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2

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

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20 **Acknowledgments:** This paper is dedicated to Prof. Rauno Veli Alatalo who passed away
21 on November 9th 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.

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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 as 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 ≥ 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 ± 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

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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