

Saami reindeer herders cooperate with social group members and genetic kin

Journal:	<i>Behavioral Ecology</i>
Manuscript ID:	BEHECO-2014-0634.R2
Manuscript Type:	Original article
Keywords:	humans, cooperation, economic games, kin selection, reciprocal altruism, social groups

SCHOLARONE™
Manuscripts

New Only

1 Saami reindeer herders cooperate with social group members and genetic kin

2 Abstract

3 Cooperative behaviors evolve by ultimately increasing the inclusive fitness of performers as well as
4 recipients of those behaviors. Such increases can occur via direct or indirect fitness benefits,
5 theoretically explained by reciprocal altruism and kin selection respectively. However, humans are
6 known for cooperating with individuals who are not necessarily genetic relatives, which seemingly
7 precludes kin selection as an explanation. Here, we aim to quantify the relative importance of
8 kinship and social group membership as mediators of cooperative behavior. Using an experimental
9 gift game, we test whether indigenous Saami reindeer herders in Norway give gifts to genetic
10 relatives or to members of their cooperative herding group (the 'siida'), or both. Membership of the
11 same siida strongly increased the odds of gift-giving. Kinship had a smaller, albeit positive, effect.
12 Gifts were not preferentially given to younger family members, contrary to predictions relating to
13 inter-generational resource transfers as a form of parental investment. These patterns suggest that
14 social grouping can be at least as important as genetic factors in mediating cooperative behavior in
15 this population. This is likely to reflect the importance of herding groups in day-to-day subsistence.
16 Key words: humans, cooperation, economic games, kin selection, reciprocal altruism, social groups

17 Lay Summary

18 Humans cooperate extensively and flexibly. The extent to which we prefer helping kin over non-kin
19 (or vice versa) remains an open question. Our experiments with indigenous reindeer herders in
20 north Norway investigated the relative importance of kin and non-kin in determining cooperative
21 behavior. Our results suggest that herders give gifts to members of their herding alliances regardless
22 of whether or not the recipient is a genetic relative, although within groups, kin were favored.

23

24 Introduction

25 Cooperation is prevalent in a wide range of taxa, including humans. Cooperative behaviors benefit
26 other individuals, either at a cost to the cooperator or not; such behaviors can be favored by
27 selection due to their effects on others (West et al. 2007). The most long-standing explanations of
28 the evolution of cooperative behavior are kin selection (Hamilton 1964) and reciprocal altruism
29 (Trivers 1971), both of which are likely to play a role in human social interactions. A panoply of
30 theoretical models of these and other effects have shown how the existence of cooperation is
31 relatively easy to explain in evolutionary terms (Lehmann & Keller 2006; Nowak 2006; West et al.
32 2007). Ultimately, cooperative behaviors will evolve if they increase the inclusive fitness of the
33 individuals performing the behavior. Exactly with whom one should cooperate, and to what extent,
34 remains a contentious issue that is expected to depend on context.

35 Humans cooperate extensively in many regards. For example, cooperation is vital for survival and
36 reproduction among humans following a pastoralist way of life: a subsistence strategy involving a
37 dependence on livestock. Across the world, most pastoralist societies work in cooperative herding
38 groups formed from multiple families in multiple households (Næss 2012). Ariaal and Rendille
39 pastoralists of East Africa herd in cooperative units typically formed of siblings' families that, among
40 the Ariaal at least, can fission from the wider settlement (Fratkin 1986). In Tibet, the *rukor* (or *ru*
41 *skor*) is a cooperative group which tends to form for the summer and disband during winter
42 (Nietupski 2012). Mongolian nomadic herders cluster into groups known as *Khot-Ail*, living and
43 managing livestock as a socio-economic unit (Upton 2008). Saami pastoralists, the focus of this
44 study, work in a cooperative institution known as the *siida* (Paine 1994).

45 Working in cooperative groups has many advantages, allowing herders to pool risk, defend herds
46 from raiders or predators, protect pastureland, share knowledge and information, loan or gift
47 animals to those in need, and exchange labor (Dyson-Hudson & Dyson-Hudson 1980; Paine 1994;
48 Aktipis et al. 2011; Næss 2012). These forms of cooperative behavior may be a least-cost strategy

1
2
3 49 compared to herding alone, allowing herding groups to achieve economies of scale, i.e. an increase
4
5 50 in the percentage of output coupled with a reduction in the costs related to labor investment (Næss
6
7 51 et al. 2009; Næss 2012).

8
9
10 52 Kin selection theory (Hamilton 1964) predicts that cooperative behaviors would evolve between
11
12 53 genetic relatives as long as the fitness benefits, tempered by the degree of relatedness between
13
14 54 them, outweigh the costs. Previous work on Saami reindeer pastoralists has shown that decisions to
15
16 55 slaughter are mediated through kin relations (Næss et al. 2012) and that the presence of genetic
17
18 56 relatives, along with the availability of workers, had a positive effect on herd size (Næss et al. 2010).
19
20 57 Such an effect is important for year-on-year household viability as well as during crisis periods; those
21
22 58 with large pre-collapse herd sizes also had the largest post-collapse herds (Næss & Bårdsen 2010;
23
24 59 Næss & Bårdsen 2013).

25
26
27
28 60 Group living can lead to a social dilemma where rational actors might choose not to contribute to a
29
30 61 common enterprise (i.e. defect) but still try to reap the benefits of other's contributions, eventually
31
32 62 leading to a breakdown in cooperation. Avoidance of defectors can allow cooperators to assort
33
34 63 together, either through mobility (Aktipis 2011), severing social links (Wang et al. 2012) or choosing
35
36 64 partners (Stiff & Van Vugt 2008). The ability to choose from a 'marketplace' (Noë & Hammerstein
37
38 65 1994) of competing potential partners can lead individuals to act more cooperatively in relation to
39
40 66 others, resulting in an escalation of 'competitive cooperation' (Barclay & Willer 2007). Individuals
41
42 67 may direct cooperative behaviors to others based on their knowledge of the recipient's reputation
43
44 68 (indirect reciprocity (Nowak 2006)). In biological markets, being cooperative could act as an indicator
45
46 69 of status, as can factors such as skill, prestige or experience.

47
48
49
50 70 Once partners have been chosen, rewards (such as gifts) and punishment may be important
51
52 71 mechanisms for maintaining cooperation through partner control (Trivers 1971; West et al. 2007).
53
54 72 However, gift exchange might also function as a method of pooling risk in unpredictable
55
56
57
58
59
60

1
2
3 73 environments in order to benefit all social group members. For pastoralists, exchanging gifts of
4
5 74 livestock has been theoretically shown to boost long-term herd survival (Aktipis et al. 2011).
6
7

8 75 **Predictions**

9
10 76 Previous work on Saami pastoralists has looked at how genetic relatedness and labor availability
11
12 77 affect cooperation across districts, which are administrative clusters of herding groups (Næss et al.
13
14 78 2010; Næss et al. 2012). We extend this to investigate the relative effects of kinship and cooperative
15
16 79 group membership on gift giving behavior between individuals within a district. Saami pastoralists
17
18 80 organize themselves into groups – composed of kin and non-kin – for the purposes of cooperative
19
20 81 herding, their primary means of subsistence. Given the reliance on herding groups, we predict a
21
22 82 strong cooperative bias towards fellow group members, regardless of whether or not the recipients
23
24 83 are genetic relatives.
25
26
27

28
29 84 However, this hypothesis does not imply that kinship will be unimportant. One manifestation of kin
30
31 85 selection in humans may take the form of inter-generational resources flows from older to younger
32
33 86 family members, especially from parents to children (Kaplan 1994). Thus, we predict that resources
34
35 87 such as gifts would be given preferentially to younger people when they are given within families.
36
37

38
39 88 We aim to quantify the relative effects of factors predicting cooperative behavior by conducting a
40
41 89 culturally salient experimental gift game among Saami reindeer herders living in Finnmark, Northern
42
43 90 Norway. Participants could choose between one and three other reindeer herders to receive a gift of
44
45 91 money. In order to ensure the game had contextual relevance to participants, we framed the gifts in
46
47 92 terms of how much gasoline they could be used to purchase, since gasoline is a valuable commodity
48
49 93 for Saami pastoralists.
50
51

52 94 **Methods**

53
54
55
56 95 This research was approved by the University College London research ethics committee.
57
58
59
60

1
2
3 96 **Study Area**
4

5 97 The term Saami describes a group of people indigenous to the areas that comprise northern
6
7 98 Fennoscandia (Norway, Sweden and Finland), as well as the westernmost part of Russia. Today only
8
9 99 a minority of Saami people subsist on reindeer pastoralism; as of 2013, there were 533 licensed
10
11 100 reindeer herders (Norwegian: *siidaandeler*) living in Norway and 3,112 other Saami people
12
13
14 101 connected to reindeer husbandry (Anonymous 2013).
15
16

17 102 The *siida* is an important economic and cultural unit of cooperation and subsistence (Paine 1994).
18

19 103 Membership is, for the most part, influenced by long-standing relationships between families, some
20
21 104 of whom will be genealogically related. Traditionally, the *siida* was based on conjugal and sibling
22
23 105 solidarity, which could be extended to include cousins and other affinal relatives of the same
24
25 106 generation (Bergman et al. 2008). Unmarried people and unrelated wage laborers may also join
26
27 107 *siidas* on a facultative basis. Therefore, *siidas* can include both kin and non-kin.
28
29

30
31 108 People from different *siidas* can interact in a number of ways. With the adoption of snowmobiles
32
33 109 and other vehicles as well as communication technologies, herders now live more sedentary lives:
34

35 110 Members from several *siidas* live in the same towns for much of the year. In addition, herders from
36
37 111 different *siidas* may help one another by splitting up mixed herds or finding lost reindeer. Conflicts
38
39 112 may also arise, which has resulted in the destruction of fences separating the pasture areas of
40
41 113 different *siidas*, among other issues.
42
43

44 114 In general, herders belong to two *siidas*: summer and winter. Summer *siidas* are large groups of
45

46 115 households whose reindeer graze on the coastal pastures and islands of Norway. The summer *siida*
47
48 116 became a legal entity in 2007 and can be thought of akin to a corporation with elected boards of
49
50 117 leaders. Before the legal consolidation of *siidas*, membership was more flexible and could change
51
52 118 over time; of the herders in our study sample, only 1 person had moved summer *siida* within the
53
54 119 past 15 years. Every year, summer *siidas* split into 1 or more smaller winter *siidas* whose herds graze
55
56
57
58
59
60

1
2
3 120 in the interior of the country (Paine 1994). Summer siidas are grouped into administrative regions
4
5 121 defined by the government, known as districts (Næss et al. 2009).
6
7
8 122 In the present study, we focus on a single district in Finnmark County – the northernmost and largest
9
10 123 reindeer herding area in Norway (Figure 1). Our sample was formed of licensed herd owners within
11
12 124 summer siidas. The Norwegian Government provides licenses to a subset of herders within each
13
14 125 summer siida/district. These license owners are legally allowed to keep reindeer and the Norwegian
15
16 126 Agriculture Agency (*Landbruksdirektoratet*) tracks the productivity of their herds over time. As of
17
18 127 2013, there were 377 license owners in the county of Finnmark (Anonymous 2013).
19
20
21 128 Saami herders face occupational stresses from predators, weather conditions, financial pressures,
22
23 129 changing land tenures, conflicts, and ethnic discrimination (Bjerkli 2010; Hansen et al. 2010; Allard
24
25 130 2011; Pape & Löffler 2012). A recent report found that the high levels of reindeer mortality observed
26
27 131 in Finnmark might be due not to predation, as commonly believed, but rather overcrowding of
28
29 132 reindeer and the poor condition of the animals (Tveraa et al. 2013). Conflicts can involve
30
31 133 governments, industry (e.g., mineral extraction or logging companies), landowners, researchers, as
32
33 134 well as other reindeer herders. Within the reindeer husbandry community, conflicts can arise over
34
35 135 encroachment onto a rival siida's pasture, theft of reindeer, and destruction of fences, among other
36
37 136 things (Paine 1970).
38
39
40
41
42 137 Siidas are also loci for collective action. Siida group members work together on maintenance
43
44 138 activities, run slaughterhouses, and gathering herds into corrals so as to weigh and administer
45
46 139 medicine to the animals, determine the number and quality of pregnant cows, and split herds by sex
47
48 140 before seasonal migrations. Given the conflicts and cooperative behaviors described above, we
49
50 141 would expect the siida to represent more than a decision-making body: rather, it would act as an
51
52 142 important social unit. The focus of our study is the summer siida.
53
54

55 56 143 **Gift Game** 57 58 59 60

1
2
3 144 In July and August 2013, the first author interviewed 30 licensed reindeer herders across all 9
4
5 145 summer siidas in 1 district in Finnmark, Norway (Figure 1) with the help of a Saami field assistant.
6
7 146 Participants were endowed with vouchers (see below) and were then asked to give these as
8
9 147 anonymous gifts to other licensed herd owners in their district. Respondents were presented with a
10
11 148 list of license owners in the district (collected by a combination of publically available contact
12
13 149 information and snowball sampling, whereby one participant suggested other potential participants)
14
15 150 coded with randomly generated ID numbers. Respondents read the ID numbers of their desired gift
16
17 151 recipients to the field assistant. This procedure aimed to minimize experimenter bias, since the
18
19 152 assistant was also a member of the district, although not a licensed herd owner.
20
21
22
23 153 We gave players 3 vouchers, each representing 5 liters of gasoline. At the time, 1 liter of petrol cost
24
25 154 approximately NOK 15 (US\$ 2.54). Players could choose to give the vouchers to 1-3 other license
26
27 155 owners – in multiples of 5 liters. They were not allowed to keep anything for themselves; they had to
28
29 156 give the vouchers to at least 1 recipient. Players also gave reasons for their distribution of gifts. We
30
31 157 coded these open answers into 1-3 keywords, blind to the giver's name, siida and distribution of gifts
32
33 158 (see Supplementary Methods). At the end of the experimental period, all recipients were given their
34
35 159 rewards in the form of cash, since the vouchers were created for the purposes of this study and
36
37 160 were not legal tender, although all gift decisions were framed in terms of liters of gasoline.
38
39
40
41 161 Communication was not allowed within the parameters of the experiment. However, due to the
42
43 162 vagaries of the herding lifestyle, we were unable to conduct all interviews within a sufficiently short
44
45 163 time to rule out for the chance that herders did not communicate with one another.
46
47
48
49 164 Experimental materials were translated into Norwegian by an independent person and back-
50
51 165 translated by the second author. The first and second authors agreed on the final translations.
52
53 166 Norwegian and English materials are available on request.
54

167 **Kinship Data**

1
2
3 168 Genealogical data were collected in May 2014 detailing how each license owner in the district (n =
4
5 169 75) was related to one another. We linked license owners to their previously assigned ID numbers
6
7 170 and calculated a coefficient of relatedness (r_{ij}) for each pair of herders (i, j). This resulted in a full
8
9 171 kinship network of licensed herd owners in the target district.

12 172 **Herd Size Data**

13
14
15 173 Herd sizes held by individual license owners were collected from data published by the Norwegian
16
17 174 Broadcasting Corporation (*Norsk rikskringkasting AS*; Aslaksen (2014)). We used the numbers of
18
19 175 reindeer held by individuals in 2012 – the most recent data available. We were able to match herd
20
21 176 sizes for 62 of the 75 people in our database, not achieving complete coverage due to changes in
22
23 177 license owners between 2012 and our study period. Herd sizes were group-mean centered across
24
25 178 the district.

28 179 **Statistical Analysis**

29
30
31 180 We fitted generalized estimating equation (GEE) models to all potential gift-giving dyads, where the
32
33 181 egos were the 30 gift game participants and alters were the 75 licensed owners, giving $30 \times (75 -$
34
35 182 $1) = 2,220$ possible dyads. The binary response variable in all models was whether or not a gift
36
37 183 was given within a dyad. We present unstandardized and standardized estimates, where in the latter
38
39 184 case, binary factors were mean-centered and continuous variables were standardized over 2
40
41 185 standard deviations to allow estimates to be compared within models, following the
42
43 186 recommendations of Gelman (2008) and Schielzeth (2010).

44
45
46
47 187 GEE is a population-averaged approach that accounts for multiple observations of each ego by
48
49 188 clustering standard errors. We specified an exchangeable working correlation matrix, which models
50
51 189 the dependence of observations within clusters. GEE does not use full likelihood estimates, so we
52
53 190 computed and compared the quasi-likelihood under the independence model information criterion
54
55 191 (QIC) for model selection (Pan 2001). Note that we did not fit models containing the individual-level

1
2
3 192 predictors gathered from our questionnaires since doing so would have dramatically reduced the
4
5 193 number of dyads in our analysis.
6
7
8 194 Analyses were conducted in R 3.2.0 (R Core Team 2012). Details of packages and additional software
9
10 195 used, as well as where to download archived data and analysis code, are available in the
11
12 196 Supplementary Information.
13
14
15

16 17 197 **Results**

18 19 20 198 **Description of the District and the Gift Network**

21
22 199 61 of the 75 herd owners in the district were male, with a median age of 53 (see Supplementary Fig.
23
24 200 S1 for the age distribution and Table S1 for descriptive statistics). The median number of reindeer
25
26 201 owned by herders in the district in 2012 was 456.5, ranging between 55 and 1,604 reindeer
27
28 202 (Supplementary Fig. S2). The 30 herders interviewed gave 71 gifts to 43 people (Figure 2a), some of
29
30 203 whom were also participants. Of the 71 gifts, 45 (63.4%) were given to members of the same
31
32 204 summer siida. A significantly higher proportion of gifts were given within siidas ($\chi^2_1 = 4.563, P =$
33
34 205 0.033). The majority of gifts (59) were for 5 liters of gasoline and were given by 18 of the 30 people
35
36 206 interviewed. 5 gifts, given by 5 separate individuals, were worth 10 liters, while 7 gifts, given by 7
37
38 207 different people, were for 15 liters.
39
40
41
42

43 208 The number of gifts received by individuals (in-degree) ranged from 0 to 7 (median = 1, mean = 0.95,
44
45 209 standard deviation [SD] = 1.16). We do not report the number of gifts given (out-degree) or include
46
47 210 it in the models since only the 30 people interviewed were able to give gifts. Gift givers received
48
49 211 more gifts; that is, out-degree significantly correlated with in-degree (Pearson's product-moment
50
51 212 correlation, $r = 0.415, P < 0.001, 95\% CI [0.208, 0.587]$). One outlier received 7 gifts totaling 50
52
53 213 liters of gasoline – twice as much as the second most popular herder. The reasons given for his gifts
54
55 214 fell on a wide spectrum, from "Deserves it" and "Good reindeer herder" to "Always empty of fuel".
56
57
58
59
60

1
2
3 215 Ten gifts (28.2%) were reciprocated (Figure 2b), despite communication not featuring in the
4
5 216 experiment. Of the reciprocated gifts, only 1 was given to a member of another siida. In this case,
6
7 217 both were males living in the same town who clearly had a history of working together based on
8
9 218 their stated reasons for giving the gifts. Supplementary Table S2 shows descriptive statistics for the
10
11 219 gift network.

12
13
14 220 Siida leaders did not receive more gifts than others (Table 1). There was a significant sex difference
15
16 221 between number of gifts received where males on average received more (Mann-Whitney test,
17
18 222 $W = 258.500, P = 0.015$), although the sample contains substantially fewer females (4 of the 43
19
20 223 herders who received gifts).

224 **Relatedness in the District**

225 The smallest two siidas ('a' and 'f' in Figure 3) were formed entirely of siblings and/or parents with
226 children ($r_{ij} = 0.5$). These siidas contained, respectively, 2 and 3 licensed owners. As the number of
227 members increases, there was no discernible trend in relatedness across the nine siidas. The mean
228 relatedness across the district was $r_{ij} = 0.02$ (i.e., between 2nd and 3rd cousins), whereas the grand
229 mean of mean relatedness within siidas was $r_{ij} = 0.19$. Due to the small number of groups and their
230 small sizes, we did not perform analyses grouped by individual siidas.

231 **Analysis of gift giving**

232 Table 2 shows the distribution of gifts, split by whether recipients were genetically related to the
233 giver and/or belonged to the same siida. We calculated correlation coefficients between the
234 networks of gifts, relatedness and siida membership (Supplementary Table S3). Summer siida
235 membership correlated with genetic relatedness ($r = 0.39, P \ll 0.01, 95\% CI [0.35, 0.42]$). The
236 coefficient of relatedness between givers and receivers correlates with receiving a gift ($r =$
237 $0.32, P \ll 0.01, 95\% CI [0.29, 0.36]$) and with siida membership
238 ($r = 0.42, P \ll 0.01, 95\% CI [0.38, 0.45]$).

1
2
3 239 In the best-fitting GEE model (Table 3), belonging to the same summer siida as the other person in a
4
5 240 dyad was the strongest predictor of gift-giving (standardized log odds = 1.875, S.E. = 0.447)
6
7 241 compared to genetic relatedness (standardized log odds = 0.691, S.E. = 0.187). Note that these
8
9 242 estimates are only biologically interpretable in their unstandardized form (Table 3).
10
11
12 243 From the full set of candidate models, the model containing only a term for siida membership
13
14 244 (model 5 in Supplementary Table S4) fitted the data better than the model containing only a term
15
16 245 for relatedness (model 6 in Supplementary Table S4). Models with an interaction between
17
18 246 relatedness and siida membership (models 3 and 4 in Supplementary Table S4) and models
19
20 247 containing herd sizes for the potential giver and recipient (models 2 and 4 in Supplementary Table
21
22 248 S4) did not provide a better fit compared to the model containing additive terms for relatedness and
23
24 249 siida membership (Table 3; model 1 in Supplementary Table S4).

25
26
27
28 250 We hypothesized that gifts would preferentially be given to younger herders within families (where
29
30 251 gifts to younger herders are scored as a negative age difference). Contrary to expectations, gifts
31
32 252 were not preferentially given to younger kin ($\chi^2_1 = 0.78, P = 0.38$; Table 4). Age also had no
33
34 253 significant effect on the number of gifts received (Spearman's rank correlation, $\rho = -0.235, P =$
35
36 254 0.211 ; Figure 4).

37 38 39 40 255 **Why give?**

41
42 256 Table 5 lists the coded translations of all reasons for giving gifts (Supplementary Table S5 provides
43
44 257 the full text). The most common category ($n = 24$) for giving a gift, regardless of kinship and siida
45
46 258 membership, was current or future reciprocity. Thirteen gifts were given to recipients with good
47
48 259 reputations.

50
51
52 260 An interesting case is the gifts given to non-kin belonging to other siidas. Over half of these gifts
53
54 261 were split between those with reputations of being a 'good herder' and young license owners who
55
56 262 were newly established in reindeer husbandry.
57
58
59
60

263 Discussion

264 Summer siidas are stable cooperative groups. Only 1 person of 30 interviewed had moved between
265 summer siidas within the last 15 years. Belonging to the same summer siida was the stronger
266 predictor for gift-giving compared to being genetically related (Table 3). Interactions between
267 relatedness and siida membership (models 3 and 4 in Supplementary Table S4) did not provide a
268 better fit to the data. Similarly, including the herd sizes for the potential gift giver and recipient did
269 not improve the fit (models 2 and 4 in Supplementary Table S4). Siida membership may be
270 important for this population if strategies that benefit direct fitness are optimal compared to those
271 increasing indirect fitness. Alternatively, herders might receive inclusive fitness benefits by virtue of
272 assorting into the same groups as kin, whereas cooperation with non-kin might need to be
273 maintained via reward mechanisms such as gift giving.

274 There was no preference for giving gifts to younger herders within families (Table 4 and Figure 4),
275 contrary to our prediction derived from parental investment theory regarding the flow of resources
276 down generations within families. The absence of this pattern is likely due to participants not
277 viewing the gifts as resources to be invested in younger relatives. It should be noted that some close
278 relatives (such as a son and heir) might be jointly herding with the herd owner and therefore not
279 eligible to receive a gift as they are not yet a licensed herd owner themselves.

280 Twenty-four of the 71 gifts (33.8%) were given for reasons related to existing reciprocal relationships
281 or developing future relationships (Table 5). In addition, 10 gifts (28.2%) were reciprocated although
282 the experimental setup did not allow communication between participants (Figure 2b). This form of
283 direct reciprocity has been conceptualized as an important mechanism behind the evolution of
284 cooperation (Trivers 1971; Nowak 2006). Our experiment did not explicitly account for either
285 indirect (reputational) or direct reciprocity as mechanisms underlying cooperation; rather, we
286 investigated the relative importance of kinship and social group membership in predicting gift giving.
287 Membership of the same siida may imply multiple opportunities for reciprocation.

1
2
3 288 While the stated reasons for why participants gave particular gifts were *ad hoc*, we argue they
4
5 289 provide valuable insight into behavior in the games. Thirteen of the 71 gifts (18.3%) were given to
6
7 290 those with the reputation of being a 'good herder' (Table 5), something important to Saami
8
9 291 pastoralists (Paine 1970). Gifts were not given preferentially to siida leaders (Table 2). In this study,
10
11 292 we were not able to control for potential confounds such as prestige, skills, experience, etc. that may
12
13 293 have biased gift giving behaviors, although we did control for herd size as a proxy of wealth. Given
14
15 294 this indication that cultural factors such as reputation may be important mediators of cooperative
16
17 295 behavior for Saami reindeer herders, future work could attempt to define measures of reputation
18
19 296 and prestige that are meaningful to this population. One approach would be to ask herders,
20
21 297 preferably in group interviews, to rank others by their experience, skill, history of good decisions,
22
23 298 etc. These culturally derived measures could then be linked to quantitative measures of wealth and
24
25 299 used to predict gift giving.
26
27
28

29
30 300 Gifts in our study were small and anonymous, and communication between participants was not
31
32 301 allowed. This makes it unlikely that costly signals, reputation or competitive altruism were driving
33
34 302 the observed behaviors, although we were unable to test this formally. However, indirect reciprocity
35
36 303 and competitive cooperation play important roles in human social groups, especially when
37
38 304 cooperative behaviors are public (Barclay 2013; Sylwester & Roberts 2013). Our study investigated
39
40 305 the factors underlying partner choice but did not look at mechanisms of partner control that might
41
42 306 enforce or maintain cooperation. Future work should attempt to understand the relative importance
43
44 307 of partner control compared with partner choice as well as the roles of indirect reciprocity, partner
45
46 308 choice and direct reciprocity (especially reciprocity based on reputation, i.e., competitive
47
48 309 cooperation) in real-world contexts.
49
50

51
52 310 This work represents a first step towards quantifying the forms and diversity of cooperative
53
54 311 strategies among Saami people. Saami pastoralists face many social and ecological challenges.
55
56 312 Competition for access to winter pastures may explain herd accumulation as the only viable risk-
57
58
59
60

1
2
3 313 reducing strategy, although the efficacy of this strategy may be limited by quotas on maximum herd
4
5 314 size (Næss & Bårdsen 2010). This suggests the future of reindeer husbandry presents a collective
6
7 315 action problem for the herders: one that may be solved from within the community without
8
9 316 necessitating the privatization of pastures (Bjørklund 1990; Marin 2006; Hausner et al. 2012). At
10
11 317 present, management policies seem to be designed to attain sustainability by targeting only
12
13 318 individual reindeer owners (e.g. providing subsidies to increase slaughter rates), while disregarding
14
15 319 the cooperative nature of reindeer pastoralism (Næss et al. 2012). Understanding the mechanisms
16
17 320 of cooperation in this population will be an important task for its future viability.
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

321

322 **References**

- 323 Aktipis, C.A., 2011. Is cooperation viable in mobile organisms? Simple Walk Away rule favors the
324 evolution of cooperation in groups. *Evolution and Human Behavior*, **32**, 263–276.
- 325 Aktipis, C.A., Cronk, L. & Aguiar, R., 2011. Risk-pooling and herd survival: An agent-based model of a
326 Maasai gift-giving system. *Human Ecology*, **39**, 131–140.
- 327 Allard, C., 2011. The Nordic countries' law on Sámi territorial rights. *Arctic Review on Law and*
328 *Politics*, **3**, 159–183.
- 329 Anonymous, 2013. *Ressursregnskap for Reindriftsnæringen (Ecological statistics of reindeer*
330 *husbandry)*,
- 331 Aslaksen, E., 2014. Her er reintallene. *NRK Sápmi*.
- 332 Barclay, P., 2013. Strategies for cooperation in biological markets, especially for humans. *Evolution*
333 *and Human Behavior*, **34**, 164–175.
- 334 Barclay, P. & Willer, R., 2007. Partner choice creates competitive altruism in humans. *Proceedings of*
335 *the Royal Society B: Biological Sciences*, **274**, 749–53.
- 336 Bergman, I. et al., 2008. Kinship and settlements: Sami residence patterns in the Fennoscandian
337 alpine areas around A.D. 1000. *Arctic Anthropology*, **45**, 97–114.
- 338 Bjerkli, B., 2010. Landscape and resistance. The transformation of common land from dwelling
339 landscape to political landscape. *Acta Borealia*, **27**, 221–236.
- 340 Bjørklund, I., 1990. Sámi reindeer pastoralism as an indigenous resource management system in
341 Northern Norway: A contribution to the common property debate. *Development and Change*,
342 **21**, 75–86.
- 343 Dyson-Hudson, R. & Dyson-Hudson, N., 1980. Nomadic pastoralism. *Annual Review of Anthropology*,
344 **9**, 15–61.
- 345 Fratkin, E., 1986. Stability and resilience in East African pastoralism: The Rendille and the Ariaal of
346 northern Kenya. *Human Ecology*, **14**, 269–286.
- 347 Gelman, A., 2008. Scaling regression inputs by dividing by two standard deviations. *Statistics in*
348 *Medicine*, **27**, 2865–2873.
- 349 Hamilton, W.D., 1964. The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, **7**,
350 1–16.
- 351 Hansen, K.L., Melhus, M. & Lund, E., 2010. Ethnicity, self-reported health, discrimination and socio-
352 economic status: a study of Sami and non-Sami Norwegian populations. *International journal of*
353 *circumpolar health*, **69**, 111–28.

- 1
2
3 354 Hausner, V.H., Fauchald, P. & Jernsletten, J.-L., 2012. Community-based management: under what
4 355 conditions do sámí pastoralists manage pastures sustainably? *PLoS ONE*, **7**, e51187.
- 5
6 356 Kaplan, H., 1994. Evolutionary and wealth flows theories of fertility: Empirical tests and new models.
7 357 *Population and Development Review*, **20**, 753–791.
- 8
9
10 358 Lehmann, L. & Keller, L., 2006. The evolution of cooperation and altruism--a general framework and
11 359 a classification of models. *Journal of Evolutionary Biology*, **19**, 1365–76.
- 12
13 360 Marin, A.F., 2006. Confined and sustainable? A critique of recent pastoral policy for reindeer herding
14 361 in Finnmark, Northern Norway. *Nomadic Peoples*, **10**, 209–232.
- 15
16 362 Næss, M.W. et al., 2010. Cooperative pastoral production — the importance of kinship. *Evolution*
17 363 *and Human Behavior*, **31**, 246–258.
- 18
19 364 Næss, M.W., 2012. Cooperative pastoral production: reconceptualizing the relationship between
20 365 pastoral labor and production. *American Anthropologist*, **114**, 309–321.
- 21
22
23 366 Næss, M.W. & Bårdsen, B.-J., 2010. Environmental stochasticity and long-term livestock viability—
24 367 herd-accumulation as a risk reducing strategy. *Human Ecology*, **38**, 3–17.
- 25
26 368 Næss, M.W. & Bårdsen, B.-J., 2013. Why herd size matters - mitigating the effects of livestock
27 369 crashes. *PLoS ONE*, **8**, e70161.
- 28
29 370 Næss, M.W., Bårdsen, B.-J. & Tveraa, T., 2012. Wealth-dependent and interdependent strategies in
30 371 the Saami reindeer husbandry, Norway. *Evolution and Human Behavior*, **33**, 696–707.
- 31
32 372 Næss, M.W., Fauchald, P. & Tveraa, T., 2009. Scale dependency and the “marginal” value of labor.
33 373 *Human Ecology*, **37**, 193–211.
- 34
35
36 374 Nietupski, P.K., 2012. *Labrang Monastery: A Tibetan Buddhist Community on the Inner Asian*
37 375 *Borderlands, 1709-1958*, Lexington Books.
- 38
39 376 Noë, R. & Hammerstein, P., 1994. Biological markets: supply and demand determine the effect of
40 377 partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology*, **35**,
41 378 1–11.
- 42
43 379 Nowak, M.A., 2006. Five rules for the evolution of cooperation. *Science*, **314**, 1560–3.
- 44
45
46 380 Paine, R., 1994. *Herds of the tundra: A portrait of Saami reindeer pastoralism*, Smithsonian
47 381 Institution Press.
- 48
49 382 Paine, R., 1970. Lappish decisions, partnerships, information management, and sanctions: A nomadic
50 383 pastoral adaptation. *Ethnology*, **9**, 52–67.
- 51
52 384 Pan, W., 2001. Akaike’s information criterion in generalized estimating equations. *Biometrics*, **57**,
53 385 120–125.
- 54
55
56 386 Pape, R. & Löffler, J., 2012. Climate change, land use conflicts, predation and ecological degradation
57 387 as challenges for reindeer husbandry in northern Europe: what do we really know after half a
58 388 century of research? *Ambio*, **41**, 421–34.

- 1
2
3 389 R Core Team, 2012. R: A Language and Environment for Statistical Computing.
4
5 390 Schielzeth, H., 2010. Simple means to improve the interpretability of regression coefficients.
6 391 *Methods in Ecology and Evolution*, **1**, 103–113.
7
8
9 392 Stiff, C. & Van Vugt, M., 2008. The power of reputations: The role of third party information in the
10 393 admission of new group members. *Group Dynamics: Theory, Research, and Practice*, **12**, 155–
11 394 166.
12
13 395 Sylwester, K. & Roberts, G., 2013. Reputation-based partner choice is an effective alternative to
14 396 indirect reciprocity in solving social dilemmas. *Evolution and Human Behavior*, **34**, 201–206.
15
16 397 Trivers, R., 1971. The evolution of reciprocal altruism. *Quarterly review of biology*, **46**, 35–57.
17
18 398 Tveraa, T. et al., 2013. *Beregning av produksjon og tap i reindriften - NINA Rapport 938*,
19
20 399 Upton, C., 2008. Social capital, collective action and group formation: Developmental trajectories in
21 400 post-socialist Mongolia. *Human Ecology*, **36**, 175–188.
22
23
24 401 Wang, J., Suri, S. & Watts, D.J., 2012. Cooperation and assortativity with dynamic partner updating.
25 402 *Proceedings of the National Academy of Sciences*, **109**, 14363–8.
26
27 403 West, S.A., Griffin, A.S. & Gardner, A., 2007. Social semantics: altruism, cooperation, mutualism,
28 404 strong reciprocity and group selection. *Journal of Evolutionary Biology*, **20**, 415–32.
29
30 405
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3 406 **Figure Legends**
4
5

6 407 Figure 1: Location of the study site, situated in the county of Finnmark, Norway (shown in blue). The
7
8 408 study site was a single district (dashed ellipse and inset). The inset map shows the study site, with
9
10 409 the black outline representing the district border and red outlines representing summer siida
11
12 410 pasture boundaries. Pastures are labelled with the siida code used in this study. Note that siida 'd'
13
14 411 has two pastures since it was two siidas at the time the map was drawn; it is now considered a single
15
16 412 siida. Map credits are listed in the supplementary information.
17
18

19 413 Figure 2: Gift networks showing license owners in the district (nodes) colored by siida membership
20
21 414 for (a) the entire district and (b) reciprocated gifts only. Filled circles represent the 30 license owners
22
23 415 interviewed for this study. Edges are gifts, where edge thickness corresponds to gift size (5, 10 or 15
24
25 416 liters of gasoline) and color shows the siida from which the gift came.
26
27

28
29 417 Figure 3: Relatedness within the 9 siidas. Points are the mean coefficients of relatedness between
30
31 418 licensed herd owners within each siida. Error bars show standard deviation. Data are ordered, from
32
33 419 left to right, in increasing group sizes (also shown within the data points). The grey dotted line shows
34
35 420 the mean relatedness in the entire district (i.e. across all siidas); the red dotted line shows the grand
36
37 421 mean (i.e. mean of the mean within-siida relatedness coefficients).
38
39

40 422 Figure 4: Age differences between givers and receivers of gifts where the pair are (a) kin or (b) non-
41
42 423 kin. Positive values represent gifts given to older herders (brown bars) whereas negative values
43
44 424 represent gifts to younger herders (blue bars). No gifts were given to herders of the same age.
45
46

47
48 425
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

426 **Tables**

427 Table 1: Number of gifts received (In-degrees) split by whether the herder is on their siida’s leadership board or not.

Leader?	N	In-degree		
		Median	Mean	SD
Yes	18	1	1.28	1.02
No	12	1	1.75	1.91
Unknown	45	0	0.60	0.78

428

429

For Review Only

430

431 Table 2: Counts of people receiving a gift or not, split by whether they are genetic relatives and/or members of the same

432 summer siida, for all possible dyads in the district.

Same siida?	Related?	Received gift?		% receiving gift
		No	Yes	
Yes	Yes	74	30	28.8%
	No	153	15	8.9%
No	Yes	88	3	3.3%
	No	1,834	23	1.2%

433

434

For Review Only

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

435

436 Table 3: Results from the best-fitting generalized estimating equation. Column 2 shows unstandardized log odds (S.E.);
437 column 3 shows log odds (S.E.) standardized over 2 SD (Schiezeth 2010; Gelman 2008) so that the effect sizes can be
438 directly compared. The predictors are the coefficient of relatedness, r , and a binary factor coding whether or not a dyad
439 belongs to the same summer siida. The siida membership predictor most strongly predicts gift giving, although relatedness
440 also has a positive effect. See Supplementary Table S4 for a comparison of all candidate models.

Parameter	Log odds (S.E.)	Standardized log odds (S.E.)
Intercept	-4.178 (0.225)	-3.868 (0.184)
r	4.263 (1.152)	0.691 (0.187)
Same siida?	1.875 (0.447)	1.875 (0.447)

441

442

443

1
2
3 444 Table 4: Number of gifts given to older or younger herders, split by whether or not the dyad were kin.
4
5

Gift to...	Older	Younger	Unknown
... kin	19	13	1
... non-kin	16	14	8

6
7
8
9
10
11 445

12
13 446
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

For Review Only

447

448 Table 5: Coded reasons for giving gifts, split by whether or not the recipient is a genetic relative and/or belongs to the same

449 summer siida.

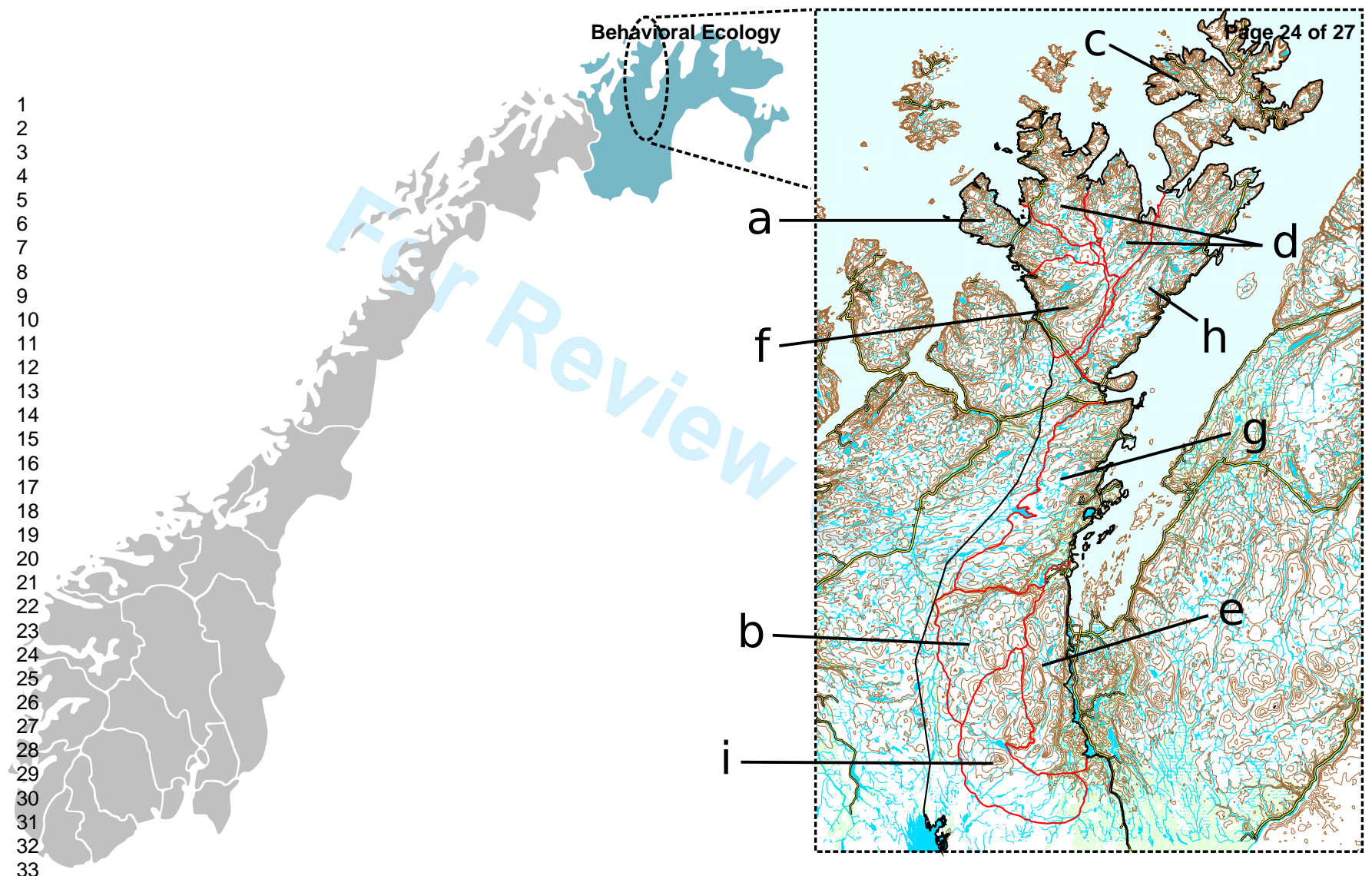
Reason category	Kin in same siida	Non-kin in same siida	Kin in another siida	Non-kin in another siida	Total
Good herders	3	2		8	13
Young/new owners	1	1		5	7
Current or future reciprocity	12	9	1	2	24
Old friend				1	1
Need help		1		1	2
Deserving	2	1			3
Lazy				3	3
Selfish	1				1
Family	7		2	2	11
No reason given	4	1		1	6
Total	30	15	3	23	

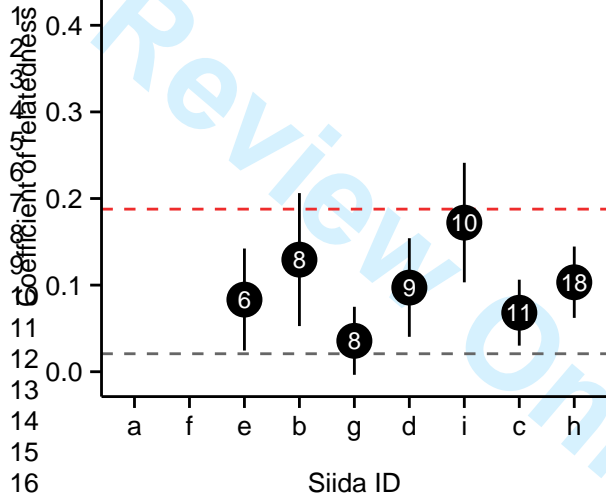
450

451

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33

For Review





Behavioral Ecology

