



## Original Article

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

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

**Key words:** cooperation, economic games, humans, kin selection, reciprocal altruism, social groups.

## INTRODUCTION

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

Humans cooperate extensively in many regards. For example, cooperation is vital for survival and reproduction among humans following a pastoralist way of life: a subsistence strategy involving a dependence on livestock. Across the world, most pastoralist

societies work in cooperative herding groups formed from multiple families in multiple households (Næss 2012). Ariaal and Rendille pastoralists of East Africa herd in cooperative units typically formed of siblings' families that, among the Ariaal at least, can fission from the wider settlement (Fratkin 1986). In Tibet, the *rukor* (or *ru skor*) is a cooperative group, which tends to form for the summer and disband during winter (Nietupski 2012). Mongolian nomadic herders cluster into groups known as *Khot-Ail*, living and managing livestock as a socioeconomic unit (Upton 2008). Saami pastoralists, the focus of this study, work in a cooperative institution known as the *siida* (Paine 1994).

Working in cooperative groups has many advantages, allowing herders to pool risk, defend herds from raiders or predators, protect pastureland, share knowledge and information, loan or gift animals to those in need, and exchange labor (Dyson-Hudson R and Dyson-Hudson N 1980; Paine 1994; Aktipis et al. 2011; Næss 2012). These forms of cooperative behavior may be a least-cost strategy compared with herding alone, allowing herding groups to achieve economies of scale: that is, an increase in the percentage of output coupled with a reduction in the costs related to labor investment (Næss et al. 2009; Næss 2012).

Kin selection theory (Hamilton 1964) predicts that cooperative behaviors would evolve between genetic relatives as long as the

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fitness benefits, tempered by the degree of relatedness between them, outweigh the costs. Previous work on Saami reindeer pastoralists has shown that decisions to slaughter are mediated through kin relations (Næss et al. 2012) and that the presence of genetic relatives, along with the availability of workers, had a positive effect on herd size (Næss et al. 2010). Such an effect is important for year-on-year household viability as well as during crisis periods; those with large precollapse herd sizes also had the largest postcollapse herds (Næss and Bårdsen 2010, 2013).

Group living can lead to a social dilemma where rational actors might choose not to contribute to a common enterprise (i.e., defect) but still try to reap the benefits of other's contributions, eventually leading to a breakdown in cooperation. Avoidance of defectors can allow cooperators to assort together, either through mobility (Aktipis 2011), severing social links (Wang et al. 2012), or choosing partners (Stiff and Van Vugt 2008). The ability to choose from a "marketplace" (Noë and Hammerstein 1994) of competing potential partners can lead individuals to act more cooperatively in relation to others, resulting in an escalation of "competitive cooperation" (Barclay and Willer 2007). Individuals may direct cooperative behaviors to others based on their knowledge of the recipient's reputation (indirect reciprocity [Nowak 2006]). In biological markets, being cooperative could act as an indicator of status, as can factors such as skill, prestige, or experience.

Once partners have been chosen, rewards (such as gifts) and punishment may be important mechanisms for maintaining cooperation through partner control (Trivers 1971; West et al. 2007). However, gift exchange might also function as a method of pooling risk in unpredictable environments in order to benefit all social group members. For pastoralists, exchanging gifts of livestock has been theoretically shown to boost long-term herd survival (Aktipis et al. 2011).

## Predictions

Previous work on Saami pastoralists has looked at how genetic relatedness and labor availability affect cooperation across districts, which are administrative clusters of herding groups (Næss et al. 2010; Næss et al. 2012). We extend this to investigate the relative effects of kinship and cooperative group membership on gift-giving behavior between individuals within a district. Saami pastoralists organize themselves into groups—composed of kin and nonkin—for the purposes of cooperative herding, their primary means of subsistence. Given the reliance on herding groups, we predict a strong cooperative bias towards fellow group members, regardless of whether or not the recipients are genetic relatives.

However, this hypothesis does not imply that kinship will be unimportant. One manifestation of kin selection in humans may take the form of intergenerational resources flows from older to younger family members, especially from parents to children (Kaplan 1994). Thus, we predict that resources such as gifts would be given preferentially to younger people when they are given within families.

We aim to quantify the relative effects of factors predicting cooperative behavior by conducting a culturally salient experimental gift game among Saami reindeer herders living in Finnmark, Northern Norway. Participants could choose between 1 and 3 other reindeer herders to receive a gift of money. In order to ensure the game had contextual relevance to participants, we framed the gifts in terms of how much gasoline they could be used to purchase because gasoline is a valuable commodity for Saami pastoralists.

## METHODS

This research was approved by the University College London research ethics committee.

### Study area

The term Saami describes a group of people indigenous to the areas that comprise northern Fennoscandia (Norway, Sweden, and Finland) as well as the westernmost part of Russia. Today only a minority of Saami people subsist on reindeer pastoralism; as of 2013, there were 533 licensed reindeer herders (Norwegian: *siidaandeler*) living in Norway and 3112 other Saami people connected to reindeer husbandry (Anonymous 2013).

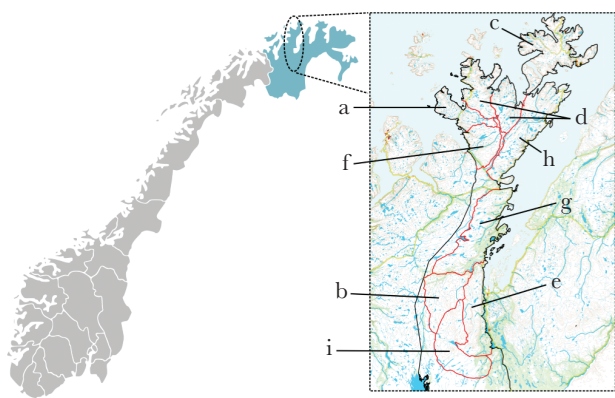
The siida is an important economic and cultural unit of cooperation and subsistence (Paine 1994). Membership is, for the most part, influenced by long-standing relationships between families, some of whom will be genealogically related. Traditionally, the siida was based on conjugal and sibling solidarity, which could be extended to include cousins and other affinal relatives of the same generation (Bergman et al. 2008). Unmarried people and unrelated wage laborers may also join siidas on a facultative basis. Therefore, siidas can include both kin and nonkin.

People from different siidas can interact in a number of ways. With the adoption of snowmobiles and other vehicles as well as communication technologies, herders now live more sedentary lives: Members from several siidas live in the same towns for much of the year. In addition, herders from different siidas may help one another by splitting up mixed herds or finding lost reindeer. Conflicts may also arise, which has resulted in the destruction of fences separating the pasture areas of different siidas, among other issues.

In general, herders belong to 2 siidas: summer and winter. Summer siidas are large groups of households whose reindeer graze on the coastal pastures and islands of Norway. The summer siida became a legal entity in 2007 and can be thought of akin to a corporation with elected boards of leaders. Before the legal consolidation of siidas, membership was more flexible and could change over time; of the herders in our study sample, only 1 person had moved summer siida within the past 15 years. Every year, summer siidas split into 1 or more smaller winter siidas whose herds graze in the interior of the country (Paine 1994). Summer siidas are grouped into administrative regions defined by the government, known as districts (Næss et al. 2009).

In the present study, we focus on a single district in Finnmark County—the northernmost and largest reindeer herding area in Norway (Figure 1). Our sample was formed of licensed herd owners within summer siidas. The Norwegian Government provides licenses to a subset of herders within each summer siida/district. These license owners are legally allowed to keep reindeer, and the Norwegian Agriculture Agency (*Landbruksdirektoratet*) tracks the productivity of their herds over time. As of 2013, there were 377 license owners in the county of Finnmark (Anonymous 2013).

Saami herders face occupational stresses from predators, weather conditions, financial pressures, changing land tenures, conflicts, and ethnic discrimination (Bjerkli 2010; Hansen et al. 2010; Allard 2011; Pape and Löffler 2012). A recent report found that the high levels of reindeer mortality observed in Finnmark might be due not to predation, as commonly believed, but rather overcrowding of reindeer and the poor condition of the animals (Tveraa et al. 2013). Conflicts can involve governments, industry (e.g., mineral extraction or logging companies), landowners, researchers, and



**Figure 1**

Location of the study site, situated in the county of Finnmark, Norway (shown in blue). The study site was a single district (dashed ellipse and inset). The inset map shows the study site, with the black outline representing the district border and red outlines representing summer siida pasture boundaries. Pastures are labeled with the siida code used in this study. Note that siida “d” has 2 pastures because it was 2 siidas at the time the map was drawn; it is now considered a single siida. Map credits are listed in the [Supplementary Material](#).

other reindeer herders. Within the reindeer husbandry community, conflicts can arise over encroachment onto a rival siida’s pasture, theft of reindeer, and destruction of fences, among other things (Paine 1970).

Siidas are also loci for collective action. Siida group members work together on maintenance activities, running slaughterhouses, and gathering herds into corrals so as to weigh and administer medicine to the animals, determine the number and quality of pregnant cows, and split herds by sex before seasonal migrations. Given the conflicts and cooperative behaviors described above, we would expect the siida to represent more than a decision-making body: rather, it would act as an important social unit. The focus of our study is the summer siida.

## Gift game

In July and August 2013, the first author interviewed 30 licensed reindeer herders across all 9 summer siidas in 1 district in Finnmark, Norway (Figure 1) with the help of a Saami field assistant. Participants were endowed with vouchers (see below) and were then asked to give these as anonymous gifts to other licensed herd owners in their district. Respondents were presented with a list of license owners in the district (collected by a combination of publicly available contact information and snowball sampling, whereby 1 participant suggested other potential participants) coded with randomly generated ID numbers. Respondents read the ID numbers of their desired gift recipients to the field assistant. This procedure aimed to minimize experimenter bias because the assistant was also a member of the district, although not a licensed herd owner.

We gave players 3 vouchers, each representing 5 L of gasoline. At the time, 1 L of petrol cost approximately NOK 15 (US\$2.54). Players could choose to give the vouchers to 1–3 other license owners—in multiples of 5 L. They were not allowed to keep anything for themselves; they had to give the vouchers to at least 1 recipient. Players also gave reasons for their distribution of gifts. We coded these open answers into 1–3 keywords, blind to the giver’s name, siida, and distribution of gifts (see [Supplementary Methods](#)). At the end of the experimental period, all recipients were given their

rewards in the form of cash because the vouchers were created for the purposes of this study and were not legal tender, although all gift decisions were framed in terms of liters of gasoline.

Communication was not allowed within the parameters of the experiment. However, due to the vagaries of the herding lifestyle, we were unable to conduct all interviews within a sufficiently short time to rule out the chance that herders did not communicate with one another.

Experimental materials were translated into Norwegian by an independent person and back-translated by the second author. The first and second authors agreed on the final translations. Norwegian and English materials are available on request.

## Kinship data

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

## Herd size data

Herd sizes held by individual license owners were collected from data published by the Norwegian Broadcasting Corporation (*Norsk rikskringkasting AS*; [Aslaksen 2014](#)). We used the numbers of reindeer held by individuals in 2012—the most recent data available. We were able to match herd sizes for 62 of the 75 people in our database, not achieving complete coverage due to changes in license owners between 2012 and our study period. Herd sizes were group-mean centered across the district.

## Statistical analysis

We fitted generalized estimating equation (GEE) models to all potential gift-giving dyads, where the egos were the 30 gift game participants and alters were the 75 licensed owners, giving  $30 \times (75 - 1) = 2220$  possible dyads. The binary response variable in all models was whether or not a gift was given within a dyad. We present unstandardized and standardized estimates, where in the latter case, binary factors were mean centered and continuous variables were standardized over 2 standard deviations (SDs) to allow estimates to be compared within models, following the recommendations of [Gelman \(2008\)](#) and [Schielzeth \(2010\)](#).

GEE is a population-averaged approach that accounts for multiple observations of each ego by clustering standard errors (SEs). We specified an exchangeable working correlation matrix, which models the dependence of observations within clusters. GEE does not use full likelihood estimates, so we computed and compared the quasi-likelihood under the independence model information criterion for model selection ([Pan 2001](#)). Note that we did not fit models containing the individual-level predictors gathered from our questionnaires since doing so would have dramatically reduced the number of dyads in our analysis.

Analyses were conducted in R 3.2.0 ([R Core Team 2012](#)). Details of packages and additional software used, as well as where to download archived data and analysis code, are available in the [Supplementary Material](#).

## RESULTS

### Description of the district and the gift network

Sixty-one of the 75 herd owners in the district were male, with a median age of 53 (see [Supplementary Figure S1](#) for the age

distribution and [Supplementary Table S1](#) for descriptive statistics). The median number of reindeer owned by herders in the district in 2012 was 456.5, ranging between 55 and 1604 reindeer ([Supplementary Figure S2](#)). The 30 herders interviewed gave 71 gifts to 43 people ([Figure 2a](#)), some of whom were also participants. Of the 71 gifts, 45 (63.4%) were given to members of the same summer siida. A significantly higher proportion of gifts were given within siidas ( $\chi^2 = 4.563$ ,  $P = 0.033$ ). The majority of gifts (59) were for 5L of gasoline and were given by 18 of the 30 people interviewed. Five gifts, given by 5 separate individuals, were worth 10L, whereas 7 gifts, given by 7 different people, were for 15L.

The number of gifts received by individuals (in-degree) ranged from 0 to 7 (median = 1, mean = 0.95, SD = 1.16). We do not report the number of gifts given (out-degree) or include it in the models since only the 30 people interviewed were able to give gifts. Gift givers received more gifts; that is, out-degree significantly correlated with in-degree (Pearson's product-moment correlation,  $r = 0.415$ ,  $P < 0.001$ , 95% confidence interval [CI] [0.208, 0.587]). One outlier received 7 gifts totaling 50L of gasoline—twice as much as the second most popular herder. The reasons given for his gifts fell on a wide spectrum, from “Deserves it” and “Good reindeer herder” to “Always empty of fuel.”

Ten gifts (28.2%) were reciprocated ([Figure 2b](#)), despite communication not featuring in the experiment. Of the reciprocated gifts, only 1 was given to a member of another siida. In this case, both were males living in the same town who clearly had a history of working together based on their stated reasons for giving the gifts. [Supplementary Table S2](#) shows descriptive statistics for the gift network.

Siida leaders did not receive more gifts than others ([Table 1](#)). There was a significant sex difference between number of gifts received where males on average received more (Mann–Whitney test,  $W = 258.500$ ,  $P = 0.015$ ), although the sample contains substantially fewer females (4 of the 43 herders who received gifts).

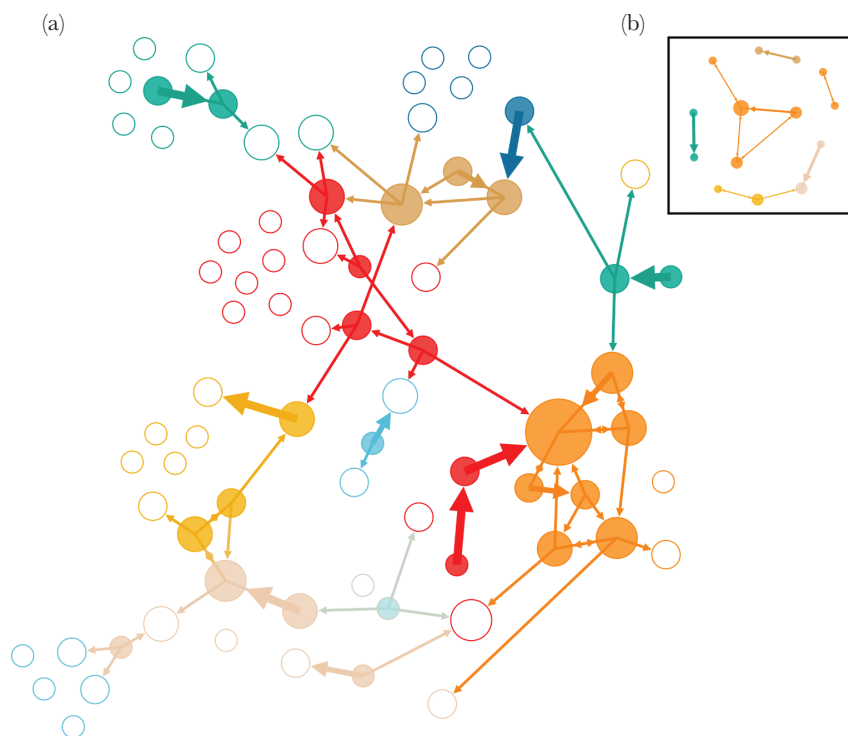
### Relatedness in the district

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

### Analysis of gift giving

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

In the best-fitting GEE model ([Table 3](#)), belonging to the same summer siida as the other person in a dyad was the strongest predictor of gift giving (standardized log odds = 1.875, SE = 0.447)



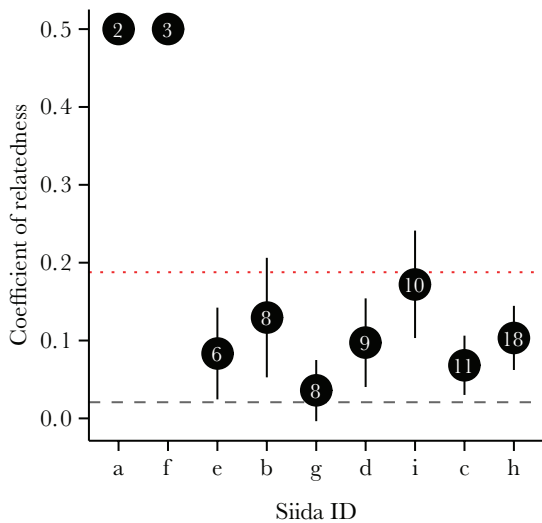
**Figure 2**

Gift networks showing license owners in the district (nodes) colored by siida membership for (a) the entire district and (b) reciprocated gifts only. Filled circles represent the 30 license owners interviewed for this study. Edges are gifts, where edge thickness corresponds to gift size (5, 10, or 15L of gasoline), and color shows the siida from which the gift came.



**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 |



**Figure 3**  
Relatedness within the 9 siidas. Points are the mean coefficients of relatedness between licensed herd owners within each siida. Error bars show SD. Data are ordered, from left to right, in increasing group sizes (also shown within the data points). The gray dotted line shows the mean relatedness in the entire district (i.e., across all siidas); the dotted line shows the grand mean (i.e., mean of the mean within-siida relatedness coefficients).

compared with genetic relatedness (standardized log odds = 0.691, SE = 0.187). Note that these estimates are only biologically interpretable in their unstandardized form (Table 3).

From the full set of candidate models, the model containing only a term for siida membership (model 5 in Supplementary Table S4) fitted the data better than the model containing only a term for relatedness (model 6 in Supplementary Table S4). Models with an interaction between relatedness and siida membership (models 3 and 4 in Supplementary Table S4) and models containing herd sizes for the potential giver and recipient (models 2 and 4 in Supplementary Table S4) did not provide a better fit compared with the model containing additive terms for relatedness and siida membership (Table 3; model 1 in Supplementary Table S4).

We hypothesized that gifts would preferentially be given to younger herders within families (where gifts to younger herders were scored as a negative age difference). Contrary to expectations, gifts were not preferentially given to younger kin ( $\chi^2_1 = 0.05, P = 0.82$ ; Table 4). Age also had no significant effect on the number of gifts received (Spearman rank correlation,  $\rho = -0.140, P = 0.279$ ; Figure 4).

**Why give?**

Table 5 lists the coded translations of all reasons for giving gifts (Supplementary Table S5 provides the full text). The most common category ( $n = 24$ ) for giving a gift, regardless of kinship and siida

**Table 2**  
Counts of people receiving a gift or not, split by whether they are genetic relatives and/or members of the same 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       | 1834           | 23  | 1.2              |

**Table 3**  
Results from the best-fitting GEE

| Parameter   | Log odds (SE)  | Standardized log odds (SE) |
|-------------|----------------|----------------------------|
| 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)              |

Column 2 shows unstandardized log odds (SE); column 3 shows log odds (SE) standardized over 2 SD (Schielzeth 2010; Gelman 2008) so that the effect sizes can be directly compared. The predictors are the coefficient of relatedness,  $r$ , and a binary factor coding whether or not a dyad belongs to the same summer siida. The siida membership predictor most strongly predicts gift giving, although relatedness also has a positive effect. See Supplementary Table S4 for a comparison of all candidate models.

**Table 4**  
Number of gifts given to older or younger herders, split by whether or not the dyads were kin

| Gift to | Older | Younger | Unknown |
|---------|-------|---------|---------|
| Kin     | 19    | 13      | 1       |
| Nonkin  | 16    | 14      | 8       |

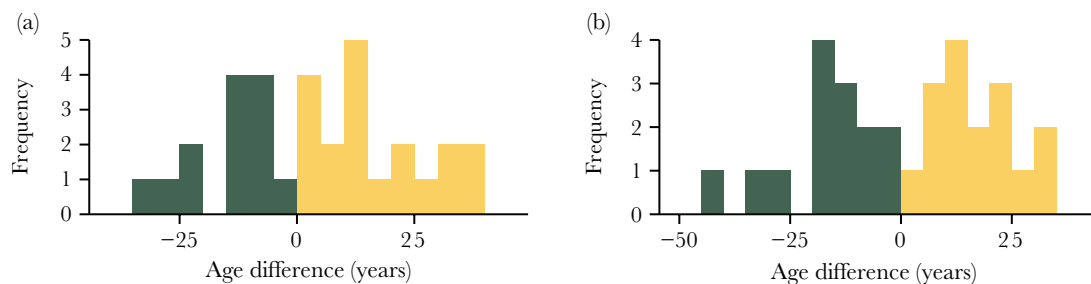
membership, was current or future reciprocity. Thirteen gifts were given to recipients with good reputations.

An interesting case is the gifts given to nonkin belonging to other siidas. Over half of these gifts were split between those with reputations of being a “good herder” and young license owners who were newly established in reindeer husbandry.

**DISCUSSION**

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

There was no preference for giving gifts to younger herders within families (Table 4, Figure 4), contrary to our prediction



**Figure 4**

Age differences between givers and receivers of gifts where the pair are (a) kin or (b) nonkin. Positive values represent gifts given to older herders whereas negative values represent gifts to younger herders. No gifts were given to herders of the same age.

**Table 5**

**Coded reasons for giving gifts, split by whether or not the recipient is a genetic relative and/or belongs to the same summer siida**

| Reason category               | Kin in same siida | Nonkin in same siida | Kin in another siida | Nonkin 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                    |                         | 11    |
| No reason given               | 4                 | 1                    |                      | 1                       | 6     |
| Total                         | 30                | 15                   | 3                    | 23                      |       |

derived from parental investment theory regarding the flow of resources down generations within families. The absence of this pattern is likely due to participants not viewing the gifts as resources to be invested in younger relatives. It should be noted that some close relatives (such as a son and heir) might be jointly herding with the herd owner and therefore not eligible to receive a gift as they are not yet a licensed herd owner themselves.

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

While the stated reasons for why participants gave particular gifts were *ad hoc*, we argue they provide valuable insight into behavior in the games. Thirteen of the 71 gifts (18.3%) were given to those with the reputation of being a “good herder” (Table 5), something important to Saami pastoralists (Paine 1970). Gifts were not given preferentially to siida leaders (Table 2). In this study, we were not able to control for potential confounds such as prestige, skills, experience, etc. that may have biased gift-giving behaviors, although we did control for herd size as a proxy of wealth. Given this indication that cultural factors such as reputation may be important mediators of cooperative behavior for Saami reindeer herders, future work could attempt to define measures of reputation and prestige that are meaningful to this population. One approach would be to

ask herders, preferably in group interviews, to rank others by their experience, skill, history of good decisions, etc. These culturally derived measures could then be linked to quantitative measures of wealth and used to predict gift giving.

Gifts in our study were small and anonymous, and communication between participants was not allowed. This makes it unlikely that costly signals, reputation, or competitive altruism were driving the observed behaviors, although we were unable to test this formally. However, indirect reciprocity and competitive cooperation play important roles in human social groups, especially when cooperative behaviors are public (Barclay 2013; Sylwester and Roberts 2013). Our study investigated the factors underlying partner choice but did not look at mechanisms of partner control that might enforce or maintain cooperation. Future work should attempt to understand the relative importance of partner control compared with partner choice as well as the roles of indirect reciprocity, partner choice and direct reciprocity (especially reciprocity based on reputation, i.e., competitive cooperation) in real-world contexts.

This work represents a first step toward quantifying the forms and diversity of cooperative strategies among Saami people. Saami pastoralists face many social and ecological challenges. Competition for access to winter pastures may explain herd accumulation as the only viable risk-reducing strategy, although the efficacy of this strategy may be limited by quotas on maximum herd size (Næss and Bårdsen 2010). This suggests the future of reindeer husbandry presents a collective action problem for the herders: one that may be solved from within the community without necessitating the privatization of pastures (Bjørklund 1990; Marin 2006; Hausner et al. 2012). At present, management policies seem to be designed to attain sustainability by targeting only individual reindeer owners (e.g., providing subsidies to increase slaughter rates), while disregarding the cooperative nature of reindeer pastoralism (Næss et al.

2012). Understanding the mechanisms of cooperation in this population will be an important task for its future viability.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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## REFERENCES

- Aktipis CA. 2011. Is cooperation viable in mobile organisms? Simple Walk Away rule favors the evolution of cooperation in groups. *Evol Hum Behav.* 32:263–276.
- Aktipis CA, Cronk L, Aguiar R. 2011. Risk-pooling and herd survival: an agent-based model of a Maasai gift-giving system. *Human Ecol.* 39:131–140.
- Allard C. 2011. The Nordic countries' law on Sámi territorial rights. *Arctic Rev Law Polit.* 3:159–183.
- Anonymous. 2013. Ressursregnskap for Reindriftsnæringen (Ecological statistics of reindeer husbandry). Alta (Norway): Reindriftsforvaltningen. p. 114.
- Aslaksen E. 2014. Her er reintallene. NRK Sápmi Available from: <http://www.nrk.no/sapmi/her-er-reintallene-1.12050012> (Accessed 4 May 2015).
- Barclay P. 2013. Strategies for cooperation in biological markets, especially for humans. *Evol Human Behav.* 34:164–175.
- Barclay P, Willer R. 2007. Partner choice creates competitive altruism in humans. *Proc Biol Sci.* 274:749–753.
- Bergman I, Liedgren L, Östlund L, Zackrisson O. 2008. Kinship and settlements: Sami residence patterns in the Fennoscandian alpine areas around A.D. 1000. *Arctic Anthropol.* 45:97–114.
- Bjerkli B. 2010. Landscape and resistance. The transformation of common land from dwelling landscape to political landscape. *Acta Borealia.* 27:221–236.
- Bjørklund I. 1990. Sámi reindeer pastoralism as an indigenous resource management system in Northern Norway: a contribution to the common property debate. *Dev Change.* 21:75–86.
- Dyson-Hudson R, Dyson-Hudson N. 1980. Nomadic pastoralism. *Annu Rev Anthropol.* 9:15–61.
- Fratkin E. 1986. Stability and resilience in East African pastoralism: the Rendille and the Ariaal of northern Kenya. *Human Ecol.* 14:269–286.
- Gelman A. 2008. Scaling regression inputs by dividing by two standard deviations. *Stat Med.* 27:2865–2873.
- Hamilton WD. 1964. The genetical evolution of social behaviour. I. *J Theor Biol.* 7:1–16.
- Hansen KL, Melhus M, Lund E. 2010. Ethnicity, self-reported health, discrimination and socio-economic status: a study of Sami and non-Sami Norwegian populations. *Int J Circumpolar Health.* 69:111–128.
- Hausner VH, Fauchald P, Jernsletten JL. 2012. Community-based management: under what conditions do Sámi pastoralists manage pastures sustainably? *PLoS One.* 7:e51187.
- Kaplan H. 1994. Evolutionary and wealth flows theories of fertility: empirical tests and new models. *Popul Dev Rev.* 20:753–791.
- Lehmann L, Keller L. 2006. The evolution of cooperation and altruism—a general framework and a classification of models. *J Evol Biol.* 19:1365–1376.
- Marin AF. 2006. Confined and sustainable? A critique of recent pastoral policy for reindeer herding in Finnmark, Northern Norway. *Nomadic Peoples.* 10:209–232.
- Næss MW. 2012. Cooperative pastoral production: reconceptualizing the relationship between pastoral labor and production. *Am Anthropol.* 114:309–321.
- Næss MW, Bårdsen BJ. 2010. Environmental stochasticity and long-term livestock viability—herd-accumulation as a risk reducing strategy. *Human Ecol.* 38:3–17.
- Næss MW, Bårdsen BJ. 2013. Why herd size matters—mitigating the effects of livestock crashes. *PLoS One.* 8:e70161.
- Næss MW, Bårdsen BJ, Fauchald P, Tveraa T. 2010. Cooperative pastoral production—the importance of kinship. *Evol Human Behav.* 31:246–258.
- Næss MW, Bårdsen BJ, Tveraa T. 2012. Wealth-dependent and interdependent strategies in the Saami reindeer husbandry, Norway. *Evol Human Behav.* 33:696–707.
- Næss MW, Fauchald P, Tveraa T. 2009. Scale dependency and the “marginal” value of labor. *Human Ecol.* 37:193–211.
- Nietupski PK. 2012. Labrang Monastery: a Tibetan Buddhist community on the inner Asian borderlands, 1709–1958. Plymouth (UK): Lexington Books.
- Noë R, Hammerstein P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav Ecol Sociobiol.* 35:1–11.
- Nowak MA. 2006. Five rules for the evolution of cooperation. *Science.* 314:1560–1563.
- Paine R. 1970. Lappish decisions, partnerships, information management, and sanctions: a nomadic pastoral adaptation. *Ethnology.* 9:52–67.
- Paine R. 1994. Herds of the tundra: a portrait of Saami reindeer pastoralism. London: Smithsonian Institution Press.
- Pan W. 2001. Akaike's information criterion in generalized estimating equations. *Biometrics.* 57:120–125.
- Pape R, Löffler J. 2012. Climate change, land use conflicts, predation and ecological degradation as challenges for reindeer husbandry in northern Europe: what do we really know after half a century of research? *Ambio.* 41:421–434.
- R Development Core Team. 2014. R: a language and environment for statistical computing [Internet]. Vienna (Austria): R Foundation for Statistical Computing. Available from: <http://www.r-project.org>.
- Schielzeth H. 2010. Simple means to improve the interpretability of regression coefficients. *Methods Ecol Evol.* 1:103–113.
- Stiff C, Van Vugt M. 2008. The power of reputations: the role of third party information in the admission of new group members. *Group Dyn: Theory Res Pract.* 12:155–166.
- Sylwester K, Roberts G. 2013. Reputation-based partner choice is an effective alternative to indirect reciprocity in solving social dilemmas. *Evol Human Behav.* 34:201–206.
- Trivers R. 1971. The evolution of reciprocal altruism. *Q Rev Biol.* 46:35–57.
- Tveraa T, Ballesteros M, Bårdsen BJ, Fauchald P, Lagergren M, Langeland K, Pedersen E, Stien A. 2013. Beregning av produksjon og tap i reindriften—NINA Rapport 938 Tromsø (Norway): Norsk Institutt for Naturforskning.
- Upton C. 2008. Social capital, collective action and group formation: developmental trajectories in post-socialist Mongolia. *Human Ecol.* 36:175–188.
- Wang J, Suri S, Watts DJ. 2012. Cooperation and assortativity with dynamic partner updating. *Proc Natl Acad Sci USA.* 109:14363–14368.
- West SA, Griffin AS, Gardner A. 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J Evol Biol.* 20:415–432.