

Næss, M. W., Bårdsen, B.-J., and Tveraa, T. (2012). Wealth-dependent and interdependent strategies in the Saami reindeer husbandry, Norway. *Evolution and Human Behavior* 33(6):696-707.

1 **Wealth-dependent and interdependent strategies in the Saami reindeer husbandry,**

2 **Norway¹**

3

4 **Marius Warg Næss^{1,2,*}, Bård-Jørgen Bårdsen² & Torkild Tveraa²**

5 ¹ *CICERO - Center for International Climate and Environmental Research, Fram Centre, N-*
6 *9296 Tromsø, Norway.*

7 ² *Norwegian Institute for Nature Research (NINA), Arctic Ecology Department, Fram Centre,*
8 *N-9296 Tromsø, Norway.*

9 **Corresponding author, E-Mail: m.w.nass@cicero.uio.no; Phone: (+47) 90721907.*

10 Word Count: 8528 (main text + references)

¹ This is the accepted version of the paper and as such may differ from the final corrected proof which can be accessed at <http://dx.doi.org/10.1016/j.evolhumbehav.2012.05.004>.

11 **ABSTRACT**

12 It has been argued that decisions in relation to choosing strategies to a large degree depend
13 on an organism's state. For nomadic pastoralists, wealth is an important state variable, since
14 it has been argued that differences in observed behaviours reflect alternative strategies
15 dependent on varying socioeconomic circumstances. From a game theoretical point of view,
16 however, strategies are also interdependent, i.e. the choice of a strategy cannot be made
17 wisely without considering what other actors are doing, since the outcome of a given
18 strategy is not only dependent on individual state but also on the strategies of others. This
19 study investigated to what degree slaughter strategies in the Saami reindeer husbandry are
20 both state dependent and interdependent. The main findings in this study was that: (1) the
21 probability; (2) the amount; and (3) the type of animal slaughtered was to a large degree
22 influenced by both individual herders' herd size and the number of animals slaughtered by
23 neighbouring herders. Moreover, this study also found that kinship represents a
24 coordinating principle since the degree of genealogical relatedness had a positive effect on
25 the slaughtering strategies adopted by herders.

26

27

28 **Keywords:** Tragedy of the commons; Prisoners' Dilemma; Cooperation; Kinship; Reindeer
29 abundance; Wealth.

30 1.0 INTRODUCTION

31 1.1 State dependent strategies

32 It has been argued that decisions in relation to choosing strategies to a large degree depend
33 on the organism's state (e.g. McNamara and Houston, 1996) and for nomadic pastoralists
34 some measure of wealth (e.g. herd size) may be an important state variable. Differences in
35 observed herder behaviours among nomadic pastoralist may, for example, reflect alternative
36 strategies aimed at achieving similar objectives dependent on varying socioeconomic
37 circumstances (Borgerhoff Mulder and Sellen, 1994). Grandin (1983:240), for example,
38 argues that a herder with 400 animals have different options available than one with 4. In a
39 model investigating how household wealth should be divided between small stock and
40 camels in order to maximise long term household viability, Mace & Houston (1989) found
41 that while it paid off for relatively poor pastoral households to maximize small stock, this
42 changed above a certain threshold of wealth where it paid off to invest in camels. In another
43 study, Mace (1993) found that wealthier pastoralists use flexible herd management
44 strategies to accommodate long-term household survival by controlling breeding rates of
45 sheep. This practice can be explained by the cost of reproduction, especially during
46 occasions of harsh weather conditions where the survival rate of neonates and even
47 pregnant and/or lactating females can be substantially lowered (Bårdsen et al., 2010;
48 Bårdsen and Tveraa, 2012; Tveraa et al., 2003; Bårdsen et al., 2011). Poor households cannot
49 engage in this practice since they have no choice but to increase herd size. Moreover,
50 Borgerhoff Mulder & Sellen (1994:214) argues that rich herders among the Kipsigis and
51 Datoga often extend livestock as gifts to clansmen or neighbours having an emergency.
52 While this practice reduces wealthy households' short term access to livestock and livestock

Næss, M. W., Bårdsen, B.-J., and Tveraa, T. (2012). Wealth-dependent and interdependent strategies in the Saami reindeer husbandry, Norway. *Evolution and Human Behavior* 33(6):696-707.

53 products, it may increase long term household survival through delayed reciprocity, a
54 strategy that is only available to wealthier households (Borgerhoff Mulder and Sellen,
55 1994:214; see also Moritz et al., 2011). Grandin (1983:241-2, Table 2) has presented
56 evidence that indicate that in Kenya percentage off take is negatively related to wealth, but
57 that wealthy household have greater per capita slaughter. In other words, wealthy
58 households slaughter a larger number of animals but proportionally less of their herds than
59 poor households.

60

61 **1.2 Interdependent strategies**

62 While wealth seems to be an important state variable affecting production strategies in
63 several pastoral societies, decisions in relation to, for example, the number of animals to
64 slaughter also have to be made in relation to the actions of neighbouring herders because
65 the outcome of a given strategy is not only dependent on the herders' own state but also on
66 what others are doing (Schelling, 1980; see also Axelrod, 1984; Dixit and Skeath, 2004;
67 Colman, 1995; Wydick, 2008). In general terms, this interdependency lies on a continuum
68 with pure coordination at one end (convergent interests) and pure conflict at the other end
69 (divergent interests, Schelling, 1980:86).

70

71 *1.2.1 Mixed motives: Prisoners' Dilemma and the tragedy of the commons*

72 Nevertheless, most situations lies somewhere in between these two extremes where
73 individuals are faced with incentives both to cooperate and compete. A case point is
74 Hardin's (1968) concept of 'the tragedy of the commons' since it captures the social dilemma
75 inherent in utilizing communally owned resources: all herders would be better off by

76 cooperating to restrict herd size and consequently preserve the common grazing area, but
77 individuals can do better by taking advantage of the cooperative efforts of others.

78 The tragedy of the commons is an example of a Prisoners' Dilemma and Hardin
79 (1968) observed that Prisoners' Dilemma problems occur in many, if not most, situations
80 that call for some kind of collective sacrificial restraint or action, but where *the underlying*
81 *incentive lies in gaining and individual advantage through a lack of individual restraint*
82 (Wydick, 2008:27-8). In short, the Prisoners' Dilemma captures a broad class of settings in
83 which the welfare of the individual and the welfare of the group are in conflict with another
84 (Wydick, 2008:28). Thus, decisions in relation to the number of animals to slaughter also
85 have to be made in relation to the actions of other herders. This is especially pertinent in
86 areas with common pastures, such as e.g. the reindeer husbandry in Finnmark, where
87 pasture access to a large degree is dependent on herd size (Riseth et al., 2004). Larger herds
88 use more extensive pasture areas and may thereby exclude other herds from grazing in the
89 same area. In such a system a unilateral strategy of slaughtering many animals have negative
90 implications if *everybody else slaughters few or no animals*. In other words, in areas where
91 pastures are common, decisions in relation to slaughter can be expressed as a tragedy of the
92 commons: individuals perform better by adding additional animals on the common pastures
93 since the cost of overexploitation is shared by all users while the benefits of increased herd
94 size is accrued to individual herders (Næss and Bårdsen, 2010). One way of achieving such a
95 benefit is to restrict slaughter.

96

97 *1.2.2 Kinship – evolutionary aspects of cooperation*

98 In general terms, benefits not easily obtainable by individuals may be available to
99 cooperating groups (Axelrod, 1984).² The problem, as illustrated by the tragedy of the
100 commons, is related to “free riding” where individuals that can benefit from cooperation can
101 do better by exploiting the cooperative behaviour of others (Axelrod, 1984:92).

102 From an evolutionary point of view important mechanisms facilitating cooperative
103 behaviour are kin selection and inclusive fitness (see e.g. Hamilton, 1964; Alvard, 2003; for a
104 review, see Griffin and West, 2002). Other prominent mechanism facilitating cooperation
105 are (1) reciprocity (Trivers, 1971), (2) signalling (Smith and Bird, 2005), and (3) punishment
106 (Axelrod, 1986). Moreover, (4) asymmetry in social relations have been argued to play a
107 part in the emergence of cooperative social institutions (Richerson et al., 2003; see also
108 Borgerhoff Mulder and Coppolillo, 2005), where some individuals have both the means and
109 the incentives to enforce e.g. costly punishment that facilitate cooperative behaviour.
110 Punishment, however, represent a second-order collective action problem because the
111 means to solve a collective action problem itself poses a collective action problem since
112 punishment is a public good open for free riding (see Smith, 2003). More to the point, while
113 punishment may favour cooperation it is less evident why natural selection would favour
114 such a trait (West et al., 2011). Nevertheless, experimental evidence indicate that, in the
115 long run, both groups and individuals are better off when punishing non-cooperative
116 behaviour since the cost of punishment becomes negligible and is also outweighed by the
117 increased benefits that comes from cooperation (Gächter et al., 2008). Moreover,
118 punishment may provide: (1) direct fitness advantage by seceding interactions with

² Following Smith (2003:402) cooperation can be defined as collective action for mutual benefit, where collective action can be defined as when two or more individuals have to interact to achieve a specific goal.

119 uncooperative individuals to the benefit of interactions with cooperative individuals; and (2)
120 indirect fitness advantages as punished individuals may change behaviour in response to
121 punishment and may thus be more likely to cooperate in the future (cf. West et al., 2011).

122 Kin relations may thus provide a powerful coordinating principle (Gintis et al., 2005;
123 Griffin and West, 2002; Alvard, 2003; Smith, 2003; Hamilton, 1964) because groups
124 organized on the basis of kinship are usually small where individuals have: (1) close and long-
125 term contact; (2) the possibility to monitor the behaviour of others with the possibility to;
126 (3) punish people who break the rules (Borgerhoff Mulder and Coppolillo, 2005, see below
127 for arguments in relation to why reciprocity, kinship and punishment may not explain large
128 scale cooperation). Kin relationship may thus be conducive for making it possible for
129 herders to monitor and punish rule breakers and thus mitigate the inherent social dilemma
130 in utilizing common pool resources.

131

132 **1.3 Predictions**

133 In sum, it could be argued that, *ceteris paribus*, herders' strategies are formed by a
134 combination of the household's own state, such as herd size, and by the strategies adopted
135 by neighbouring households. Consequently, this paper aims at investigating how slaughter
136 strategies in the Saami reindeer husbandry in Norway are influenced by: (1) reindeer
137 herder's own wealth, where herd size is expected to be a positive predictor for slaughtering.
138 (2) The actions of other herders, since negative density-dependence influence the reindeer
139 husbandry (Næss, 2009; Næss et al., 2010; Tveraa et al., 2007; Bårdsen and Tveraa, 2012;
140 Bårdsen et al., 2010) and the situation facing reindeer herders can thus be characterized as a

141 tragedy of the commons³ we expected that the number of animals slaughtered by
142 neighbouring herders to be a negative predictor for slaughtering. (3) The degree of kinship
143 within groups, if kinship works as a coordinating principle (as shown by Næss et al., 2010) we
144 expected kinship to be a positive predictor for slaughter. Finally, (4) the interaction between
145 the actions of other herders and kin relations, should be positively related to slaughter
146 because as kin relations increase, conflicts are reduced and thereby weakens the negative
147 effect of the amount of slaughter undertaken by other herders.

148

149 2.0 METHODS

150 2.1 Study area

151 Reindeer husbandry has been said to be the cornerstone of the Saami culture in northern
152 Fennoscandia (Bostedt, 2001). Reindeer husbandry is, however, historically relatively recent
153 (300-400 years old) and probably evolved from a hunting culture based on wild reindeer (cf.
154 Næss et al., 2010). Over the years, Saami reindeer husbandry has changed, most
155 significantly, from milk and meat production with smaller herds to meat production alone
156 with larger herds (Paine, 1994). Traditionally, reindeer pastoralism was based on households
157 that followed their herds year-round and the pastoral economy was primarily tied to
158 reindeer products (Vorren, 1978). Between 1960 and 1990 reindeer husbandry underwent
159 major technological, economic, and political changes leading to a motorized and market
160 oriented industry (Riseth, 2003).

³ According to McPeak (2005:188-9) the fact that the herd size of other herders exerts a negative influence on the production of the target household herd captures the essence of the negative externality, i.e. the tragedy of the commons posited for pastoral areas.

161 At present Saami reindeer husbandry operates at three different levels of social
162 organization: (1) husbandry unit; (2) siida; and (3) district. The husbandry unit is the basic
163 unit of the social organization, and is licensed by the government to manage a herd of
164 reindeer within a delimited area (Ulvevadet and Klovov, 2004). The husbandry unit is similar
165 to the household as defined by Dahl (1979:70), but as the herd can also contain reindeer
166 belonging to family members of the husbandry unit's manager, it resembles an extended
167 family unit. The siida is a cooperative unit composed of one or more reindeer management
168 families, and is part of the traditional reindeer husbandry system⁴ (cf. Næss et al., 2010). The
169 siida is usually organized on the basis of kinship joined together in social and labor
170 communities for keeping control of herds of reindeer through herding (cf. Næss et al., 2010).
171 Saami kinship system is extensive and includes terms for consanguinal and affinal
172 relationships (Pehrson, 1964). Traditionally, Saami kinship system was bilateral, i.e. kinship
173 defined through both the male and female lines (Gjessing, 1975:326). Sibling solidarity,
174 however, could be extended to include cousins and other affinal relatives of the same
175 generation (Paine 1964:256-257 in Bergman et al., 2008:101).

176 Saami reindeer husbandry districts are formal management units with responsibility
177 to provide the Norwegian reindeer husbandry administration with information. The district
178 is also responsible for ensuring that reindeer husbandry is managed in accordance with
179 government regulations (Bull, 1997). As such the district might be better described as the
180 lowest level of government management of the reindeer industry rather than a level of
181 social organization (Ulvevadet, 2008) even though members of reindeer districts have to

⁴ This level of social organization is *formally* recognized by the Norwegian government in the new Reindeer Management Act as what has previously been designated as *husbandry unit* will change to *siida share* (Ulvevadet, 2008; Anonymous, 2007a).

182 cooperate in, e.g., maintaining fences or fulfilling governmental quotas on the maximum
183 number of reindeer per district (Næss et al., 2010; Næss et al., 2009).

184

185 **2.2 Study design**

186 Different reindeer summer pasture districts represent heterogeneous units that differ in
187 both climate and herding strategies (e. g. Bårdsen and Tveraa, 2012). Previous studies have
188 used differences in density as a basis of a paired-block design between neighbouring districts
189 with low and high density. This quasi-experimental design, consisting of 10 pairs and 20
190 districts, have been adopted to separate the effects of reindeer density from other
191 environmental factors (see Ims et al., 2007; Bråthen et al., 2007a; Bråthen et al., 2007b for
192 details). While not estimating the effects of the design directly, the present study used the
193 same districts to ensure that the analyses were based on a subsample of heterogeneous
194 districts.

195

196 **2.3 Study protocol**

197 This study is based on two datasets: the first consist of governmental statistics compiled and
198 published annually by the Norwegian reindeer husbandry administration (31 of March, see
199 e.g. Anonymous, 2007b). This dataset contains data pertaining to husbandry unit numbers,
200 herd size (total number of reindeer in the spring) and number of reindeer slaughtered. These
201 data covers the period 1998-2007 with data from 20 reindeer husbandry summer districts.
202 Data on husbandry unit numbers and herd size are based on counts made by herders that
203 are regularly checked by the authorities (Anonymous, 2007b), while data in relation to
204 slaughter are recorded by slaughterhouses approved by the government (Tveraa et al.,

205 2007). The second dataset consist of data pertaining to the genealogical relatedness
206 between active reindeer herders within summer districts, i.e. herders that have a license to
207 practice reindeer husbandry. Data pertaining to kinship denote the average coefficient of
208 relatedness within a reindeer husbandry district (for details pertaining to this dataset and
209 how it was collected see Næss et al., 2010:250 & Appendix B). As in our previous studies we
210 made a selection of husbandry units with ≥ 70 reindeer (Næss and Bårdsen, 2010; Næss et
211 al., 2010; Næss et al., 2009). The dataset contains the following variables:

212 S_{off_t} (response).-- A (*husbandry unit level*) variable that either acts as a binary variable
213 (0 = no slaughter & 1 = slaughter) or as a continuous variable denoting the total
214 number of slaughtered offspring in each husbandry unit per year.

215 S_{σ_t} (response).-- Similar to S_{off_t} except that this (*husbandry unit level*) variable denotes
216 the number of slaughtered adult males.

217 S_{φ_t} (response).-- Similar to S_{off_t} except that this (*husbandry unit level*) variable denotes
218 the number of slaughtered adult females.

219 N_t .-- A continuous (*husbandry unit level*) variable denoting the total herd size at the
220 beginning of the year.

221 S_{around_t} .-- A continuous (*district level*) variable denoting the number of slaughtered
222 reindeer in the district (after subtracting the number of slaughtered animals in the
223 husbandry unit itself). This variable measures the number of animals being
224 slaughtered around each husbandry unit per year.

225 $r_{district}$.-- A continuous (*district level*) variable denoting the average coefficient of
226 relatedness, where we used kinship information up to second cousins, within each
227 district (see Næss et al., 2010 for details).

228 $ID_{district}$.-- This is a factor variable with each district acting as levels.

229 ID_{unit} -- This is a factor variable with each husbandry unit acting as levels.

230

231 2.4 Statistical analyses

232 2.4.1 An overview of the statistical analyses

233 Selecting a slaughter strategy entails several decisions: (1) the choice to slaughter or not;
234 and (2) if slaughtering, the herder has to choose: (i) how many animals to slaughter; and (ii)
235 the type of animal to slaughter. Consequently, we divided our statistical analyses in three
236 steps:

237 *Step 1:* evaluating the probability that a husbandry unit slaughtered or not.

238 *Step 2:* by using information solely from units that slaughtered at least one animal
239 belonging to each category, we tried to identify slaughter strategies by identifying
240 possible gradients along the three variables S_{off_t} , S_{σ_t} and S_{φ_t} (taking into account
241 correlation between them).

242 *Step 3:* by using information from Step 2 we tried to identify important predictors
243 affecting slaughter strategies.

244

245 In Step 1 & 3 we selected the fixed model structure based on *a priori* expectations as
246 follows: $N_t + S_{around_t} + r_{district} + S_{around_t} \times r_{district}$. This structure was chosen due to the
247 expectation that: (1) N_t represents an important state variable as it is related to wealth; (2)
248 S_{around_t} represents the actions of other herders (see above); (3) $r_{district}$ represents an
249 important coordinating principle (cf. Næss et al., 2010); and (4) $S_{around_t} \times r_{district}$
250 represents the interaction between the actions of other herders and kinship. In Step 1 both
251 S_{σ_t} and S_{φ_t} contained too few zeroes in all years in order to model slaughtering

252 probabilities, and this was due to the fact that most herders slaughters adult reindeer every
253 year. S_{off_t} contained too few zeros in most years, but when year was removed as a
254 grouping variable the proportion of zeros became more satisfactory (Table 1). We thus chose
255 to remove year as a fixed effect in all subsequent mixed models since we wanted to keep the
256 fixed effects structure similar across analyses. We do not, however, view this as problematic
257 as herd size and year are related to each other (see below for discussion).

258 The random effects in a mixed-effects model can conceptually be viewed as a way of
259 controlling for additional sources of variation (or error) that cannot be estimated (Luke,
260 2004), were ID_{unit} , $ID_{district}$ and ID_{unit} nested in $ID_{district}$ were included as potential
261 random effects in all analyses. In order to select the most appropriate random structure we
262 selected the most parsimonious model (i.e. the model with the lowest AIC value; results not
263 shown) from a set of models in which the random structure varied [following the procedure
264 described in Zuur et al. (2009)]. In the analyses of slaughter probability (Step 1) we fitted
265 models using the Laplace approximation, whereas in the other analyses (Step 2-3) we fitted
266 all models using a restricted maximum likelihood fitted model (REML) as we kept the fixed
267 effects structure constant across models (Pinheiro and Bates, 2000). Statistical analyses and
268 plotting of results were carried out in *R* (R Development Core Team, 2009). All tests were
269 two-tailed and the null-hypothesis was rejected at an α -level of 0.05, we used Wald statistics
270 to test if estimated parameters were significantly different from zero.

271

272 *2.4.2 Step 1: Predicting slaughtering probabilities*

273 Generalized linear mixed effect models (using a logit link function and a binomial
274 distribution), applied using the *glmer* function of the *lme4* package (Bates and Maechler,

275 2009) were used in the analysis with a binary response variable (0 = 'no slaughter', 1 =
276 'slaughter', Bolker et al., 2009).

277

278 *2.4.3 Step 2: Gradients in slaughtering strategies – amounts vs. offspring/male proportions*

279 Principal component analysis (PCA) of the three response variables was applied using the
280 *princomp* function (Everitt, 2004; Venables and Ripley, 2002). PCA is not a statistical test, but
281 a heuristic procedure aiming at representing as much information in the data as possible
282 using a reduced number of axes or abstract variables (Borcard, 2006; Everitt, 2004). PCA
283 describes variation in a set of correlated variables by creating a new set of uncorrelated, or
284 orthogonal variables, which is a linear combination of the original variables: these new
285 uncorrelated variables are derived in a decreasing order of importance with respect to the
286 amount of variation they contain relative to the original variables (Everitt, 2004). These
287 abstract variables, called principal components (PC), will then be used to ease our
288 interpretation of the structure in the original data. We applied PCA on a subset of the data
289 containing only husbandry units who slaughtered at least one individual per slaughtering
290 category, i.e. $S_{off_t} > 0$, $S_{\sigma_t} > 0$ and $S_{\varphi_t} > 0$. The PCA was performed on \log_e transformed values
291 for the three variables and by using the correlation matrix. The first PC and possible also the
292 second PC will, if they explain more than their proportion of the variance in the original
293 variables (i.e. $> 2/3$ of the total variance), be used as proxies for the three variables in further
294 formal statistical testing of relationships (see below). We evaluated the results from the
295 principal component analysis by plotting the scores from principal component 2 (PC2) as a
296 function of principal component 1 (PC1) and by evaluating the loadings for the principal

297 components and the Pearson's product moment correlations between the components and
298 the original variables.

299

300 *2.4.4 Step 3: Predicting gradients in slaughtering strategies*

301 Linear mixed-effect models (*lme*) applied using the *nlme* package (Pinheiro and Bates, 2000;
302 Pinheiro et al., 2006) were used in the analyses of the scores from the principal component
303 analyses.

304

305 **3.0 RESULTS**

306 **3.1 Step 1: Predicting slaughtering probabilities**

307 Husbandry units with larger herds had a higher slaughtering probability (the positive effect
308 of N_t : Table 2) indicating that husbandry units with few animals were more reluctant to
309 slaughter compared to larger herds (but note the relative lack of variability in the response
310 indicating that most herders slaughtered at least one animal, see Table 1 for details).

311 Slaughtering also appeared to be correlated with what others were doing since the number
312 of slaughtered animals around each husbandry unit was a positive predictor of slaughtering
313 probability (the positive effect of S_{around_t} : Table 2). Moreover, the average degree of
314 kinship within the district had a positive, although not statistically significant, effect on
315 slaughter probability (the positive effect of $r_{district}$: Table 2). We also found a positive, but
316 not statistically significant, effect of the interaction between the number of slaughtered
317 animals around each husbandry and the average degree of kinship within the district (the

318 positive effect of $S_{around_t \times r_{district}}$: Table 2). In sum, a combination of individual state and
319 interdependent factors affected whether reindeer owners slaughtered or not.

320

321 **3.2 Step 2: Gradients in slaughtering strategies – amount vs. offspring/male proportions**

322 PC1 and PC2 jointly explained 83.41% of the original variation (Table 3a), and as judged by
323 the correlations between PC1, PC2 and the original data (Table 3b) and the loadings for the
324 PCs (Table 3c) we identified two main gradients in the data (Figure 1): (1) an ‘amount
325 gradient’ in which husbandry units with the most negative scores for PC1 on average
326 slaughtered many animals in all categories (the loadings for S_{off_t} , S_{σ_t} and S_{φ_t} were all
327 negative, see Fig. A1.1); and (2) an ‘offspring-male gradient’ in which husbandry units with
328 the most negative PC2 scores on average slaughtered few offspring and many males (the
329 loadings for S_{off_t} were highly positive whereas the loadings for S_{σ_t} and S_{φ_t} were negative,
330 see Fig. A1.2).

331

332 **3.3 Step 3: Predicting gradients in slaughtering strategies**

333 **3.3.1 PC1: amount gradient**

334 In the analysis of the scores from PC1, the effect of herd size was negative [N_t : -1.382 (Table
335 4a; Figure 2a)], which indicates that husbandry units with larger herds slaughtered more
336 animals than smaller ones (as PC1 was negatively related to S_{off_t} , S_{σ_t} and S_{φ_t}). The amount
337 of slaughter was also positively affected by what others were doing since the scores from
338 PC1 was negatively correlated to the number of animals slaughtered by neighbouring
339 husbandry units [S_{around_t} : -0.617 (Table 4a; Figure 2b)]. We also found a positive effect of

340 kinship as the scores from PC1 was negatively correlated with the average coefficient of
341 relatedness in districts [$r_{district}$: -6.224 (Table 4a; Figure 2c)]. In other words, husbandry
342 units surrounded by more closely related kin slaughtered more animals compared to those
343 being surrounded by more distantly related kin. Finally, we also found a positive (but not
344 statistical significant) interaction between number of animals slaughtered by neighbouring
345 husbandry units and average coefficient of relatedness since the interaction term had a
346 negative effect on PC1 [$S_{around_t} \times r_{district}$: -0.546 (Table 4a; Figure 2c)].

347

348 *3.3.2 PC2: offspring-male gradient*

349 In the analysis of the scores from PC2, the effect of herd size was positive [N_t : 0.104 (Table
350 4b; Figure 3a)], indicating that husbandry units with larger herds slaughtered on average
351 more offspring and fewer males than husbandry units with smaller herds (PC2 was positively
352 correlated with S_{off_t} and negatively correlated with S_{δ_t}). The number of animals
353 slaughtered by neighbouring husbandry units affected the offspring-male proportion
354 positively [S_{around_t} : 0.333 (Table 4b; Figure 3b)]. We also found a positive effect of kinship
355 on PC2, even though this effect was only near to reach statistical significance [$r_{district}$: 5.316
356 (Table 4a; Figure 3c)]. The same was also the case with the interaction between number of
357 animals slaughtered around each husbandry unit and average coefficient of relatedness in
358 the district [$S_{around_t} \times r_{district}$: 0.401 (Table 4a; Figure 2c)], but this effect was not
359 statistically significant.

360

361 **4.0 DISCUSSION**

362 The main finding in this study was that Saami reindeer herders' slaughter strategies are
363 shaped by a combination of the herder's own state and the actions undertaken by
364 neighbouring herders. First, when assessing the probability of slaughtering, both wealth and
365 the amount of slaughter undertaken by neighbouring herders had a positive effect on the
366 probability of slaughtering. Moreover, we found a weak positive, i.e. only nearly significant,
367 effect of kinship on the probability of slaughtering. We also identified two main gradients in
368 the data in the PCA, which show that husbandry units who chose to slaughter were faced at
369 least two strategic choices: (1) the amount of reindeer to slaughter; and (2) the type of
370 animal to slaughter. Second, the amount of reindeer slaughtered increased with increasing
371 values for herd size, the amount slaughtered by neighbouring herders and kinship. Third, we
372 found that husbandry units with larger herds slaughtered more offspring and fewer males
373 than husbandry units with smaller herds. Moreover, when the number of animals
374 slaughtered by neighbouring units increased individual husbandry units slaughtered more
375 offspring and fewer males.

376

377 **4.1 State dependent strategies**

378 The amount of slaughter was positively correlated with own herd size, indicating that
379 wealthy husbandry units slaughtered more than poor ones (see also Grandin, 1983).
380 Moreover, we also found that wealth was a positive predictor for the type of reindeer
381 slaughtered as wealthier units slaughtered more calves and fewer males. This was expected
382 as calves typically represent the majority of slaughtering within the Norwegian reindeer
383 husbandry (at least in recent years, see Anonymous, 2008a). Nevertheless, this result can be

384 interpreted with reference to pastoral risk management. In general, it has been found that
385 herd accumulation maximizes long term household survival and is therefore an effective risk
386 reducing strategy (e.g. Templer et al., 1993; McPeak, 2005; Mace, 1993; cf. Næss and
387 Bårdsen, 2010; Næss et al., 2011). Mace (1993) found, for example, that wealthy herders
388 maintain large herds by controlling breeding rates: by reducing the number of offspring per
389 year the longevity of females is increased. The underlying rationale is linked to the cost of
390 reproduction (see above for details) and a herder can reduce this cost by controlling
391 breeding rates (Mace, 1993) or by slaughtering calves (this study). Just as poor Gabbara
392 households cannot control breeding rates since they have no choice but to increase their
393 herds to maximize long-term household survival, poor husbandry units have to maximize
394 herd size by restricting calf slaughter since those with the larger herds have the highest
395 probability of staying in the pastoral game (Næss and Bårdsen, 2010).

396

397 **4.2 Interdependent strategies**

398 The results from this study indicate that slaughtering strategies is not only influenced by the
399 husbandry units' own state but also by the amount of slaughter undertaken by neighbouring
400 herders. Consequently, our results support the game theoretical expectation that strategies
401 are interdependent (see above)

402 Nevertheless, previous studies have indicated the presence of a tragedy of the
403 commons in the reindeer husbandry since density dependence has been shown to influence
404 the reindeer husbandry negatively (Næss, 2009; Næss et al., 2010; Tveraa et al., 2007;
405 Bårdsen and Tveraa, 2012; Bårdsen et al., 2010). Consequently, if the cost of
406 overexploitation by adding additional reindeer is shared by all (negative density

407 dependence) but the benefit (increased long term viability and access to common pastures)
408 from increasing herd size is individually accrued, it could be argued that when other
409 husbandry units slaughter, the best response is to restrict own slaughter and thereby exploit
410 the cooperative effort of others. In contrast, the positive association between the amount of
411 slaughtering undertaken by individual husbandry units and the amount of slaughter by
412 neighbouring units indicate that slaughtering in the reindeer husbandry is *not* characterized
413 as a tragedy of the commons situation. This interpretation is valid because in a Prisoners'
414 Dilemma the best strategy is to always restrict slaughtering regardless of what others are
415 doing. For reindeer herders, however, the appropriate question may not be whether to
416 slaughter or not (as most units slaughter at least a few animals) but rather how much to
417 slaughter. *This decision may entail balancing the need for income from slaughter with the*
418 *risk beneficial aspects of accumulating herd size.* As such the situation facing reindeer
419 herders is neither characterised as a Prisoners' Dilemma where it is always better to exploit
420 the cooperative efforts of others nor by the same mutualistic aspect as cooperative labour
421 input among pastoralists (Næss et al., 2010) or cooperative hunting (Alvard and Nolin, 2002;
422 Smith, 1997) where individuals are always better off cooperating. Rather decisions in
423 relation to slaughtering may entail a level of risk aversion where reindeer herders are more
424 concerned with not doing worse (slaughtering more than neighbours and be outcompeted
425 e.g. by losing access to grazing) than being the best (slaughtering less than neighbours and
426 thus outcompete neighbours e.g. by gaining access to more grazing). If this is the case, the
427 best strategy may be to monitor how much others are slaughtering and synchronise
428 slaughter accordingly. This should give rise to a synchronous pattern in slaughtering, which
429 can be revealed by looking at temporal trends in the amount of slaughter undertaken by
430 neighbouring husbandry units (Fig. 4).

431

432 **4.3 Kinship and cooperation – indirect and direct benefits**

433 While kin selection is a powerful force promoting cooperation and helping behaviour, one
434 could question the universality of genetic kinship as an organizing principle for social
435 cooperation among humans (Bock, 2009). Alvard (2003), for example, found that among
436 whale hunters in Lamalera, Indonesia, lineage membership rather than genetic kinship
437 determined hunting group formation (see also Allen-Arave et al., 2008). In contrast, when
438 reanalysing the Chagnon's famous analysis of the axe fight among the Yanomamös living in
439 the rainforests of southern Venezuela, Alvard (2009) found, in support of Chagnon and
440 Bugos's (1979, cited in Alvard, 2009) original conclusion, that genetic relatedness rather than
441 lineage identity was a primary organizing principle for individuals' choosing sides in the fight
442 (for other studies documenting the importance of kinship see e.g. Borgerhoff Mulder, 2007;
443 Crognier et al., 2002; Sear and Mace, 2008; Tymicki, 2004). Alvard (2009) concludes that for
444 problems that require small groups (which seems to characterise summer districts in the
445 reindeer husbandry, cf. Næss et al., 2010:253-4), genetic kinship is sufficient (for the
446 problem of large-scale cooperation see e.g. Paciotti and Hadley, 2004; Alvard, 2009).

447 The results from this study suggest that that kinship is an important measure of
448 cooperation in the Saami reindeer husbandry since the amount of reindeer slaughtered was
449 positively correlated with the degree of relatedness between husbandry units within districts
450 (see also Næss et al., 2010). Nevertheless, the lack of evidence for any interaction between
451 kinship and the amount of slaughter undertaken by neighbouring herders indicate that while
452 kinship may be an important coordinating principle in general, it may be important to
453 synchronise slaughter regardless of kin relations. In other words, it could be argued that

454 individuals may cooperate because it is in their own direct self-interest and not necessarily
455 because of the benefits indirectly acquired through kin relations (Griffin and West, 2002:20;
456 Alvard, 2003; Allen-Arave et al., 2008). Coordinated slaughter can thus be interpreted as
457 being based on gaining direct benefits from cooperation, where the benefits can be
458 expressed as both income from the reindeer slaughtered and a reduced probability of losing
459 access to grazing areas, e.g. winter pastures, by not slaughtering more than others (Næss et
460 al., 2010:254-5). This is substantiated when looking at the relative importance of the
461 different predictors: while slaughter undertaken by neighbouring herders accounted for 13
462 % of the variation in the amount of slaughtering undertaken by individual husbandry units
463 alone, kinship alone explained no variation (models refitted not accounting for the grouping
464 structure, see Table A1.1 for details). Nevertheless, the results from this study indicate that
465 kinship plays a part in shaping slaughter strategies since husbandry units with larger herds in
466 districts where neighbouring husbandry units slaughtered more animals and with more close
467 related kin slaughtered more animals compared to those with smaller herds surrounded by
468 husbandry units slaughtering fewer animals and with more distantly related kin (see Fig. 2a
469 & b).

470

471 **4.4 Confounding and limitations**

472 All observational studies have potential problems in relation to confounding, which may lead
473 to spurious relationships between the included predictors and the response and to biased
474 estimation of effects (Cohen et al., 2003). Problems related to confounders were, however,
475 reduced as we had *a priori* expectations to all predictors included in the analyses (Anderson,
476 2008; Burnham and Anderson, 2002). Nevertheless, there are several important known

477 factors not included in our models that can potentially influence slaughtering. First, variation
478 in climate may affect slaughtering as survival is particularly constrained during harsh winters
479 (Tveraa et al., 2003); and husbandry units experiencing negative winter conditions may be
480 less reluctant to slaughter. While this needs to be further investigated, reindeer populations
481 in Finnmark seems not to be severely limited by negative winter conditions since overall
482 reindeer abundance in Finnmark (and nationally) has increased from ~2001 and onwards
483 (e.g. Næss et al., 2011:Fig. 1; Næss and Bårdsen, 2010; Bårdsen et al., 2010). As such the
484 inability to account for possible negative effects of winter climate should not affect our
485 conclusions.

486 Second, temporal trends in the number of animals slaughtered can confound our
487 analyses. While we have not included year as a covariate in our analyses, by including herd
488 size we did, however, partially control for such temporal trends due to the positive
489 association between herd size and year, which is apparent at the national level (Næss et al.,
490 2011) as well as for many districts (Bårdsen et al., 2010; Tveraa et al., 2007) and husbandry
491 units in Finnmark (Næss and Bårdsen, 2010).

492 Third, both mortality and reproduction are important potential confounders as they
493 may influence slaughter strategies. We suspect that we also partially controlled for this
494 effect through the inclusion of herd size in the analyses since both the number of individuals
495 born and dying during a year are related to herd size.⁵

⁵ Herd size was positively correlated with both number of calves (marked) [mean correlation estimated per unit: 0.682 (95% CI, 0.635, 0.728, $n = 206$) and reported loss to predation [mean correlation estimated per unit: 0.454 (95% CI, 0.406, 0.501, $n = 206$)]. Note: data pertaining to number of calves and reported loss is from a different dataset covering the period 2000-2008.

496 Fourth, variation in vegetation quantity and quality may have important
497 consequences for slaughtering since good pasture conditions may lead to an increased calf
498 production (Bårdsen and Tveraa, 2012). While we have not explicitly controlled for this
499 source of variation we control for some measure of between district variations by including
500 districts as a random effect in our analyses (cf. Næss et al., 2009).

501 Fifth, we have not taken into account important economic measures that may
502 substantially influence slaughter in the reindeer husbandry. For example, several economic
503 subsidies aim at stimulating production: operating subsidies; production premiums;
504 subsidies for slaughtering calves; slaughter during autumn; and general subsidies for
505 stimulating overall production (Ulvevadet and Hausner, 2011). The underlying rationale for
506 this is connected to the explicit management goal to develop a sustainable reindeer
507 husbandry by reducing the number of reindeer in Finnmark (Ulvevadet, 2008). One tool used
508 to achieve this goal is the aforementioned subsidies (Anonymous, 2007c:6; 2008a:56).
509 Furthermore, from 1997 to 2007 producer prices for reindeer meat has been steadily
510 increasing (net price per kg meat paid by slaughterhouses increased from 41.85 NOK in 1997
511 to 64.51 NOK in 2007 in Finnmark, see Anonymous, 2001; 2004b; 2008b).⁶ From an
512 economical point of view it is to be expected that when the price of a product raises
513 suppliers offers more of the product for sale (i.e. the “law of supply”, see Frank, 2006),
514 indicating that as prices for reindeer meat increases reindeer herders should be willing to
515 slaughter and sell more reindeer. Nevertheless, in spite of both economical subsidies and
516 the overall temporal trend in meat prices, the number of reindeer has still increased (see
517 above). In other words, economical factors assumed to influence slaughter positively are
518 apparently not enough to decrease the number of reindeer in the region. Results from this

⁶ 100 NOK = \$17.9 per 28.02.12.

519 study indicate that one reason for this may be that slaughter strategies are not selected
520 solely on the basis of monetary considerations.

521 This is not the first study where we have experienced problems related to confounding
522 (see e.g. Næss and Bårdsen, 2010; Næss et al., 2011). Even though the most likely
523 confounders (based on experience) have varied between studies, the solution has been the
524 same. While including more, if not all, relevant predictors in a statistical model is the
525 preferred solution as this leads to reduced bias (Berry and Feldman, 1985), in reality this lead
526 to collinearity problems (cf. Næss et al., 2011: Appendix II in relation to the reindeer
527 husbandry; and Zuur et al., 2010 for general considerations). We thus chose to include the
528 set of predictors we have *a priori* expectations to (from a theoretical point of view, as
529 recommended by e.g. Licht, 1995).

530

531 **5.0 CONCLUDING REMARKS AND MANAGEMENT IMPLICATIONS**

532 In sum, this study found that pastoral slaughter strategies are both *state dependent* and
533 *interdependent* since both amount and type of animal slaughtered was influenced by the
534 husbandry units' own wealth and what other husbandry units were doing and kin relations
535 within districts. In light of the results from this paper and the governmental goal of reducing
536 the number of reindeer by stimulating slaughter, one could question the one-sided
537 governmental focus on targeting individual husbandry units through production subsidies.⁷
538 As we have shown that what others do is an important factor in explaining slaughter, it could

⁷ To be eligible to receive the different subsidies reindeer herders have to fulfil two demands: (1) they need to slaughter a quota of reindeer meat, which in 2007 was set to the value of 50 000 NOK; and (2) the husbandry units should possess no more than 600 reindeer in the spring (Anonymous, 2008a:56).

539 be argued that the government should also focus on strengthening the already existing
540 institutional framework represented by summer districts. In terms of subsidies it could be
541 argued that districts as a whole should achieve some productivity measures before
542 individual units are eligible for receiving subsidies. Such an approach would take into
543 account and strengthen the coordinating principles already present in districts. Since
544 subsidies are based on individual husbandry unit's willingness to slaughter, a husbandry unit
545 is not dependent on other units slaughtering for receiving subsidies. The present subsidy
546 system may thus not properly account for how decisions in relation to slaughter are made.

547 If subsidies are, on the other hand, conditional on some district level quota⁸ one
548 should be able to reduce the effect of a few herders restricting slaughter: if a majority of
549 herders within a district depend on or are interested in receiving subsidies they will have an
550 incentive to encourage all herders to contribute to attaining the goal set for the district. The
551 failure of others to follow the rules will, in contrast to the current scenario, have negative
552 effects on individual possibility for receiving economic subsidies. The results from this study
553 may be taken to indicate that slaughter strategies are shaped by processes at different
554 hierarchical levels, and subsidies targeting only one level, i.e. the husbandry level, may be
555 argued to be doomed from the outset. In other words, subsidies cannot be aimed at
556 reinforcing behaviour at only the level of individual actors but also have to take into account
557 that individuals behave strategic in relation to other people.

⁸ Note, however, that from 1999-2003 there was a possibility for districts to submit a *joint* slaughter plan where the districts had to fulfil the slaughter demand before individual husbandry units could receive subsidies. This approach was based on *voluntarily* participation (Anonymous, 2002:§10) and no statistics exists as to how many actually participated, although by the end of 1999 no districts had submitted a joint slaughter plan in West-Finnmark (Anonymous, 2004a:57).

Næss, M. W., Bårdsen, B.-J., and Tveraa, T. (2012). Wealth-dependent and interdependent strategies in the Saami reindeer husbandry, Norway. *Evolution and Human Behavior* 33(6):696-707.

558

559 6.0 ACKNOWLEDGMENT

560 The present study was financed by the Directorate for Nature Management, Norway; the
561 Fram Centre, Norway; and the Research Council of Norway (the FRIMUF program). We thank
562 the Norwegian Reindeer Administration for providing the data, and people employed at the
563 Reindeer Administration's office in Kautokeino and Karasjok for providing us with additional
564 information. We would also like to thank Ellen Margrete Oskal for help with data collection.

565

566 7.0 REFERENCES

567 Aiken, L. S., and West, S. G. (1991). *Multiple regression: testing and interpreting interactions*,
568 Sage, Newbury Park, Calif.

569 Allen-Arave, W., Gurven, M., and Hill, K. (2008). Reciprocal altruism, rather than kin
570 selection, maintains nepotistic food transfers on an Ache reservation. *Evolution And*
571 *Human Behavior*, 29, 305-318.

572 Alvard, M. (2009). Kinship and Cooperation The Axe Fight Revisited. *Human Nature*, 20, 394-
573 416.

574 Alvard, M. S. (2003). Kinship, lineage, and an evolutionary perspective on cooperative
575 hunting groups in Indonesia. *Human Nature*, 14, 129-163.

576 Alvard, M. S., and Nolin, D. A. (2002). Rousseau's whale hunt? Coordination among big-game
577 hunters. *Current anthropology*, 43, 533-559.

578 Anderson, D. R. (2008). *Model based inference in the life sciences: a primer on evidence*,
579 Springer Science, New York, United States of America.

580 Anonymous. (2001). Totalregnskap for reindriftnæringen. Reindriftnæringen p. 145.

Næss, M. W., Bårdsen, B.-J., and Tveraa, T. (2012). Wealth-dependent and interdependent strategies in the Saami reindeer husbandry, Norway. *Evolution and Human Behavior* 33(6):696-707.

- 581 —. (2002). "FOR-2002-07-10-870: Forskrift om tilskudd til driftsenheter og tamreinlag," in
582 hefte 10: LMD (Landbruks- og matdepartementet)
- 583 —. (2004a). "Dokument nr. 3:12 (2003–2004) Riksrevisjonens undersøkelse av bærekraftig
584 bruk av reinbeiteressursene i Finnmark," pp. 95: Riksrevisjonen.
- 585 —. (2004b). Totalregnskap for reindriftsnæringen. Reindriftsforvaltningen p. 143.
- 586 —. (2007a). Lov om reindrift av 15. juni. 2007 nr 40.
- 587 —. (2007b). Ressursregnskap for reindriftsnæringen. Reindriftsforvaltningen, p.159.
- 588 —. (2007c). "St.prp. nr. 74: Om reindriftsavtalen 2007/2008, om dekning av kostnader
589 vedrørende radioaktivitet i reinkjøtt, og om endringer i statsbudsjettet for 2007 m.m.
590 ," pp. 36: Det Kongelige Landbruks- og Matdepartement.
- 591 —. (2008a). Ressursregnskap for reindriftsnæringen. Reindriftsforvaltningen, p.164.
- 592 —. (2008b). Totalregnskap for reindriftsnæringen. Reindriftsforvaltningen p. 126.
- 593 Axelrod, R. (1984). *The evolution of cooperation*, Basic Books, New York.
- 594 Axelrod, R. (1986). An Evolutionary Approach to Norms. *American Political Science Review*,
595 80, 1095-1111.
- 596 Bates, D. M., and Maechler, M. (2009) lme4: linear mixed-effects models using S4 classes.
- 597 Bergman, I., Liedgren, L., Östlund, L., and Zackrisson, O. (2008). Kinship and Settlements:
598 Sami Residence Patterns in the Fennoscandian Alpine Areas around A.D. 1000. *Arctic*
599 *Anthropology*, 45, 97-110.
- 600 Berry, W. D., and Feldman, S. (1985). *Multiple regression in practice*. Quantitative
601 applications in the social sciences 50, Sage Publications, Beverly Hills.
- 602 Bock, J. (2009). Evolutionary Studies of Cooperation Introduction to the Special Issue. *Human*
603 *Nature*, 20, 351-353.

Næss, M. W., Bårdsen, B.-J., and Tveraa, T. (2012). Wealth-dependent and interdependent strategies in the Saami reindeer husbandry, Norway. *Evolution and Human Behavior* 33(6):696-707.

- 604 Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulson, J. R., Stevens, M. H. H., and
605 White, S. S. (2009). Generalized linear mixed models: a practical guide for ecology
606 and evolution. *Trends in Ecology & Evolution*, 24, 127-135.
- 607 Borcard, D. (2006). Multivariate analysis. Département de sciences biologiques, Université
608 de Montréal.
- 609 Borgerhoff Mulder, M. (2007). Hamilton's rule and kin competition: the Kipsigis case.
610 *Evolution And Human Behavior*, 28, 299-312.
- 611 Borgerhoff Mulder, M., and Coppolillo, P. (2005). *Conservation: linking ecology, economics,*
612 *and culture*, Princeton University Press, Princeton.
- 613 Borgerhoff Mulder, M., and Sellen, D. W. (1994). Pastoralist decision making: A behavioral
614 ecological perspective. In E. Fratkin, K. A. Galvin, and E. A. Roth (eds.), *African*
615 *Pastoralist Systems: An Integrated Approach* (pp. 205-229). Boulder, London.
- 616 Bostedt, G. (2001). Reindeer husbandry, the Swedish market for reindeer meat, and the
617 Chernobyl effects. *Agricultural Economics*, 26, 217-226.
- 618 Bråthen, K. A., Gonzalez, V. T., Iversen, M., Killengreen, S., Ravolainen, V. T., Ims, R. A., and
619 Yoccoz, N. G. (2007a). Endozoochory varies with ecological scale and context.
620 *Ecography*, 30, 308-320.
- 621 Bråthen, K. A., Ims, R. A., Yoccoz, N. G., Fauchald, P., Tveraa, T., and Hausner, V. H. (2007b).
622 Induced shift in ecosystem productivity? Extensive scale effects of abundant large
623 herbivores. *Ecosystems*, 10, 773-789.
- 624 Bull, K. S. (1997). *Studier i reindriftsrett*, Tano Aschehoug (in Norwegian), Oslo.
- 625 Burnham, K. P., and Anderson, D. R. (2002). *Model selection and multimodel inference: a*
626 *practical information-theoretic approach*, Springer, Inc., New York, USA.

Næss, M. W., Bårdsen, B.-J., and Tveraa, T. (2012). Wealth-dependent and interdependent strategies in the Saami reindeer husbandry, Norway. *Evolution and Human Behavior* 33(6):696-707.

- 627 Bårdsen, B.-J., Henden, J.-A., Fauchald, P., Tveraa, T., and Stien, A. (2011). Plastic
628 reproductive allocation as a buffer against environmental stochasticity – linking life
629 history and population dynamics to climate. *Oikos*, 20, 245-257.
- 630 Bårdsen, B.-J., and Tveraa, T. (2012). Density dependence vs. density independence – linking
631 reproductive allocation to population abundance and vegetation greenness. *Journal*
632 *of Animal Ecology*, 81, 364-376.
- 633 Bårdsen, B. J., Tveraa, T., Fauchald, P., and Langeland, K. (2010). Observational evidence of a
634 risk sensitive reproductive allocation in a long-lived mammal. *Oecologia*, 162, 627-
635 639.
- 636 Cohen, J., Cohen, P., West, S. G., and Aiken, L. S. (2003). *Applied multiple*
637 *regression/correlation analysis for the behavioral sciences*, 3rd edition, Lawrence
638 Erlbaum, Mahwah, N.J.
- 639 Colman, A. M. (1995). *Game theory and its applications in the social and biological sciences*,
640 2nd edition. International series in social psychology, Butterworth-Heinemann,
641 Oxford.
- 642 Crognier, E., Villena, M., and Vargas, E. (2002). Helping patterns and reproductive success in
643 Aymara communities. *American Journal Of Human Biology*, 14, 372-379.
- 644 Dahl, G. (1979). *Suffering grass: subsistence and society of Waso Borana*. Stockholm studies
645 in social anthropology, Department of social anthropology University of Stockholm,
646 Stockholm.
- 647 Dixit, A. K., and Skeath, S. (2004). *Games of strategy*, 2nd edition, W.W. Norton, New York.
- 648 Everitt, B. (2004). *An R and S-Plus® companion to multivariate analysis*. Springer texts in
649 statistics, Springer-Verlag, London, UK.

Næss, M. W., Bårdsen, B.-J., and Tveraa, T. (2012). Wealth-dependent and interdependent strategies in the Saami reindeer husbandry, Norway. *Evolution and Human Behavior* 33(6):696-707.

- 650 Frank, R. H. (2006). *Microeconomics and behavior*, 6th edition, McGraw-Hill/Irwin, Boston,
651 Mass.
- 652 Gächter, S., Renner, E., and Sefton, M. (2008). The Long-Run Benefits of Punishment.
653 *Science*, 322, 1510-1510.
- 654 Gintis, H., Bowles, S., Boyd, R., and Fehr, E. (2005). Moral Sentiments and Material Interests:
655 Origins, Evidence, and Consequences. In H. Gintis, S. Bowles, R. Boyd, and E. Fehr
656 (eds.), *Moral sentiments and material interests: the foundations of cooperation in*
657 *economic life* (pp. 3-39). Cambridge, Mass., MIT Press.
- 658 Gjessing, G. (1975). Socio-Archeology. *Current anthropology*, 16, 323-332.
- 659 Grandin, B. E. (1983). The importance of wealth effects on pastoral production: A rapid
660 method for wealth ranking. (eds.), *Pastoral systems research in sub-Saharan Africa:*
661 *proceedings of the IDRC/ILCA workshop held at ILCA, Addis Ababa, Ethiopia 21 to 24*
662 *March, 1983* (pp. 237-262). Addis Ababa, Ethiopia, ILCA.
- 663 Griffin, A. S., and West, S. A. (2002). Kin selection: fact and fiction. *Trends In Ecology &*
664 *Evolution*, 17, 15-21.
- 665 Hamilton, W. D. (1964). Genetical Evolution of Social Behavior 2. *Journal of Theoretical*
666 *Biology*, 7, 17-52.
- 667 Hardin, G. J. (1968). The Tragedy of the Commons. *Science* 162, 1243-1248.
- 668 Ims, R. A., Yoccoz, N. G., Bråthen, K. A., Fauchald, P., Tveraa, T., and Hausner, V. (2007). Can
669 reindeer overabundance cause a trophic cascade? *Ecosystems*, 10, 607-622.
- 670 Licht, M. H. (1995). Multiple Regression and Correlation. In L. G. Grimm and P. R. Yarnold
671 (eds.), *Reading and understanding multivariate statistics* (pp. 19-64). Washington,
672 D.C., American Psychological Association.

Næss, M. W., Bårdsen, B.-J., and Tveraa, T. (2012). Wealth-dependent and interdependent strategies in the Saami reindeer husbandry, Norway. *Evolution and Human Behavior* 33(6):696-707.

673 Luke, D. A. (2004). *Multilevel modeling*. Quantitative applications in the social sciences, Sage
674 Publications, Thousand Oaks, Calif.

675 Mace, R. (1993). Nomadic pastoralists adopt subsistence strategies that maximise long-term
676 household survival. *Behavioral Ecology and Sociobiology* 33, 329-334.

677 Mace, R., and Houston, A. (1989). Pastoralist strategies for survival in unpredictable
678 environments: A model of herd composition that maximises household viability.
679 *Agricultural Systems*, 31, 185-204.

680 McNamara, J. M., and Houston, A. I. (1996). State-dependent life histories. *Nature*, 380, 215-
681 221.

682 McPeak, J. (2005). Individual and collective rationality in pastoral production: Evidence from
683 Northern Kenya. *Human Ecology*, 33, 171-197.

684 Moritz, M., Giblin, J., Ciccone, M., Davis, A., Fuhrman, J., Kimiaie, M., Madzsar, S., Olson, K.,
685 and Senn, M. (2011). Social Risk-Management Strategies in Pastoral Systems: A
686 Qualitative Comparative Analysis. *Cross-Cultural Research*, 45, 286-317.

687 Næss, M. W. (2009). Pastoral Risk Management - The Importance of Cooperative Production.
688 Philosophiae Doctor, University of Tromsø, Norway.

689 Næss, M. W., and Bårdsen, B.-J. (2010). Environmental Stochasticity and Long-Term
690 Livestock Viability-Herd-Accumulation as a Risk Reducing Strategy. *Human Ecology*,
691 38, 3-17.

692 Næss, M. W., Bårdsen, B.-J., Fauchald, P., and Tveraa, T. (2010). Cooperative pastoral
693 production - the importance of kinship. *Evolution and Human Behavior*, 31, 246-258.

694 Næss, M. W., Bårdsen, B.-J., Pedersen, E., and Tveraa, T. (2011). Pastoral herding strategies
695 and governmental management objectives: predation compensation as a risk
696 buffering strategy in the Saami reindeer husbandry. *Human Ecology*, 39, 489-508.

Næss, M. W., Bårdsen, B.-J., and Tveraa, T. (2012). Wealth-dependent and interdependent strategies in the Saami reindeer husbandry, Norway. *Evolution and Human Behavior* 33(6):696-707.

- 697 Næss, M. W., Fauchald, P., and Tveraa, T. (2009). Scale Dependency and the "Marginal"
698 Value of Labor. *Human Ecology*, 37, 193-211.
- 699 Paciotti, B., and Hadley, C. (2004). Large-Scale Cooperation among Sungusungu "Vigilantes"
700 of Tanzania: Conceptualizing Micro-Economic and Institutional Approaches. In M. S.
701 Alvard (eds.), *Socioeconomic aspects of human behavioral ecology* (pp. 119-147).
702 Amsterdam, Elsevier.
- 703 Paine, R. (1994). *Herds of the Tundra: a portrait of Saami reindeer pastoralism*. Smithsonian
704 series in ethnographic inquiry, Smithsonian Institution Press, Washington London.
- 705 Pehrson, R. N. (1964). *The bilateral network of social relations in Könkämä Lapp district*.
706 Samiske samlinger 7, Universitetsforlaget, Oslo.
- 707 Pinheiro, J. C., and Bates, D. M. (2000). *Mixed-effects models in S and S-PLUS*. Statistics and
708 computing, Springer, New York.
- 709 Pinheiro, J. C., Pinheiro, J. C., Bates, D. M., DebRoy, S., and Deepayan, S. (2006) nlme: Linear
710 and nonlinear mixed effects models.
- 711 R Development Core Team. (2009) R: a language and environment for statistical computing.
712 R Foundation for Statistical Computing, Vienna, Austria.
- 713 Richerson, P. J., Boyd, R. T., and Henrich, J. (2003). Cultural evolution of human cooperation.
714 In P. Hammerstein (eds.), *Genetic and Cultural Evolution of Cooperation* (pp. 357-
715 388). Cambridge, MA, The MIT Press.
- 716 Riseth, J. Å. (2003). Sami Reindeer Management in Norway: Modernization Challenges and
717 Conflicting Strategies. Reflections Upon the Co-management Alternative. In S.
718 Jentoft, H. Minde, and R. Nilsen (eds.), *Indigenous Peoples: Resource Management
719 and Global Rights* (pp. 229-247). Delft, Netherlands, Eburon Academic Publishers.

Næss, M. W., Bårdsen, B.-J., and Tveraa, T. (2012). Wealth-dependent and interdependent strategies in the Saami reindeer husbandry, Norway. *Evolution and Human Behavior* 33(6):696-707.

- 720 Riseth, J. Å., Johansen, B., and Vatn, A. (2004). Aspects of a two-pasture – herbivore model.
721 *Rangifer Special Issue*, 15, 65-81.
- 722 Schelling, T. C. (1980). *The strategy of conflict*, Harvard University Press, Cambridge, Mass.
- 723 Sear, R., and Mace, R. (2008). Who keeps children alive? A review of the effects of kin on
724 child survival. *Evolution And Human Behavior*, 29, 1-18.
- 725 Smith, E. A. (1997). Inuit foraging groups: some simple models incorporating conflicts of
726 interest, relatedness, and central place sharing. In L. L. Betzig (eds.), *Human nature: a*
727 *critical reader* (pp. 50-69.). New York, Oxford University Press.
- 728 —. (2003). Human cooperation: perspectives from behavioral ecology. In P. Hammerstein
729 (eds.), *Genetic and Cultural Evolution of Cooperation* (pp. 401-427). Cambridge, MA,
730 The MIT Press.
- 731 Smith, E. A., and Bird, R. B. (2005). Costly Signaling and Cooperative behavior. In H. Gintis, S.
732 Bowles, R. Boyd, and E. Fehr (eds.), *Moral sentiments and material interests: the*
733 *foundations of cooperation in economic life* (pp. 115-148). Cambridge, Mass., MIT
734 Press.
- 735 Templer, G., Swift, J., and Payne, P. (1993). The changing significance of risk in the
736 Mongolian pastoral economy. *Nomadic Peoples*, 33, 105-122.
- 737 Trivers, R. L. (1971). Evolution of Reciprocal Altruism. *Quarterly Review of Biology*, 46, 35-&.
- 738 Tveraa, T., Fauchald, P., Henaug, C., and Yoccoz, N. G. (2003). An examination of a
739 compensatory relationship between food limitation and predation in semi-domestic
740 reindeer. *Oecologia*, 137, 370-376.
- 741 Tveraa, T., Fauchald, P., Yoccoz, N. G., Ims, R. A., Aanes, R., and Hogda, K. A. (2007). What
742 regulate and limit reindeer populations in Norway? *Oikos*, 116, 706-715.

Næss, M. W., Bårdsen, B.-J., and Tveraa, T. (2012). Wealth-dependent and interdependent strategies in the Saami reindeer husbandry, Norway. *Evolution and Human Behavior* 33(6):696-707.

- 743 Tymicki, K. (2004). Kin influence on female reproductive behavior: The evidence from
744 reconstitution of the Bejsce parish registers, 18th to 20th centuries, Poland.
745 *American Journal Of Human Biology*, 16, 508-522.
- 746 Ulvevadet, B. (2008). Management of reindeer husbandry in Norway - power-sharing and
747 participation. *Rangifer*, 28, 53-78.
- 748 Ulvevadet, B., and Hausner, V. H. (2011). Incentives and regulations to reconcile
749 conservation and development: Thirty years of governance of the Sami pastoral
750 ecosystem in Finnmark, Norway. *Journal of Environmental Management*, 92, 2794-
751 2802.
- 752 Ulvevadet, B., and Klovov, K. Editors. (2004). Family-based reindeer herding and hunting
753 economies, and the status and management of wild reindeer/caribou populations.
754 Tromsø: University of Tromsø, Centre for Saami Studies
- 755 Venables, W. N., and Ripley, B. D. (2002). *Modern applied statistics with S*, Fourth edition
756 edition. Statistics and Computing, Springer-Verlag, New York.
- 757 Vorren, Ø. (1978). *Bosetning og ressursutnytting i ressursutvalgets mandatområde under*
758 *veidekulturen og dens differensiering*, Universitetsbiblioteket i Tromsø (in
759 Norwegian), Tromsø.
- 760 West, S. A., El Mouden, C., and Gardner, A. (2011). Sixteen common misconceptions about
761 the evolution of cooperation in humans. *Evolution and Human Behavior*, 32, 231-262
- 762 Wydick, B. (2008). *Games in economic development*, Cambridge University Press, Cambridge.
- 763 Zuur, A. F., Ieno, E. N., and Elphick, C. S. (2010). A protocol for data exploration to avoid
764 common statistical problems. *Methods in Ecology & Evolution*, 1, 3-14.
- 765 Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., and Smith, G. M. (2009). *Mixed effects*
766 *models and extensions in ecology with R*, Springer-Verlag New York, New York, NY.

767 **TABLES**

768 **Table 1.** The number of husbandry units that slaughtered (1) and the number who did not
 769 slaughter (0) separated by year and animal type (offspring, males and females). Numbers in
 770 **bold text** indicate where the proportion of non-slaughter (0) relative to the total (i.e. level 0
 771 + 1 for each slaughter type) was <0.15.

772

Year	S_{off_t}		S_{σ_t}		S_{φ_t}	
	0	1	0	1	0	1
1998	31	184	2	213	3	212
1999	28	192	4	216	2	218
2000	75	137	7	205	18	194
2001	44	161	12	193	18	187
2002	25	196	1	220	5	216
2003	23	199	4	218	10	212
2004	9	216	0	225	8	217
2005	10	208	1	217	3	215
2006	1	207	0	208	1	207
2007	5	207	1	211	3	209
$\Sigma(\text{year})$	251	1907	32	2126	71	2087

773

774 **Table 2.** Generalized linear mixed-effect models (*glmer*) relating offspring slaughter
 775 probability as a binary variable (i.e. a mixed GLM with binomial family and a logit link) to the
 776 total spring herd size for the husbandry units (N_t), the number of reindeer slaughtered by
 777 neighbouring herders (S_{around_t} : this variable was created by subtracting the total number of
 778 slaughtered animals in the district number from the number of reindeer slaughtered by the
 779 husbandry unit itself), the average coefficient of relatedness ($r_{district}$) and the interaction
 780 between the number of reindeer slaughtered by neighbouring herders and the average
 781 coefficient of relatedness ($S_{around_t} \times r_{district}$). All covariates were centred (see Aiken and
 782 West, 1991:35 for rationale).

Parameter	Value (SE)	P-value
<i>Slaughter probability (S_{off_t}): binary</i>		
Fixed effects		
Intercept	3.481 (0.386)	<0.001
N_t^a	1.124 (0.161)	<0.001
$S_{around_t}^a$	1.324 (0.131)	<0.001
$r_{district}$	14.328 (7.471)	0.055
$S_{around_t} \times r_{district}$	0.961 (2.668)	0.719
Random effects ^b		
Among $ID_{district}$ standard deviation (SD)	1.490	$n_{Obs.} = 260$
Among ID_{unit} nested in $ID_{district}$ SD	0.914	$n_{Obs.} = 20$
		$n_{Ind.} = 2158$

783 ^aThis variable was transformed using the natural logarithm.

784 ^bRandom effects involves only the constant term (i.e. random intercepts).

785 **Table 3.** Results from the principal component analysis on slaughtering data.

Values	PC1	PC2	PC3
(a) Importance of the components			
Standard deviation	1.271	0.942	0.706
Proportion of variance	0.539	0.300	0.166
Cumulative proportion	0.539	0.834	1.000
(b) Correlation with original variables (with 95% CI in parenthesis)			
S_{off_t}	-0.538 (-0.570,-0.505)	0.830 (0.815,0.843)	0.149 (0.104,0.193)
$S_{\text{♀}_t}$	-0.845 (-0.858,-0.832)	-0.136 (-0.180,-0.091)	-0.517 (-0.550,-0.483)
$S_{\text{♂}_t}$	-0.782 (-0.799,-0.764)	-0.424 (-0.460,-0.386)	0.456 (0.420,0.492)
(c) Loadings			
S_{off_t}	-0.423	0.881	0.211
$S_{\text{♀}_t}$	-0.665	-0.144	-0.733
$S_{\text{♂}_t}$	-0.615	-0.450	0.647

786 **Table 4.** Estimates from linear mixed-effect models (*lme*) relating gradients in (a) amount of
 787 slaughter (PC1) and (b) offspring-male proportions (PC2) to the total spring herd size for the
 788 husbandry units (N_t), the number of reindeer slaughtered by neighbouring herders
 789 (S_{around_t} : this variable was created by subtracting the total number of slaughtered animals
 790 in the district number from the number of reindeer slaughtered by the husbandry unit
 791 itself), the average coefficient of relatedness ($r_{district}$) and the interaction between the
 792 number of reindeer slaughtered by neighbouring herders and the average coefficient of
 793 relatedness ($S_{around_t} \times r_{district}$). All covariates were centred (see Aiken and West, 1991:35
 794 for rationale).

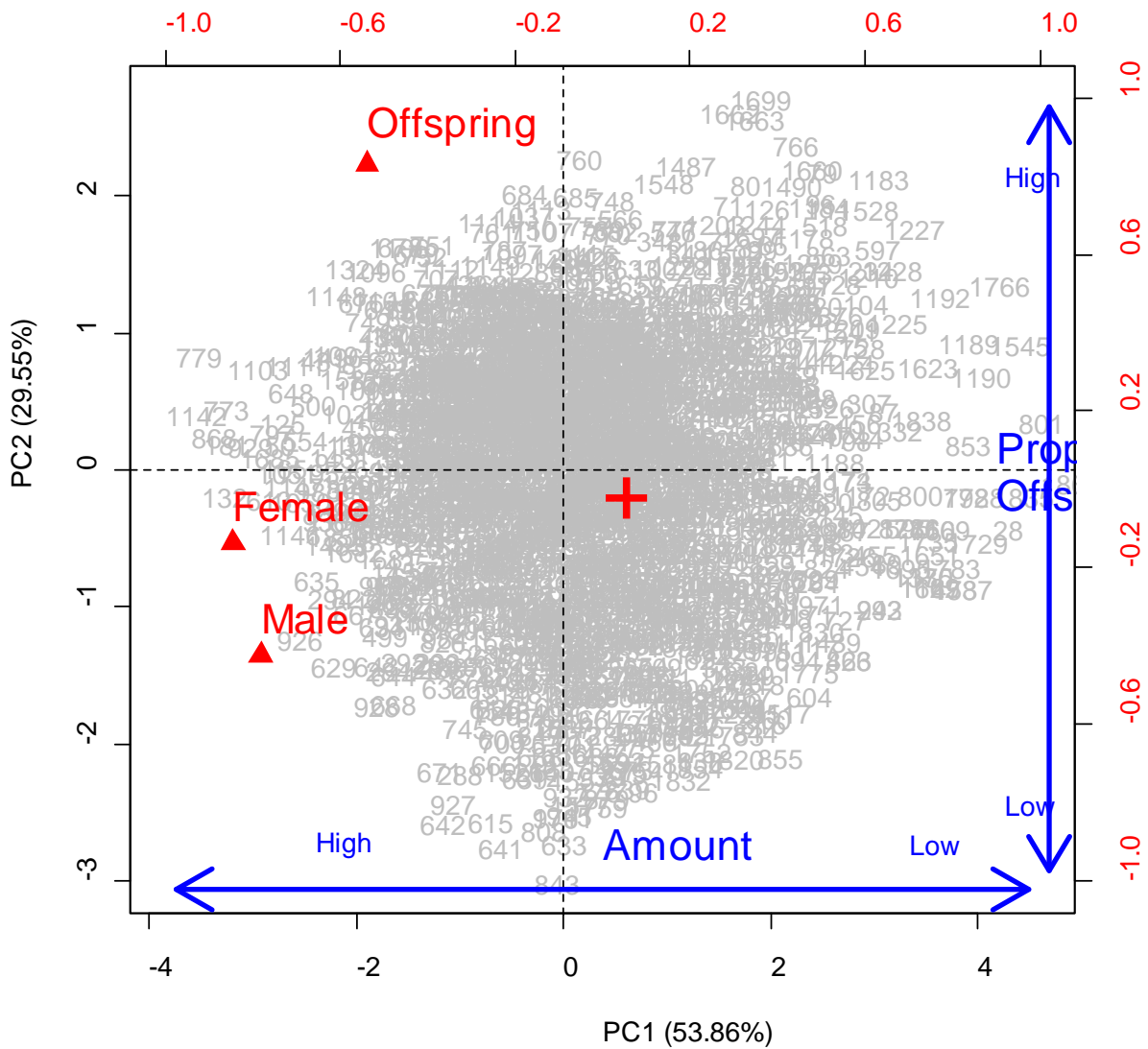
Parameter	Value (95% CI)	df	P-value
(a) PC1: 'amount gradient'			
Fixed effects			
Intercept	-0.143 (-0.391, 0.105)	1605	0.259
N_t^a	-1.382 (-1.462,-1.302)	1605	<0.001
$S_{around_t}^a$	-0.617 (-0.685,-0.548)	1605	<0.001
$r_{district}$	-6.224 (-11.145,-1.303)	18	0.016
$S_{around_t} \times r_{district}$	-0.546 (-2.002,0.909)	1605	0.462
Random effects ^b			
Among $ID_{district}$ standard deviation (SD)	0.518 (0.347, 0.775)		$n_{Obs.} = 20$
Among ID_{unit} nested in $ID_{district}$ SD	0.299 (0.244, 0.366)		$n_{Obs.} = 255$
Within group standard error (residuals)	0.740 (0.714, 0.766)		$n_{Ind.} = 1863$
(b) PC2: 'offspring-male gradient'			
Fixed effects			
Intercept	0.167 (-0.132, 0.466)	1605	0.275
N_t^a	0.104 (0.016,0.192)	1605	0.021
$S_{around_t}^a$	0.333 (0.264,0.402)	1605	<0.001
$r_{district}$	5.316 (-0.538,11.169)	18	0.073
$S_{around_t} \times r_{district}$	0.401 (-1.062, 1.864)	1605	0.591
Random effects ^b			

Næss, M. W., Bårdsen, B.-J., and Tveraa, T. (2012). Wealth-dependent and interdependent strategies in the Saami reindeer husbandry, Norway. *Evolution and Human Behavior* 33(6):696-707.

Among $ID_{district}$ standard deviation (SD)	0.629 (0.434, 0.911)	$n_{Obs.} = 20$
Among ID_{unit} nested in $ID_{district}$ SD	0.413 (0.359, 0.474)	$n_{Obs.} = 255$
Within group standard error (residuals)	0.716 (0.691, 0.741)	$n_{Ind.} = 1863$

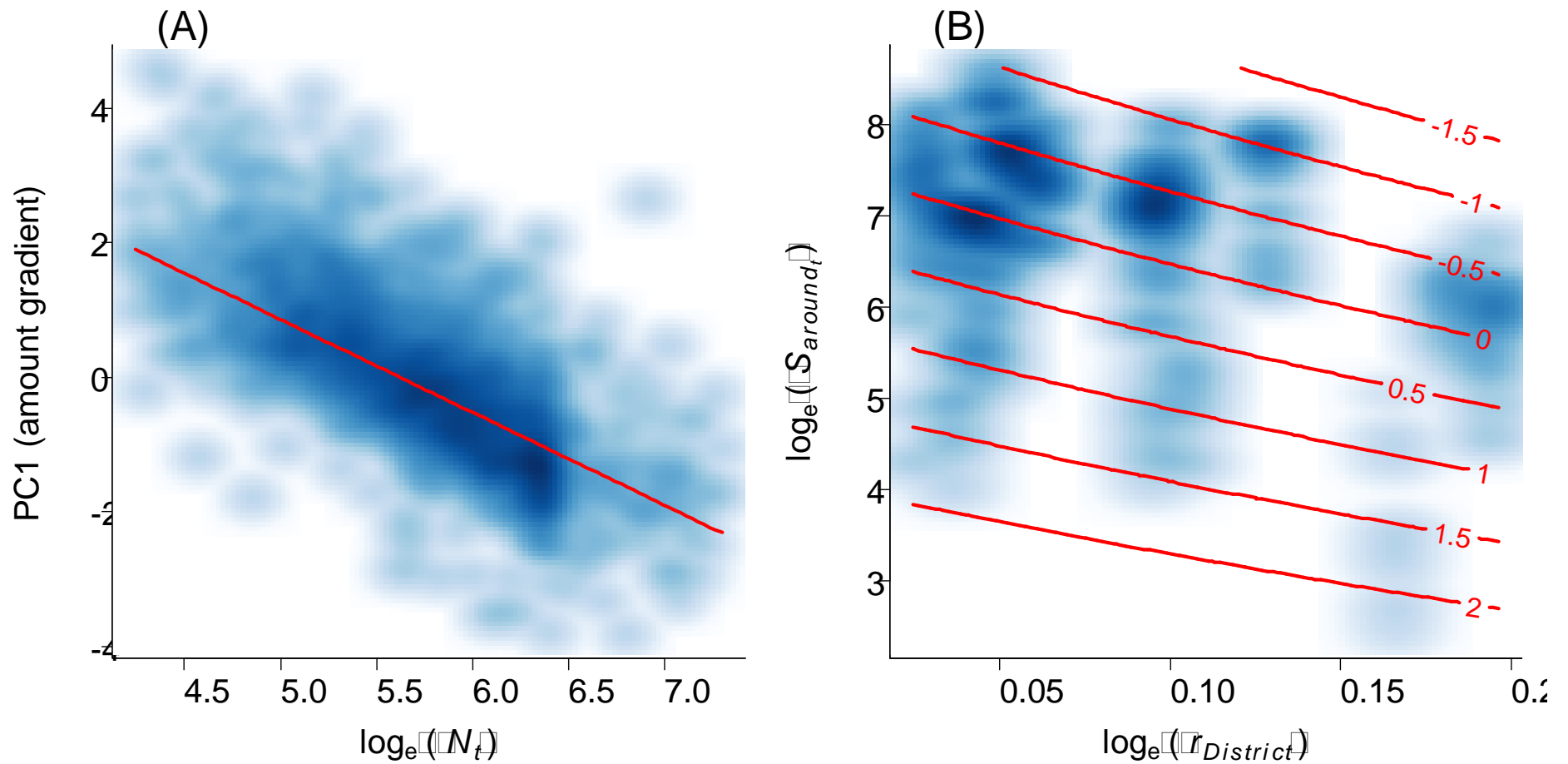
795 ^aThis variable was transformed using the natural logarithm.

796 ^bRandom effects involves only the constant term (i.e. random intercepts).



762

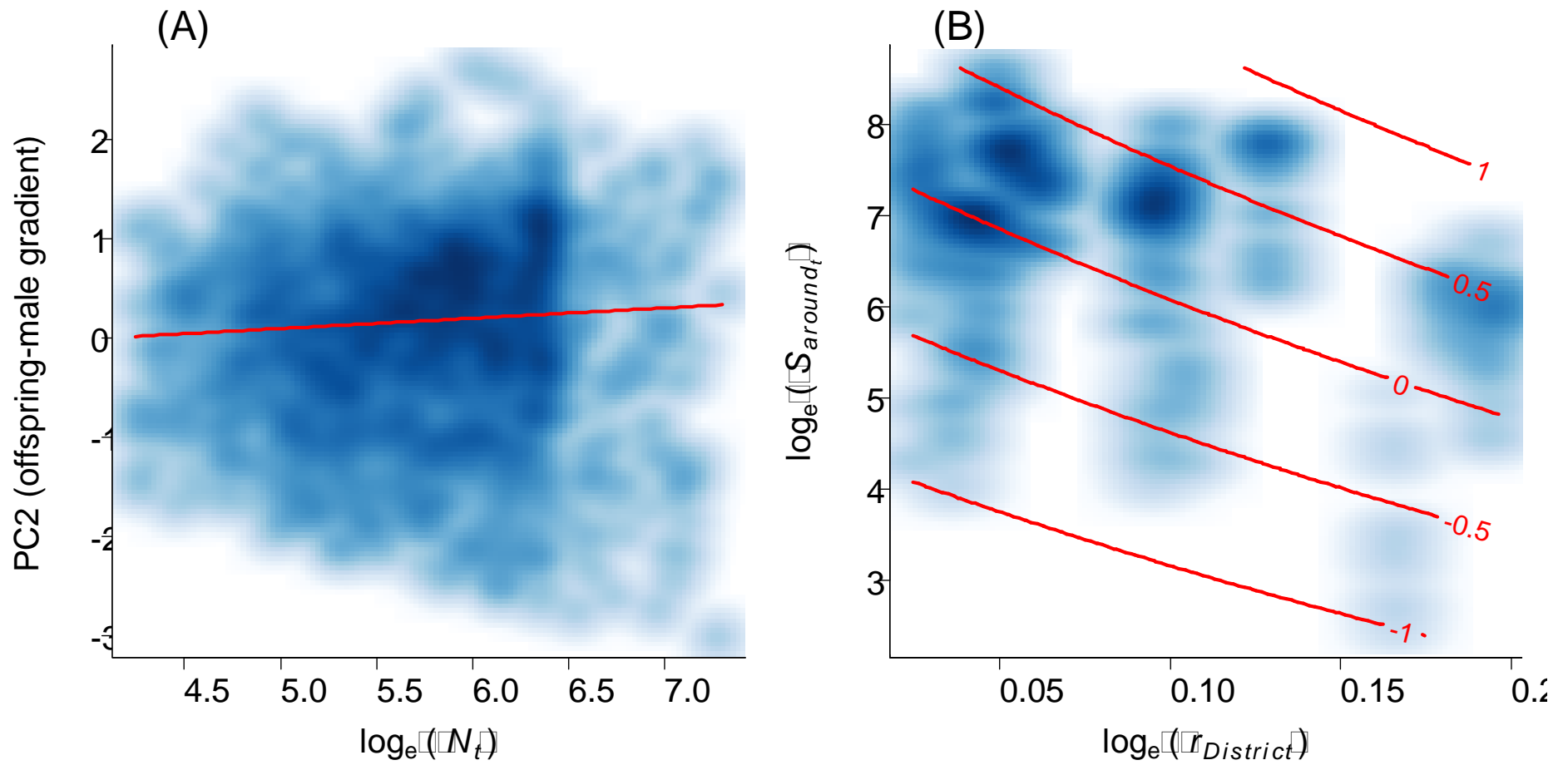
763 **Fig. 1.** A biplot showing PC2 scores as a function of PC1 scores labeled where the coordinates
 764 of the triangle for each variable show the Pearson's product moment correlations between
 765 the PCs and the original variables (red axis on the top indicated the correlation coefficient
 766 between PC1 and the original variables whereas red axis on the left indicated the same for
 767 PC2).



768

769 **Fig. 2.** A visualization of the model presented in Table 4a showing how the scores for PC1 (amount of slaughter) are predicted as a function of:
 770 (a) herd size for the husbandry units (N_t), (b) the combined effect of number of reindeer slaughtered by neighboring herders (S_{around_t}) and the
 771 average coefficient of relatedness ($r_{district}$) and the interaction between them. Please note that the model was refitted without centering any

772 variables and shows the relationships for a specific predictor keeping the other predictors at their average values. Note that even though the
773 relationship is negative, all predictors had a *positive* effect on the amount of slaughter because PC1 was negatively related to S_{off_t} , S_{σ_t} and
774 S_{φ_t} (see Fig. A1.1. for visualization of the relationship between the original variables and PC1). A smoothed density representation of the data
775 (a kernel density estimate) using the 'smoothScatter' function in the library 'geneplotter' (Gentleman and Biocore, 2011) was also added to
776 give a better visualization of the predictors.

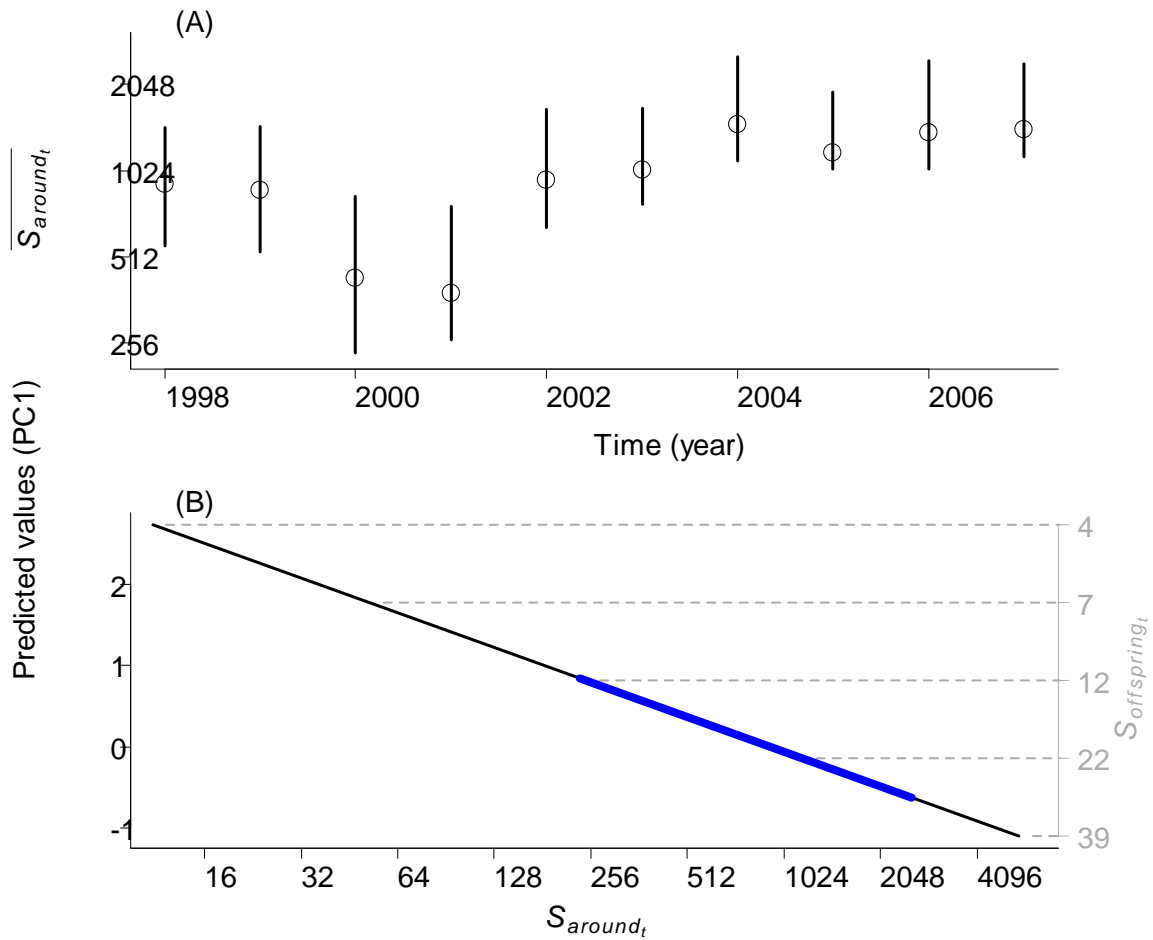


777

778 **Fig. 3.** A visualization of the model presented in Table 4b showing how the scores for PC2 ((offspring-male gradient)) are predicted as a function

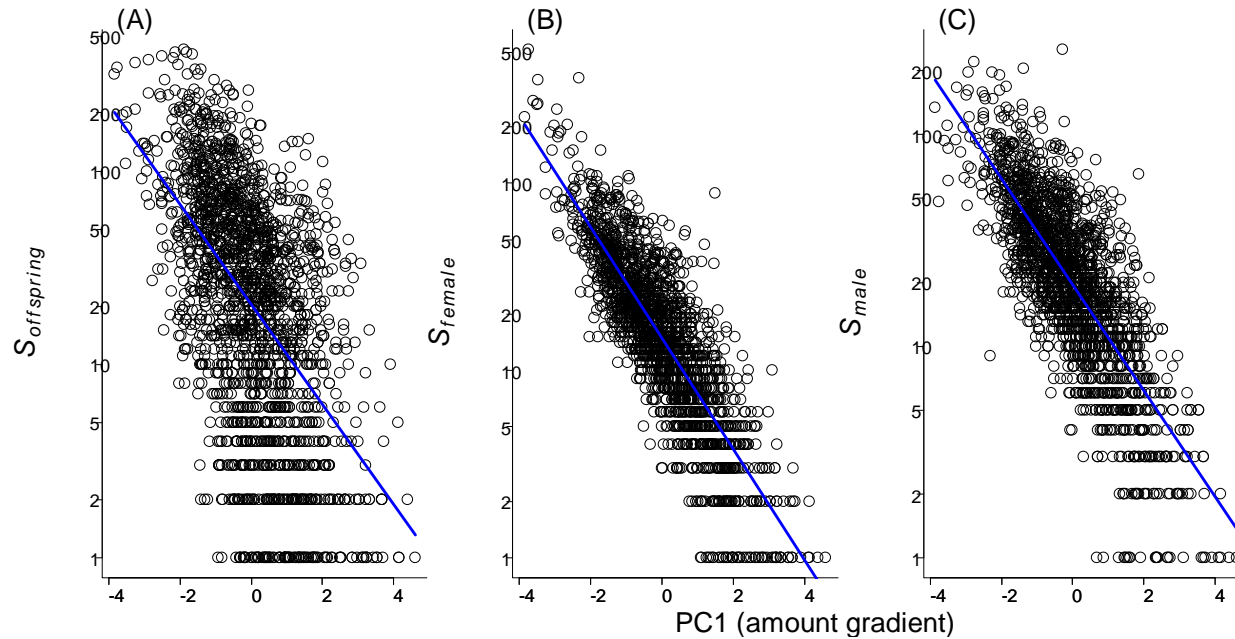
779 of: (a) herd size for the husbandry units (N_t), (b) the combined effect of number of reindeer slaughtered by neighboring herders (S_{around_t}) and

780 the average coefficient of relatedness ($r_{district}$) and the interaction between them (see Fig. A1.2. for visualization of the relationship between
781 the original variables and PC2). Legend below Fig. 2 for technical details.



782

783 **Fig. 4.** Showing (a) the temporal trend in average number of reindeer slaughtered by
 784 neighboring husbandry units (bars represent the 25 and 75 percentiles) from 1998-2007 and
 785 (b) the predicted effect of the average number of reindeer slaughtered by neighboring
 786 husbandry units on PC1 (*y-axis*) and number of slaughtered offspring (*z-axis*; based on the
 787 relationship shown in Fig. A1.1). Note: highlighted line indicates the range in the average
 788 values presented in (a).

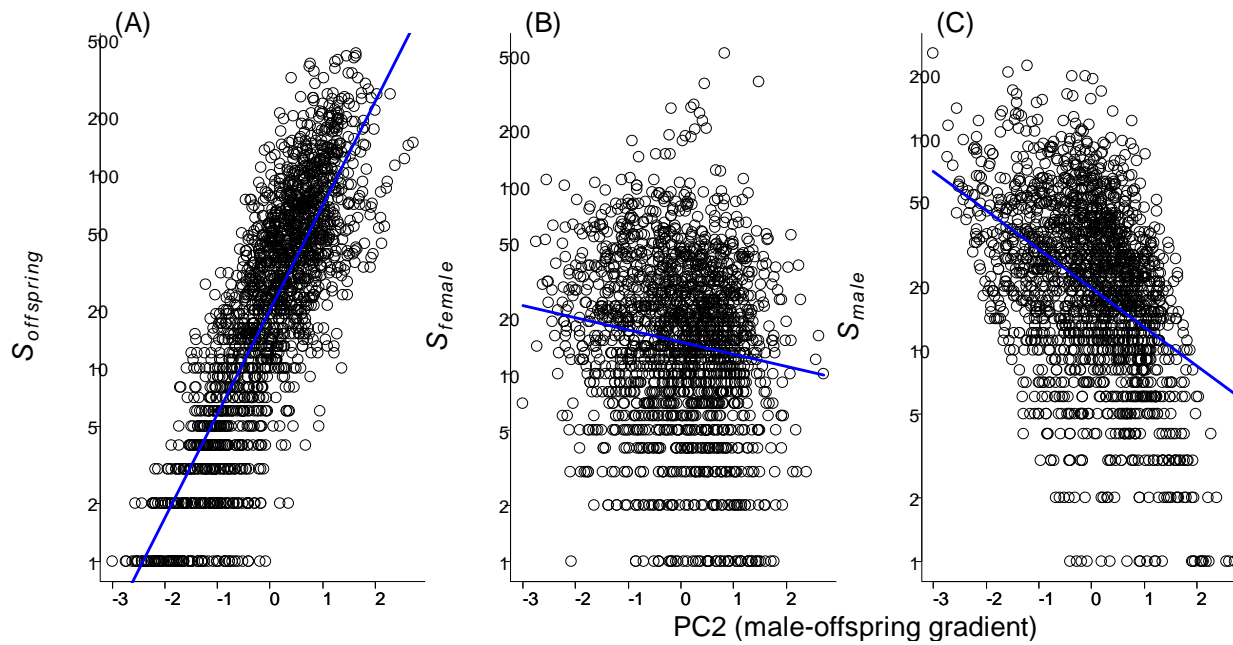


791

792 **Fig. A1.1.** Number of slaughtered (S) offspring (a), females (b) and males (c) as a function of principal component (PC) 1 for all

793 husbandry units that slaughtered at least one animal belonging to each category. The lines shows the predicted relationships between

794 the number of slaughtered animals as a function of PC 1 in a regular linear model (LM) specified as follows: $\text{response} = \alpha + \beta_1 \times \text{PC 1}$ (α 795 and β_1 represents the intercept and the slope for PC 1).



796

797 **Fig. A1.2.** Number of slaughtered (S) offspring (a), females (b) and males (c) as a function of principal component (PC) 2 for all

798 husbandry units that slaughtered at least one animal belonging to each category. The lines shows the predicted relationships between

799 the number of slaughtered animals as a function of PC 2 in a regular linear model (LM) specified as follows: $\text{response} = \alpha + \beta_1 \times \text{PC 2}$ (α

800 and β_1 represents the intercept and the slope for PC 2).

801 **Tables**

802 **Table A1.1.** Test statistics and adjusted R² values from fitting regular (a) univariate linear
 803 regression and (b) multiple regression analyses relating amount of slaughter (PC1) to the total
 804 herd size for the husbandry units (N_t), the number of reindeer slaughtered by neighbouring
 805 herders (S_{around_t}), the average coefficient of relatedness ($r_{district}$) and the interaction between
 806 them ($S_{around_t} \times r_{district}$). While not accounting for grouping structure in the data (see main
 807 text), the table gives some indication as to the relative importance of the different predictors.

PC1 ('amount gradient')

Model parameter	R ² (adjusted)	(F-statistics)	P-value
(a) Univariate analyses			
N_t^a	0.501	(F = 1868, df = 1,1861)	<0.001
$S_{around_t}^a$	0.131	(F = 281, df = 1,1861)	<0.001
$r_{district}$	-0.001	(F = 0.04, df = 1,1861)	0.845
(b) Multiple regression analyses			
$N_t + S_{around_t}$	0.554	(F = 1157, df = 2,1860)	<0.001
$N_t + r_{district}$	0.500	(F = 934, df = 2,1860)	<0.001
$N_t + S_{around_t} + r_{district}$	0.562	(F = 799, df = 3,1859)	<0.001
$N_t + S_{around_t} + r_{district} + S_{around_t} \times r_{district}$	0.567	(F = 610, df = 4,1858)	<0.001

808 ^aThis variable was transformed using the natural logarithm.

809 Note: All covariates were centred (see Aiken and West, 1991:35 for rationale).