse. Behav Ecol 5:182–187

428 Höglund J, Alatalo RV, Lundberg A, Rintamäki PT, Lindell J (1999) Microsatellite markers  
429 reveal the potential for kin selection on black grouse leks. Proc R Soc Lond B 266:813–816

430 Höglund J, Johansson T, Pelabon C (1997) Behaviourally mediated sexual selection:  
431 Characteristics of successful male black grouse. Anim Behav 54:255–264

432 Höglund J, Kålås JA, Fiske P (1992) The costs of secondary sexual characters in the lekking  
433 great snipe (*Gallinago media*). Behav Ecol Sociobiol 30:309–315

434 Höner OP, Wachter B, East ML, Streich WJ, Wilhelm K, Burke T, Hofer H (2007) Female  
435 mate-choice drives the evolution of male-biased dispersal in a social mammal. Nature  
436 448:798–801

437 Hood GM (2011) PopTools version 3.2.5, <http://www.poptools.org>

438 Hovi M, Alatalo RV, Höglund J, Lundberg A, Rintamäki PT (1994) Lek centre attracts black  
439 grouse females. Proc R Soc Lond B 258:303–305

440 Hsu Y, Earley RL, Wolf LL (2006) Modulation of aggressive behaviour by fighting experience:  
441 Mechanisms and contest outcomes. *Biol Rev* 81:33–74

442 Isvaran K, Pongshe A (2013) How general is a female mating preference for clustered males  
443 in lekking species? A meta-analysis. *Anim Behav* 86:417–425

444 Kervinen M, Alatalo RV, Lebigre C, Siitari H, Soulsbury CD (2012) Determinants of yearling  
445 male lekking effort and mating success in black grouse (*Tetrao tetrix*). *Behav Ecol*  
446 23:1209–1217

447 Kervinen M, Lebigre C, Alatalo RV, Siitari H, Soulsbury CD (2015) Life history differences in  
448 age-dependent expressions of multiple ornaments and behaviors in a lekking bird. *Am Nat*  
449 185:13–27

450 Kervinen M, Lebigre C, Soulsbury CD (2016) Simultaneous age-dependent and age-  
451 independent sexual selection in the lekking black grouse (*Lyrurus tetrix*). *J Anim Ecol*  
452 85:715–725

453 Kirkpatrick M, Ryan MJ (1991) The evolution of mating preferences and the paradox of the  
454 lek. *Nature* 350:33–38

455 Kokko H, Lindström J (1996) Kin selection and the evolution of leks: whose success do young  
456 males maximize? *Proc R Soc Lond B* 263:919–923

457 Kokko H, Lindström J, Alatalo RV, Rintamäki PT (1997) Queuing for territory positions in the  
458 lekking black grouse (*Tetrao tetrix*). *Behav Ecol* 9:376–383

459 Kokko H, Rintamäki PT, Alatalo RV, Höglund J, Karvonen E, Lundberg A (1999) Female  
460 choice selects for lifetime lekking performance in black grouse males. *Proc R Soc Lond B*  
461 266:2109–2115

462 Komdeur J (1994) The effect of kinship on helping in the cooperative breeding Seychelles  
463 warbler (*Acrocephalus sechellensis*). *Proc R Soc Lond B* 256:47–52

464 Koprowski JL (1996) Natal philopatry, communal nesting, and kinship in fox squirrels and  
465 gray squirrels. *J Mammal* 77:1006–1016

466 Krakauer AH (2005) Kin selection and cooperative courtship in wild turkeys. *Nature* 434:69–  
467 72

468 Krützen M, Sherwin WB, Barre LM, Connor RC, Van de Castele T, Mann J, Brooks R  
469 (2003) Contrasting relatedness patterns in bottlenose dolphins (*Tursiops* sp.) with different  
470 alliance strategies. *Proc R Soc Lond B* 270:497–502

471 Lebigre C, Alatalo RV, Forss HE, Siitari H (2008). Low levels of relatedness on black grouse  
472 leks despite male philopatry. *Mol Ecol* 17:4512–4521

473 Lebigre C, Alatalo RV, Kilpimaa J, Staszewski V, Siitari H (2012) Leucocyte counts variation  
474 and measures of male fitness in the lekking black grouse. *J Ornithol* 153:95–102

475 Lebigre C, Alatalo RV, Siitari H (2010) Female-biased dispersal alone can reduce the  
476 occurrence of inbreeding in black grouse. *Mol Ecol* 19:1929–1939

477 Lebigre C, Alatalo RV, Siitari H (2013) Physiological costs enforce the honesty of lek display  
478 in the black grouse (*Tetrao tetrix*). *Oecologia* 172:983–993

479 Lebigre C, Alatalo RV, Siitari H, Parri S (2007) Restrictive mating by females on black grouse  
480 leks. *Mol Ecol* 16:4380–4389

481 Lebigre C, Alatalo RV, Soulsbury CD, Höglund J, Siitari H (2014) Limited indirect fitness  
482 benefits of male group membership in a lekking species. *Mol Ecol* 23:5356–5365

483 Lion S, Gandon S (2009) Habitat saturation and the spatial evolutionary ecology of altruism.  
484 *J Evol Biol* 22:1487–1502

485 Loiselle BA, Ryder TB, Durães R, Tori W, Blake JG, Parker PG (2007) Kin selection does not  
486 explain male aggregation at leks of 4 manakin species. *Behav Ecol* 18:287–291

487 MacColl ADC, Piertney SB, Moss R, Lambin X (2000) Spatial arrangement of kin affects  
488 recruitment success in young male red grouse. *Oikos* 90:261–270

489 Magaña M, Alonso JC, Palacín C (2011) Age-related dominance helps reduce male  
490 aggressiveness in great bustard leks. *Anim Behav* 82:203–211

491 McElligott AG, Gammell MP, Harty HC, Paine DR, Murphy DT, Walsh JT, Hayden TJ (2001)  
492 Sexual size dimorphism in fallow deer (*Dama dama*): Do larger, heavier males gain  
493 greater mating success? *Behav Ecol Sociobiol* 49:266–272

494 McElligott AG, Naulty F, Clarke WV, Hayden TJ (2003) The somatic cost of reproduction:  
495 What determines reproductive effort in prime-aged fallow bucks? *Evol Ecol Res* 5:1239–  
496 1250

497 Mitteldorf J, Wilson DS (2000) Population viscosity and the evolution of altruism. *J Theor Biol*  
498 204:481–496

499 Parker GA, Sutherland WJ (1986) Ideal free distributions when individuals differ in  
500 competitive ability: phenotype-limited ideal free models. *Anim Behav* 34:1222–1242

501 Piertney SB, Lambin X, Maccoll ADC et al (2008) Temporal changes in kin structure through  
502 a population cycle in a territorial bird, the red grouse *Lagopus lagopus scoticus*. *Mol Ecol*  
503 17:2544–2551

504 Piertney SB, MacColl ADC, Lambin X, Moss R, Dallas JF (1999) Spatial distribution of  
505 genetic relatedness in a moorland population of red grouse (*Lagopus lagopus scoticus*).  
506 *Biol J Linn Soc* 68:317–331

507 Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2013) nlme: Linear and Nonlinear  
508 Mixed Effects Models. R package version 3.1-108, [https://cran.r-](https://cran.r-project.org/web/packages/nlme/index.html)  
509 [project.org/web/packages/nlme/index.html](https://cran.r-project.org/web/packages/nlme/index.html)

510 Pravosudova EV, Grubb TC, Parker PG (2001) The influence of kinship on nutritional  
511 condition and aggression levels in winter social groups of Tufted Titmice. *Condor* 103:  
512 821–828

513 Queller DC, Goodnight KF (1989) Estimating relatedness using genetic markers. *Evolution*  
514 43:258–275

515 R Core Development Team (2012) R: A language and environment for statistical computing.  
516 R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org/>

517 Reeve HK, Westneat DF, Noon WA, Sherman PW, Aquadro CF (1990) DNA 'fingerprinting'  
518 reveals high levels of inbreeding in colonies of the eusocial naked mole-rat. *P Natl Acad Sci*  
519 *USA* 87:2496–2500

520 Reynolds SM, Christman MC, Uy JAC, Patricelli GL, Braun MJ, Borgia G (2009) Lekking  
521 satin bowerbird males aggregate with relatives to mitigate aggression. *Behav Ecol*  
522 20:410–415

523 Rintamäki PT, Höglund J, Alatalo RV, Lundberg A (2001) Correlates of male mating success  
524 on black grouse (*Tetrao tetrix* L.) leks. *Ann Zool Fenn* 38:99–109

525 Russell AF, Hatchwell BJ (2001) Experimental evidence for kin-biased helping in a  
526 cooperatively breeding vertebrate. *Proc R Soc Lond B* 268:2169–2174

527 Sæther SA (2002) Kin selection, female preference and the evolution of leks: direct benefits  
528 may explain kin structuring. *Anim Behav* 63:1017–1019

529 Segelbacher G, Wegge P, Sivkov AV, Höglund J (2007) Kin groups in closely spaced  
530 capercaillie leks. *J Ornithol* 148:79–84

531 Shorey L, Piertney SB, Stone J, Höglund J (2000) Fine-scale genetic structuring on *Manacus*  
532 *manacus* leks. *Nature* 408:352–353

533 Silk JB (2002) Kin selection in primate groups. *Int J Primatol* 23:849–875

534 Smith JE, Van Horn RC, Powning KS, Cole AR, Graham KE, Memenis SK, Holekamp KE  
535 (2010) Evolutionary forces favoring intragroup coalitions among spotted hyenas and other  
536 animals. *Behav Ecol* 21:284–303

537 Taylor P (1992) Altruism in viscous populations—an inclusive fitness model. *Evol Ecol*  
538 6:352–356

539 Templeton CN, Reed VA, Campbell SE, Beecher MD (2012) Spatial movements and social  
540 networks in juvenile male song sparrows. *Behav Ecol* 23:141–152

541 Van Dyken JD (2010) The components of kin competition. *Evolution* 64:2840–2854

542 Vehrencamp SL, Bradbury JW, Gibson RM (1989) The energetic cost of display in male sage  
543 grouse. *Anim Behav* 38:885–896

544 Wahaj SA, Van Horn RC, Van Horn TL, Dreyer R, Hilgris R, Schwarz J, Holekamp KE (2004)  
545 Kin discrimination in the spotted hyena (*Crocuta crocuta*): nepotism among siblings.  
546 *Behav Ecol Sociobiol* 56:237–247

- 547 Warren PK, Baines D (2002) Dispersal, survival and causes of mortality in black grouse  
548 *Tetrao tetrix* in northern England. *Wildlife Biol* 8:91–97
- 549 West Eberhard MJ (1975) The evolution of social behavior by kin selection. *Q Rev Biol* 50:1–  
550 33
- 551 Wilson DS, Pollock G, Dugatkin L (1992) Can altruism evolve in purely viscous populations?  
552 *Evol Ecol* 6:331–341
- 553

554 **Figure captions**

555 Fig. 1 Distributions of the relatedness estimates for all neighbouring males (panel A) and  
556 number of close relatives to newly territorial males (panel B). Close relatives were  
557 conservatively defined as having a pairwise relatedness coefficient superior to 0.2

558 Fig. 2 Effect of the territory centrality difference on the fight frequency of neighbouring males

559 Fig. 3 Mean relatedness of newly territorial males to their neighbours and to the other lekking  
560 males