

A Friend in Need is a Friend Indeed: Need-Based Sharing, Rather than
Cooperative Assortment, Predicts Experimental Resource Transfers
among Agta Hunter-Gatherers

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Ethics

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Data Availability

The data and code associated with this research is available via figshare at [10.6084/m9.figshare.6960998](https://doi.org/10.6084/m9.figshare.6960998) (this link will be made active upon publication).

Competing Interests

We have no competing interests.

Authors' Contributions

A.B.M. and R.M. conceived the project; D.S., M.D., K.M., A.E.P. and A.B.M. collected the data; D.S. analysed the data; D.S., A.B.M., R.M., and L.V., wrote the manuscript with the help of all other authors. All authors contributed substantially to revisions and gave final approval for publication.

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8 among Agta Hunter-Gatherers
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14 *Abstract:* Despite much theorizing, the evolutionary reasons why humans cooperate
15 extensively with unrelated individuals are still largely unknown. While reciprocity
16 explains many instances of non-kin cooperation, much remains to be understood. A
17 recent suite of models based upon ‘cooperative assortativity’ suggest that non-kin
18 cooperation can evolve if individuals preferentially assort with certain cooperative
19 phenotypes, such as helping those who help others. Here, we test these assortative
20 hypotheses among the Agta, a population of Filipino hunter-gatherers, using an
21 experimental resource allocation game in which individuals divide resources
22 between themselves and camp-mates. Individuals preferentially shared with less
23 cooperative individuals, arguing against cooperative assortativity as a mechanism
24 sustaining resource transfers in this population. Rather, sharing was often based on
25 the recipient’s level of need, in addition to kin-based transfers and reciprocal sharing.
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27 Contrary to several recent theoretical accounts, in this real-world setting we find no
28 evidence for cooperative assortativity influencing patterns of cooperation. These
29 results may reflect the demands of living in a foraging ecology characterized by high
30 resource stochasticity, necessitating need-based sharing as a system of long-term
31 reciprocity to mitigate repeated subsistence shortfalls.
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51 *Keywords:* Cooperation; Assortativity; Need-Based Sharing; Reciprocity; Hunter-
52 Gatherers; Experimental Games.
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1. Introduction

The question of why organisms display cooperative behavior – defined as a behavior which evolved to benefit others (West, Griffin, & Gardner, 2007b) – has been central to biology for over 50 years (Hamilton, 1964; Nowak, 2006). Although kin selection, where cooperation between relatives provides indirect fitness benefits (Hamilton, 1964), and reciprocity, where repeated cooperative interactions lead to greater long-term pay-offs than short-term defection (Trivers, 1971), explain many instances of cooperation throughout the animal kingdom (West, Griffin, & Gardner, 2007a), they appear insufficient to explain the full range of observed cooperative behavior. This is especially true in humans where cooperation is often between unrelated individuals who, particularly in modern market-based economies, may not interact again in the future (Nowak & Sigmund, 2005).

One potential theory to explain the human propensity for cooperation is indirect reciprocity, which suggests that organisms may help others if this increases their reputation as a cooperative individual, resulting in greater cooperation from others in the future (Alexander, 1987; Nowak & Sigmund, 1998, 2005; Panchanathan & Boyd, 2003). Crucially, the evolution of indirect reciprocity depends upon preferential cooperation towards these cooperative individuals ('helping those who help others'). Theories such as competitive altruism (also known as 'reputation-based partner choice') make similar predictions, such that cooperative individuals should be preferentially cooperated with (Roberts, 1998; Sylwester & Roberts, 2013). However, the mechanisms are distinct; competitive altruism is based on the principle of signaling cooperativeness to form future mutually-beneficial cooperative ventures, while indirect reciprocity does not require future repeated interactions. Nonetheless,

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121 both accounts are theories of ‘cooperative assortativity’, which suggest that
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123 cooperation can evolve if individuals preferentially cooperate with cooperative others.
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126 In support of these theories, several lab studies have shown that cooperative
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128 individuals receive more help from others, even if they have never previously
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130 interacted (Milinski, 2016; Raihani & Barclay, 2016; Sylwester & Roberts, 2013).
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132 However, whether these patterns extend to real-world interactions where multiple
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134 forms of information can also be used on which to base cooperation, such as kinship
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136 or previous interactions, is largely an open question. Field studies have shown that
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138 individuals respond to threats to their reputation with increased cooperation (Yoeli,
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140 Hoffman, Rand, & Nowak, 2013), while sellers on eBay with a good reputation are
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142 more likely to attract customers (Livingston, 2005). However, whether people
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144 selectively cooperate with more cooperative individuals remains under-explored in
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146 real-world settings. Small-scale populations, where group sizes are small and acts of
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148 cooperation frequent – including food-sharing (Gurven, 2004), childcare (Hrdy,
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150 2009), cooperative foraging (Hill, 2002), labor-sharing (Jaeggi, Hooper, Beheim,
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152 Kaplan, & Gurven, 2016) and political coalitions (Patton, 2005) – are particularly
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154 useful to explore how factors such as cooperativeness, kinship, reciprocity, and other
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156 considerations, influence cooperative decision-making. Research in small-scale
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158 societies, particularly hunter-gatherers, may also provide insights regarding the
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160 social and ecological bases of human cooperative evolution prior to the development
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162 of agriculture and large-scale societies (Lee & Daly, 1999).
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166 In several foraging populations the most cooperative individuals, such as those
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168 who share the most food, do not necessarily receive more in return (Bliege Bird,
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170 Bird, Smith, & Kushnick, 2002; Kaplan & Hill, 1985). Among the Hadza, using a
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172 Public Goods Game to measure cooperation, the most cooperative individuals were
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180 not more likely to be given resources or nominated as social partners (Apicella,
181 Marlowe, Fowler, & Christakis, 2012). However, among Dominican bay oil
182 producers, individuals with a reputation for cooperativeness were preferred
183 recipients of cooperation (Macfarlan, Remiker, & Quinlan, 2012), while Hiwi who
184 invested more time in foraging received more resources than others (Gurven, 2006).
185 Although this pattern was not found among Ache foragers (Gurven, 2006), Ache who
186 consistently provisioned others were more likely to receive resources when they
187 were sick or injured (Gurven, Allen-Arave, Hill, & Hurtado, 2000). In summary, there
188 is only partial support for models of cooperative assortativity in small-scale societies.
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199 A related theory also based on assortativity posits that cooperation can evolve
200 if agents assort according to cooperative homophily; that is, cooperating with others
201 of a similar cooperative level (Apicella et al., 2012). However, it is unclear why, in the
202 absence of other mechanisms, non-cooperators would preferentially assort with
203 other non-cooperators. While cooperative homophily is an *outcome* of the above
204 processes based on cooperative assortment, via mechanisms such as 'walk away' or
205 partner choice (Aktipis, 2004; Lewis, Vinicius, Strods, Mace, & Migliano, 2014;
206 McNamara, Barta, Fromhage, & Houston, 2008), these mechanisms do not require
207 that defectors actively seek out other defectors. Nonetheless, Hadza individuals
208 were more likely to nominate to live and cooperate with others of a similar
209 cooperative level to themselves, suggesting that assortativity by cooperative
210 homophily may occur and is not merely an outcome of other assortative processes
211 (Apicella et al., 2012). There are therefore two pathways by which cooperative
212 assortment may facilitate the evolution of cooperation: cooperating with the most
213 cooperative individuals (indirect reciprocity and competitive altruism) and
214 cooperating with others of a similar cooperative level (cooperative homophily).
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239 As discussed above, contrary to expectations based on cooperative
240 assortativity in several populations the most cooperative individuals are not preferred
241 cooperative partners. This behavior may reflect need-based sharing, where those in
242 greater need receive more assistance (Aktipis, Cronk, & de Aguiar, 2011). In studies
243 of forager food-sharing, those with a larger family or with low calorific production
244 relative to family consumption, and therefore in greater need, tend to receive more
245 resources (Allen-Arave, Gurven, & Hill, 2008; Gurven, Hill, Kaplan, Hurtado, & Lyles,
246 2000), while Agta foragers were more likely to receive resources from others if they
247 were unable to procure resources on a given day (Dyble et al., 2016). Consistent
248 with this, Agta in less need were more cooperative in an experimental game (Smith
249 et al., 2016), while lower socioeconomic status has been associated with reduced
250 cooperation in developed countries (Silva & Mace, 2014). Similarly, in an
251 experimental game among Fijians, the most common reason for sharing was the
252 relative need of the recipient (Gervais, 2017).
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269 However, in the absence of other mechanisms need-based sharing is a
270 description of cooperation, not an adaptive evolutionary explanation; a strategy of
271 altruistic donations to those in need, without any subsequent future fitness gain, is
272 unlikely to be selected for. This situation is comparable to the 'Banker's Paradox'
273 (Tooby & Cosmides, 1996), where the individuals most in need of a loan (or
274 resources) are the least likely to receive them because they are a greater 'credit risk'
275 and less likely to repay the loan. Nonetheless, these observed need-based transfers
276 may be adaptive if they reflect direct reciprocity, where individuals with resources
277 help those in need – as the costs to giving are low and the benefits to the recipient
278 are high – which may be reciprocated in the future (Trivers, 1971). Although
279 research on forager food-sharing has indicated the presence of need-based
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298 transfers (Allen-Arave et al., 2008; Gurven, 2004; Hooper, Gurven, Winking, Kaplan,
299 & Hooper, 2015), from these observational studies it is difficult to assess whether
300 these patterns are a result of giving to those in need (i.e., cooperation) or needy
301 individuals taking resources from those with more resources, as predicted by models
302 of tolerated theft (Blurton Jones, 1987; Winterhalder, 1996). Experimental studies
303 which dissociate unsolicited giving from tolerated theft can be used to help answer
304 these questions.
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313 Here we explore resource transfers among Agta hunter-gatherers to test
314 predictions of indirect reciprocity/competitive altruism and cooperative homophily.
315 We use a novel experimental game in which resources are divided between self and
316 known camp-mates. Using this approach, we previously found that individuals
317 preferentially shared resources with both kin and reciprocal partners (Smith et al.,
318 2016). We now extend this analysis to explore how an individual's cooperativeness
319 influences their probability of receiving resources from others. Specifically, we test
320 whether the Agta: i) preferentially share resources with cooperative individuals (in
321 line with theories of indirect reciprocity and competitive altruism); and ii) share
322 resources with others of a similar cooperative level (as predicted by cooperative
323 homophily).
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339 2. Methods

340 2.1. *Ethnographic Background*

341 This study focuses on two Agta sub-populations, the Palanan Agta (~1,000
342 individuals) and the Maconacon Agta (~250 individuals) from the remote Northern
343 Sierra Madre Natural Park in northeast Luzon, the Philippines. They subsist
344 predominantly as hunter-gatherers, engaging in hunting, fishing and gathering of wild
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357 resources, but also in wage or agricultural labor when available. Of the time spent in
358 economic activities, 77% concerned foraging behavior, predominantly fishing (54%),
359 but also gathering (20%) and hunting (3%), while the remaining 23% of time was
360 spent engaged in non-foraging behavior, such as cultivation (13.5%) and wage labor
361 (9.5%; Page et al., 2016). Game and fish are traded with local agricultural non-Agta
362 populations for rice, other carbohydrates and luxury goods. Food-sharing is a regular
363 daily occurrence (Dyble et al., 2016). Camp sizes vary between solitary dwellings
364 (seven individuals) to large camps with 26 houses (156 individuals), with an average
365 of seven houses (49 individuals).

377 2.2. *Data Collection*

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379 An experimental resource allocation game – the ‘Sharing Game’ (SG) – was
380 played with 290 Agta (mean age=37, range=16-70, males=140) from 18 camps (324
381 Agta were included as potential recipients, but 34 Agta did not play the game due to
382 either moving camp or subsequently deciding not to take part). Participants were
383 shown their own picture, along with a maximum of 10 other randomly-selected adults
384 from camp (individuals from camps with ≤ 10 other camp-mates were shown all other
385 adults) and given a number of small wooden tokens (each representing 125g of rice;
386 approximately a meal for one individual) equal to the number of camp-mate photos
387 (i.e., in a camp of 11 individuals (10 camp-mates plus ego) each player would be
388 given 10 tokens, while in a camp of nine individuals (eight camp-mates plus ego)
389 each player would be given eight tokens). This was chosen so that not all pictures,
390 including ego, could receive rice. For each token, participants had to decide whether
391 to keep the rice (placing the token on their own picture) or give it to a camp-mate of
392 their choosing (placing the token on the camp-mate’s picture). For each resource
393 given, participants were asked why that recipient was selected. This was repeated
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416 until no tokens remained. Prior to leaving camp, the amount of rice earned by each
417 participant was given to them (the amount they kept for themselves plus the amount
418 they received from others).
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423 Decisions were made in private, with just the experimenter, translator and
424 participant aware of an individual's decisions. Other camp-mates were not made
425 aware of any other player's decisions. The experimenter read the game instructions
426 in English, which were then translated into the participant's local language (Tagalog,
427 Paranan or Ilocano). All field assistants were trained prior to fieldwork to ensure that
428 they understood the game rationale and procedures. Approximately ten days were
429 spent at each Agta camp. Upon entering the camp, Agta were informed that
430 experimental sharing games would be played with all consenting adult members of
431 the camp. Games were conducted on the last few days in order to maximize
432 familiarity with the researchers and facilitate trust, but also to minimize the potential
433 for collusion between camp-mates. We do not believe that this occurred, as there
434 were no sudden shifts in game behavior over time.
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449 This non-anonymous game structure was used to assess both levels of
450 cooperative behavior and patterns of cooperation (i.e. who individuals share with,
451 such as kin or those who shared reciprocally). The game is similar to the 'Gift Game'
452 conducted in several populations (Apicella et al., 2012; Chaudhary et al., 2015; He,
453 Wu, Ji, Tao, & Mace, 2016; Thomas, Næss, Bårdsen, & Mace, 2015) where
454 participants are given resources (e.g. sticks of honey) and have to decide who to
455 give it to. Although the game used here is structurally alike, it possesses the added
456 rule that participants could either keep a share for themselves if they wished or give
457 it to a camp-mate of their choosing. Although the Gift Game allows the choice of
458 giving to multiple individuals, it does not measure levels of cooperation as there is no
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475 option for keeping gifts for one's self, meaning that there is no conflict between
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477 individual and group interests. On the other hand, although traditional economic
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479 games, such as the Ultimatum Game, Dictator Game, and Public Goods Game,
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481 measure levels of cooperation, they include only anonymous partners, and therefore
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483 ignore the role that differences in relationship have on cooperation (Rucas, Gurven,
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485 Kaplan, & Winking, 2010) and cannot be used to explore who individuals
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487 preferentially share resources with.
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490 After preliminary trials with different resources, it was decided that rice would
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492 be used as the game resource as it is highly sought-after by the Agta and therefore
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494 carries enough value to cause a dilemma when deciding whether to share or not.
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496 Initial trials with other goods, such as honey sticks, were perceived to have little
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498 value (and were freely distributed to children). After discussing with the Agta which
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500 resources were most valued, rice was the unanimous choice. The Agta do not grow
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502 their own rice (although they may harvest it for neighboring agricultural populations),
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504 and although it is a non-foraged commodity introduced by non-Agta agricultural
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506 populations it is one of the Agta's primary sources of calories (when available) and is
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508 highly valued.
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511 512 *2.3. Statistical Analyses* 513

514 The response variable was coded in a matrix as '1' if ego (the giver) gave to
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516 alter (the recipient) and '0' if not (note that although givers could theoretically donate
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518 more than one gift to a single recipient, in practice only one individual gave two
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520 tokens to the same individual, hence the use of a binary term here). Between-camp
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522 dyads and camp-mates not presented to ego were coded as missing. The main
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524 independent variable of interest was 'alter cooperation score', reflecting the
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526 recipient's level of cooperativeness. Each individual possessed a score (between 0%
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534 and 100%) indicating the percent of gifts donated to others, with 0% meaning no
535 resources shared with camp-mates (all gifts kept for self) and 100% meaning all
536 resources shared with camp-mates (no gifts kept for self). For each individual this
537 was centered around the mean for each camp (camp mean minus individual score),
538 so that between-camp differences in cooperation did not confound within-camp
539 sharing patterns. Individuals with a positive score gave more than others in camp
540 (i.e., they were more cooperative than the camp average). 'Cooperative homophily'
541 was also included as a predictor variable to explore whether individuals gave to
542 others of a similar cooperative level. This was constructed by assessing the
543 difference in cooperativeness between ego and alter. For instance, a difference of '0'
544 meant that both individuals gave the same, while '30' indicated a difference,
545 irrespective of direction, of 30 percentage points between ego and alter. As reported
546 previously (Smith et al., 2016), the average amount of rice kept in the Sharing Game
547 was 62.6% (SD=30.5), which varied considerably between camps, with individuals
548 from the most cooperative camp keeping on average only 26.8% of rice for
549 themselves, while in the least cooperative camp no camp-mates shared any
550 resources (figure 1 in *ibid.*).

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571 Following similar methodologies in other hunter-gatherer populations (Apicella
572 et al., 2012), we make the assumptions that: i) individuals know who the most
573 cooperative people are; and ii) that this is reflected in how much individuals share in
574 the game. Given that the Agta have known their camp-mates for most of their lives
575 we believe that the first assumption is plausible. Decisions about an individual's
576 trustworthiness are made within a fraction of a second (Willis & Todorov, 2006),
577 while strangers could predict who would cooperate after interacting for only 30
578 minutes (Frank, Gilovich, & Regan, 1993). Multiple years of exposure are likely to
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593 result in more accurate judgments regarding cooperativeness among the Agta.
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595 Secondly, although traditional economic games, such as the Ultimatum, Dictator or
596 Public Good Games, often have questionable external validity (Gurven & Winking,
597 2008; Winking & Mizer, 2013; although see Peysakhovich, Nowak, & Rand, 2014),
598 we have previously demonstrated that these contextualized non-anonymous games
599 among the Agta mirror real-world food-sharing decisions (Smith et al., 2016; see also
600 Gervais, 2017). Individuals from camps who shared food reciprocally in the real-
601 world were both more likely to share resources in these games and to share these
602 experimental resources reciprocally, consistent with the idea that reciprocal sharing
603 requires producer control with individuals willing to share resources with others
604 (Smith et al., 2016). This suggests that the Agta's levels of cooperativeness in this
605 game likely reflect cooperativeness in the real-world, at least regarding food-sharing
606 decisions, providing some confidence that the second assumption is also valid.
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621 Additional variables included: kinship relation between ego and alter,
622 reciprocity, proximity, age (of ego, alter, and age difference) and sex (of ego, alter,
623 and whether same or different sex). Kinship relations were defined as: primary kin
624 (PK), with a relatedness coefficient of $r=0.5$ to ego; distant kin (DK), with a
625 relatedness coefficient between $r=0.03125$ (second cousins) and $r=0.25$ to ego;
626 spouse; spouse's primary kin/primary kin's spouse (SPK/PKS); spouse's distant
627 kin/other affines (SDK/OA), which includes distant kin of spouse or other affinal
628 relationships up to five steps away from ego (e.g., spouse's brother's wife's mother);
629 and non-relatives (NR), which includes everyone else without a kinship link to ego
630 (see Dyble et al., 2015 for further details). Each of these categories was compared
631 relative to resources given to non-kin. The matrix for reciprocity was the transpose of
632 the response variable (i.e., whether alter gave to ego), from which it is possible to
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652 assess whether individuals were more likely to share with camp-mates who also
653 shared with them. Although decisions in this game were made without knowing how
654 others behaved, we justify this definition of 'reciprocity' by noting that reciprocity
655 requires individuals sharing with camp-mates who they expect to share back in
656 return, which can be assessed using this experimental design. Proximity was coded
657 from one to four, reflecting increasing physical distance between ego and alter, with
658 categories of: living in the same house as ego (1); living in the house next to ego (2);
659 having a house between ego's and alter's (3); and living further away (4).
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669 In order to ensure that patterns of resource transfers were not confounded by
670 the amount an individual distributed, ego's cooperative score (% donated to others)
671 was included as a control variable in all models. As a consequence of the game
672 structure, reciprocity could not be measured for all individuals in larger camps,
673 resulting in 1,312 dyads (out of a total 2,752) containing the reciprocity variable.
674 Similarly, as not all 324 potential recipients played the game, alter cooperativeness
675 and cooperative homophily scores were only available for 2,530 dyads. Of these
676 1,312 dyads, the number of potential recipients in each kinship category is displayed
677 in table S1. Note also that even though 290 Agta participated in these games, these
678 analyses include only the 272 individuals with at least one potential reciprocal
679 partner.
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692 Analyses were conducted using the statistical software *R* 3.5.0 (R
693 Development Core Team, 2018). A generalized estimation equation (GEE) approach
694 was utilized to control for repeated data from the same individual (Zeger & Liang,
695 1986). Logistic regressions exploring whether ego gave to alter were conducted on
696 vectors containing the variables described above. Due to GEE analyses not utilizing
697 full-likelihood estimates, quasi-likelihood information criterion estimates (QIC; Pan,
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711 2001) were employed to compare model fit. A global model was constructed first
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713 containing all variables described above. Keeping ego cooperative score, age and
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715 sex constant in all models as control variables, all possible combinations of models
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717 containing the theoretically-relevant variables (kinship, reciprocity, proximity, alter
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719 cooperativeness, and cooperative homophily) were constructed and QIC values
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721 compared. Models within two QIC values of the top model were subsequently put
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723 forward for model averaging to account for model uncertainty and identify the factors
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725 most strongly associated with receiving resources (see ‘Supplementary Information’
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727 for further details of this model comparison approach). All models contained the
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729 same 1,312 dyads to ensure that QIC values were comparable between models.
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733 Continuous input variables were standardized over two standard deviations
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735 (SDs; Gelman, 2008). This standardization allows direct comparison of effect sizes
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737 between both continuous and binary variables, as well as between continuous
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739 variables on different scales. Unless otherwise stated, standardized estimates are
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741 used in text, while standardized and unstandardized estimates are displayed in
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743 tables (although only unstandardized coefficients are biologically meaningful;
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745 Schielzeth, 2010). To facilitate comprehension of effect sizes, log-odd coefficients
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747 are converted to odds ratios (OR) in text. Odds ratios for binary or categorical
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749 variables are compared to the reference, while odds ratios for continuous variables
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751 reflect a 2 SD difference.
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754 755 3. Results

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757 Out of 1,312 potential recipients, 492 received resources (37.5%). Of the 32
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759 candidate models, those within two QIC values of the top model are displayed in
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761 table 1. After model averaging, kinship, reciprocity and alter cooperativeness were
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763 each associated with sharing resources (figure 1; see also table S2 for log-odds
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770 estimates and confidence intervals). Consistent with a previous publication (Smith et
771 al., 2016), primary kin (OR=4.01) and distant kin (OR=1.78) were more likely to
772 receive resources than non-kin, while individuals also displayed reciprocity, as they
773 were more likely to nominate others who also gave to them (OR=1.68).
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779 A strong effect of alter cooperative score was reported, with individuals
780 increasingly likely to give to less cooperative individuals (figure 1). A 2 SD decrease
781 in alter cooperativeness was associated with an approximately 50% increase in the
782 likelihood of alter receiving resources (OR=1.58). No effects of cooperative
783 homophily or proximity were found. Other predictive effects included alter age, with a
784 2 SD increase in recipient age raising the probability of being given to by nearly 50%
785 (OR=1.49), and sex-similarity, with individuals of the same sex nearly twice as likely
786 to receive resources relative to opposite sex dyads (OR=1.89).
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796 In order to explore whether this effect of sharing with less cooperative camp-
797 mates varied by relatedness we compared the baseline global model (containing all
798 variables) to a model containing an interaction term between alter cooperativeness
799 and kinship. Compared to the global model, inclusion of an alter cooperativeness by
800 kinship interaction term resulted in a reduced model fit (global model QIC=1090.3;
801 interaction model QIC=1097), indicating that the effect of giving to less cooperative
802 individuals was approximately equivalent across all kinship categories.
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810 Although GEE models control for repeated observations of givers, they do not
811 control for repeated observations of recipients, which has the potential to bias
812 parameter estimates due to the structural non-independence of the data. Therefore,
813 to test the robustness of these results logistic mixed-effect models with both givers
814 and receivers as random effects were constructed and an identical model averaging
815 approach performed. This model is qualitatively identical to that of the GEE model,
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829 demonstrating the validity and robustness of these results (Table S3). Additionally, in
830 a simplified model containing just ego cooperative score as a fixed effect, along with
831 givers and receivers as random effects, the inclusion of camp as an additional
832 random effect did not improve model fit (camp-level random effect model
833 AIC=1125.8; model without camp-level random effect AIC=1123.8). This indicates
834 that any residual clustering of cooperative decision-making based on camp
835 membership is minimal and unlikely to bias parameter estimates, further highlighting
836 the robustness of the above findings.
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847 3.1. *Effect of Need on Resource Transfers*

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849 As discussed in the introduction, in several small-scale societies sharing with
850 less cooperative individuals (e.g., those who share less food than others) may
851 indicate need-based sharing. To directly explore the effect of need on resource
852 transfers, additional models were constructed using a composite 'recipient need'
853 variable, based on data from outside the game context. This was based on: i)
854 number of dependent offspring (those aged 15 or younger, as assessed from
855 genealogical interviews), as the amount of resources necessary to support a family
856 increases with the number of non-producing consumers in a household (Hill &
857 Hurtado, 2009); ii) resource availability (whether the household had any rice stored,
858 as assessed from household questionnaires), and iii) an age component, with all
859 individuals under 40 years of age treated as equally needy, followed by a monotonic
860 increase in need after this age. This age component was chosen because foraging
861 returns among hunter-gatherers tend to decline after this age (Dyble et al., 2016; Hill
862 & Hurtado, 2009), rates of morbidity and mortality increase (Kaplan, Hill, Lancaster,
863 & Hurtado, 2000) and individuals become weaker and more dependent on others
864 (Draper & Harpending, 1994), all of which are indicative of being in greater need.
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889 Comparable measures of need have been utilized in other studies exploring food-
890 sharing and cooperation more generally (e.g., Gurven, Hill, et al., 2000; Hames &
891 McCabe, 2007; Thomas et al., 2018).
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895 Continuous variables of family size and age were standardized over 2 SDs to
896 make them comparable with the binary resource availability variable (which was
897 standardized around its mean; Gelman, 2008). The average of these three
898 standardized variables was then taken to estimate an individual's level of need, with
899 a greater value indicating greater need. To demonstrate the validity of this composite
900 need variable, a linear regression controlling for sex found that individuals in need
901 were lighter than less-needy individuals, with a one unit increase in need predicting a
902 2.75 kilogram decrease in weight (95% CI: [-0.43; -5.06], $p=0.02$, $n=276$). After age
903 was also removed from subsequent analyses to avoid confounding with need, as the
904 two are highly correlated ($r=0.66$, $p<0.001$, $n=324$).
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916 Compared to a baseline model containing all predictor variables other than
917 need, the model with alter need possessed a superior model fit, over two QIC values
918 lower than the baseline (baseline model QIC=1093.3; need model QIC=1089.6). This
919 model found that individuals in greater need were more likely to receive resources
920 ($b=0.73$, 95% CI: [0.18; 1.29]), with a one unit increase in need associated with being
921 over twice as likely to receive resources (OR=2.08). Note that in this model we still
922 find an effect of sharing with less cooperative individuals ($b=-0.01$, 95% CI: [-0.002; -
923 0.017]). This effect of need appears largely due to sharing with older individuals, as if
924 the age component is removed from the composite need variable (keeping just
925 number of dependent offspring and stored resources) then the effect of need on
926 sharing, although still in the predicted direction, is much weaker ($b=0.3$, 95% CI: [-
927 0.19; 0.79]). Compared to the model including need, we also find that that an
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947 interaction term between need and kinship does not increase model fit (need model
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949 QIC=1089.6; interaction model QIC=1096.3), suggesting that this need-based
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951 sharing is directly towards kin and non-kin with equal frequency.
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954 3.2. *Reasons for Giving in the Sharing Game*

956 We also asked why individuals gave to recipients, resulting in 1,001 answers.
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958 These were categorized according to various criteria relevant to the evolution of
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960 cooperation, such as kinship, reciprocity, need, and personal qualities, among others
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962 (figure 2 and table S4; for a similar procedure, see Gervais, 2017; Thomas et al.,
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964 2015). The most common reason for selecting an individual was genetic relatedness,
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966 accounting for over one-quarter of all nominations, while affinal relatedness
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968 accounted for one-sixth of all nominations. Collectively, over 40% of reasons given
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970 were based on kinship. The second largest category (~25% of nominations) was
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972 need-based sharing, including reasons such as old age, pregnancy, having many
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974 children, weakness, inability to work, having no food, or simply to help them. Around
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976 one in ten nominations referred to reciprocity between ego and alter. Personal
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978 qualities, such as kindness, leadership and generosity, although present, were less
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980 frequently mentioned (8.4%).
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985 4. Discussion

987 These results demonstrate that experimental resource transfers among the
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989 Agta do not conform to predictions made by theories of cooperative assortativity. We
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991 fail to find evidence for both indirect reciprocity and cooperative homophily;
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993 individuals were neither more likely to select cooperative partners or those of a
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995 similar cooperative level. Rather, the Agta preferentially shared with less cooperative
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997 individuals, which may reflect need-based sharing. Accordingly, we also demonstrate
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1006 that individuals in need, particularly older Agta, were more likely to receive resources
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1008 (although an independent effect of sharing with less cooperative individuals was still
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1010 reported). This finding is bolstered by a qualitative analysis of the reasons individuals
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1012 gave for sharing, with approximately one-quarter of all reasons coded as need- or
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1014 helping-based (figure 2). Personal qualities, including kindness and generosity,
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1016 alongside other competencies such as leadership and foraging skills, were
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1018 mentioned three times less frequently than need-based reasons. The Agta may
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1020 therefore use reputations for kindness or generosity to some extent when deciding to
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1022 share with others, but sharing based on need appears to take precedence.
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1025 Since need-based sharing is a description of cooperation, not an adaptive
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1027 explanation, understanding the evolutionary function of these patterns is essential.
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1029 The lack of interaction between need and kinship suggests that resources in this
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1031 game were given to needy camp-mates regardless of relatedness, meaning that
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1033 indirect fitness benefits via kin selection cannot solely explain this need-based
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1035 sharing. Comparable results were reported among Ache foragers where need,
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1037 irrespective of relatedness, predicted real-world food-sharing (Allen-Arave et al.,
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1039 2008). As there was no possibility of individuals taking resources from others, the
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1041 current results also suggest that need-based sharing is not solely a consequence of
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1043 tolerated theft (although other aspects of need-based transfers outside this
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1045 experimental context may be explained by this). One potential functional explanation
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1047 concerns reciprocity, but on a longer time-scale than assessed here (although an
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1049 immediate effect of reciprocity was also observed). For instance, by helping those in
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1051 need now, where the costs to the actor are low and the benefits to the recipient high,
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1053 in the future where the roles may be reversed the former recipient may reciprocate
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1055 (Trivers, 1971). This may be particularly important in hunter-gatherer contexts where
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1065 individual stochasticity in resource acquisition is high, combined with a life history
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1067 where in families with many dependent offspring are frequently at a net deficit and in
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1069 need of resources (Hill & Hurtado, 2009). The concept of resource value, rather than
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1071 resource quantity, is pertinent here, as the same quantity of food has greater value
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1073 for a needy, compared to a satiated, individual (Gurven, 2006). Taking this value
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1075 asymmetry into consideration, rather than models where pay-offs are constant,
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1077 greatly expands the potential for reciprocal cooperation to evolve (Doebeli &
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1079 Knowlton, 1998). This implies that the quantities shared between individuals do not
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1081 need to be identical, as long as the long-term resource values are equal (Gurven,
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1083 2006). For example, skilled hunters Ache who provisioned others received
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1085 significantly more food while sick or injured relative to less-skilled hunters who
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1087 provisioned others less often (Gurven, Allen-Arave, et al., 2000), while reciprocal
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1089 non-kin sharing among vampire bats likely reflects similar evolutionary processes
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1091 (Carter & Wilkinson, 2013). This long-term reciprocity based on asymmetrical pay-
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1093 offs characterizes the need-based sharing observed among friends (Hruschka,
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1095 2010), thereby resolving the ‘Banker’s Paradox’ (Tooby & Cosmides, 1996) and
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1097 illustrating how non-kin cooperation – and friendship (Migliano et al., 2017) – can
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1099 evolve.
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1103 Other functional reasons for this need-based sharing are also possible if
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1105 benefits are not returned ‘in-kind’. For instance, ‘unconditional generosity’ towards
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1107 those in need may be a sexually selected strategy to exhibit one’s phenotypic value
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1109 by displaying qualities such as care, compassion and generosity to attract mates
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1111 (Raihani & Smith, 2015). ‘Charitable’ donations may also enhance one’s social
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1113 standing, resulting in increased support in coalitions (Milinski, Semmann, &
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1115 Krambeck, 2002; Patton, 2005) or cooperative hunting (Bliege Bird & Power, 2015).
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1124 While the benefits of being cooperative may not be apparent in the short-term 'in-
1125 kind' cooperative measure used here, a longer-term perspective investigating
1126 several different cooperative and fitness-relevant domains may highlight these
1127 benefits. Alternatively, other competencies such as foraging skill, leadership,
1128 storytelling prowess or knowledge may be more important in deciding with whom to
1129 interact and cooperate, rather than solely an individual's level of cooperativeness
1130 (Macfarlan & Lyle, 2015; Smith et al., 2017).
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1139 Although we find evidence for need-based sharing, an independent effect of
1140 sharing with less cooperative individuals was still reported. One possible reason for
1141 this is that our measure of need does not encompass all relevant components of
1142 need, such as being pregnant, nursing young infants (Hurtado, Hill, Hurtado, &
1143 Kaplan, 1992), or being ill/injured (Sugiyama & Chacon, 2000). Many of the stated
1144 reasons for sharing resources with those in need, including weakness and an
1145 inability to work, could not be explicitly included in our composite need variable due
1146 to a lack of quantitative data. Given the association between cooperativeness and
1147 other components of need (Smith et al., 2016), it is plausible that inclusion of these
1148 other factors may remove the residual effect of sharing with less cooperative
1149 individuals. Alternatively, perhaps there are reasons, other than need, why
1150 individuals would avoid sharing with cooperative individuals. For instance, foragers
1151 may shun highly-cooperative individuals to avoid being indebted to them (Woodburn,
1152 1982), comparable to societies from Papua New Guinea rejecting over-generous
1153 offers in the Ultimatum Game (Henrich et al., 2005).
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1171 Our results suggest that mechanisms of cooperative assortativity may not
1172 have universal application as explanations for the evolution of human cooperation.
1173 There are several kinds of assortativity, however, not just by cooperativeness, which
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prioritize specific partners over others. Cooperation in this experimental game is associated with assortativity by kinship and reciprocal partnerships, but in different contexts other assortative mechanisms may take precedence. For instance, in many large-scale societies kinship ties are weaker and interactions repeated less frequently, meaning that kin selection and reciprocal cooperation may be weaker forces in these contexts. Under these circumstances, mechanisms of cooperative assortment, such as indirect reciprocity, may become more important (as the proliferation of online seller rating systems attests; Livingston, 2005). As a concrete example of cross-cultural variation in cooperative strategies, both hunter-gatherer (Gurven, 2004) and pastoral (Aktipis et al., 2011) societies, which suffer repeatedly from resource shortfalls due to high levels of stochasticity in food production, appear to display need-based sharing as a risk-pooling strategy. In contrast, among the agricultural Mosuo in China needier households were not more likely to receive help (Thomas et al., 2018), potentially because the unpredictable variability in resource production required for reciprocal need-based cooperation to evolve is less pronounced in farming communities. Further cross-cultural research is required to explore how cooperative mechanisms vary with socioecological context.

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These findings also have implications for models which use lab studies to investigate the evolution of cooperation. In many previous experimental studies supporting predictions made by theories of cooperative assortativity (Milinski, 2016; Milinski et al., 2002) the theory is examined in isolation. Yet, as demonstrated here, once other factors such as relatedness, reciprocity and need are taken into consideration in a real-world setting, individuals use these traits, rather than cues of cooperativeness, when deciding with whom to cooperate. Laboratory studies are useful proofs-of-concept, but real-world data are necessary to assess their predictive

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1242 power in ecologically valid contexts and to understand the social and ecological
1243 factors which influence cooperative behavior.
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1246 These findings suggest that need-based sharing, rather than cooperative
1247 assortativity, predicts patterns of experimental resource transfers among the Agta.
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1249 However, these results possess several limitations. Firstly, we only explore one
1250 domain of cooperation (food-sharing). It is possible that cooperative assortativity may
1251 explain patterns of cooperation in other contexts, such as labor-sharing (Macfarlan et
1252 al., 2012), cooperative hunting (Bliege Bird & Power, 2015), child-care or selecting
1253 camp-mates (Apicella et al., 2012). Studies exploring multiple cooperative networks
1254 within a single society (see, for example, Jaeggi et al., 2016; Mace et al., 2018;
1255 Nolin, 2011) are required to explore this possibility. Nonetheless, the present results
1256 demonstrate that cooperative assortment is unlikely to influence ‘in-kind’ food-
1257 sharing decisions among the Agta.
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1270 Additionally, the present study does not aim to explore all facets of reputation-
1271 based cooperation. For instance, we do not assess whether individuals shared food
1272 in this game in order to gain a reputation for being cooperative, or how market
1273 effects of supply and demand influence cooperative decision-making (Barclay,
1274 2013). Rather, we assume that individuals already possess a reputation for
1275 cooperativeness in real-world interactions and test whether these individuals are
1276 more likely to receive resources. This is a central prediction of all theories of
1277 cooperative assortativity. Further studies are required to explore how individuals
1278 earn a cooperative reputation and the additional nuances of cooperation in biological
1279 markets.
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1290 In addition to kin selection and immediate reciprocity, we therefore conclude
1291 that resource transfers among the Agta are largely based on need, rather than
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1301 mechanisms of cooperative assortment such as indirect reciprocity or cooperative
1302 homophily. This need-based sharing may represent delayed reciprocity or helping
1303 needy individuals for reputational benefits in other domains. This is likely due to a
1304 forager-specific ecology of high resource stochasticity resulting in repeated food
1305 shortfalls, necessitating need-based sharing as a system of long-term reciprocal
1306 exchange. These results therefore indicate that mechanisms of cooperative
1307 assortativity may not have universal application as explanations for the evolution of
1308 human cooperation, particularly prior to the advent of increasingly-anonymized
1309 interactions in large-scale societies.
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1360 *Ethics*
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1362 Ethical clearance was granted by the University Ethics Committee (Ethics code
1363 3086/003). Fieldwork permission was granted by local government units, including
1364 the Mayors of the Municipalities visited and from the Department of Environmental
1365 and Natural Resources (DENR) as the research took place in a protected area.
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1371 *Data Availability*
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1373 The data and code associated with this research is available via figshare at
1374 10.6084/m9.figshare.6960998 (this link will be made active upon publication).
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1379 *Competing Interests*
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1381 We have no competing interests.
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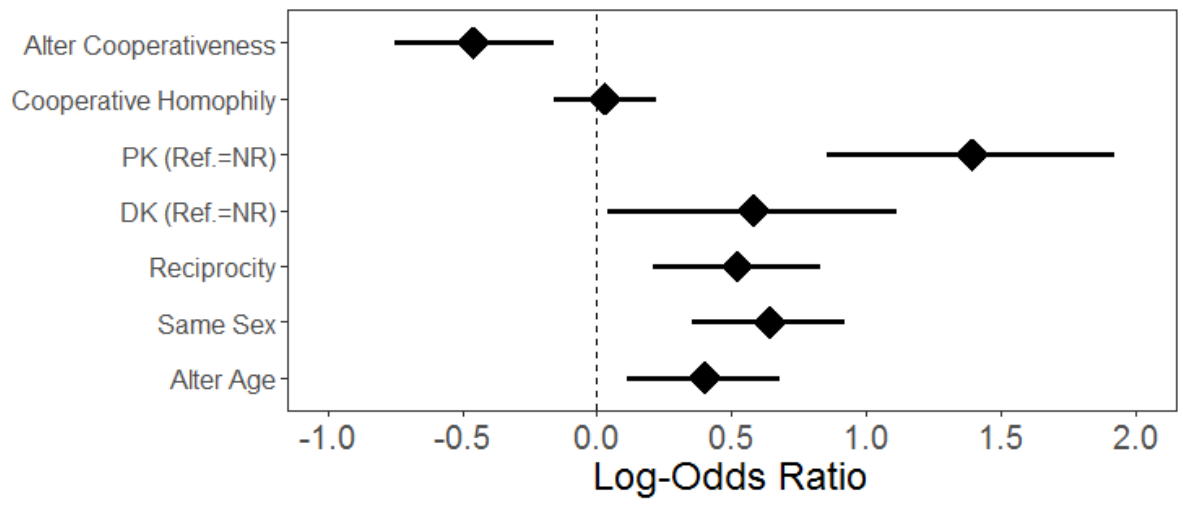
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 1773 *Table 1:* Comparison of the top models (within two QIC values of the best-fitting
 1774 model) regarding who individuals gave resources to ($n=272$, dyads=1,312). Keeping
 1775 age, sex and ego cooperativeness variables constant, 32 potential models were
 1776 constructed and QIC values compared using all combinations of the variables:
 1777 kinship, reciprocity, proximity, alter cooperativeness and cooperative homophily.
 1778 Δ QIC denotes the difference in QIC values between models (with '0' being the top
 1779 model), while model weight is a value between 0 and 1 which can be interpreted as
 1780 the probability that a given model is the best fit to the data.
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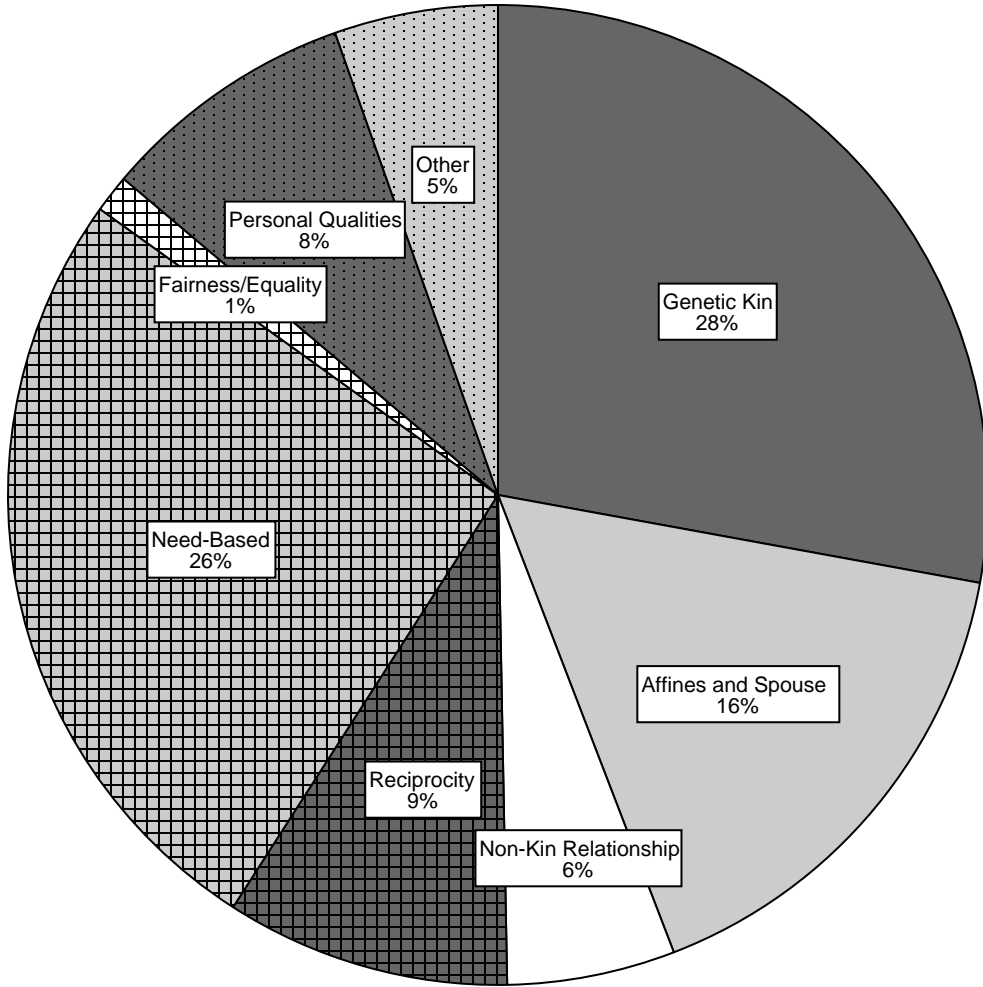
Model Variables	QIC	Δ QIC	Model Weight (w_i)
Kinship + Reciprocity + Alter Cooperativeness	1086.25	0	0.72
Kinship + Reciprocity + Alter Cooperativeness + Cooperative Homophily	1088.18	1.92	0.28

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1832 *Figure 1:* Forest plot displaying standardized log-odds estimates of giving resources
1833 to others, derived from the model averaging analysis (table S2; $n=272$, dyads=1,312;
1834 see table 1 for component models). Note that not all variables are displayed.
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1836 Abbreviations: PK=Primary kin; DK=Distant kin; NR=Non-relatives. Error bars denote
1837 95% confidence intervals.
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1856 *Figure 2:* Pie chart displaying the proportion of reasons, split by category, for giving
1857 to others (total reasons=1,001: for additional details see table S4).
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Supplementary Information for 'A Friend in Need is a Friend Indeed: Need-based Sharing, Rather than Cooperative Assortment, Predicts Experimental Resource Transfers among Agta Hunter-Gatherers'

Details of the 'Model Comparison' Statistical Approach Used

This section briefly details the 'Information Theoretic' (IT) approach used in this paper. IT approaches are distinct from traditional 'null hypothesis significance testing' approaches (also known as 'frequentist' methods) in that multiple hypotheses (models) are simultaneously evaluated and model fit assessed (Burnham & Anderson, 2002). Although several methods to assess model fit have been proposed (see Garamszegi, 2011, pg. 2), the most common method is based on the Akaike Information Criterion (AIC; Akaike, 1998) and associated metrics such as the Quasi-likelihood Information Criterion (QIC) adopted here. These methods estimate the amount of information contained in each model (i.e., how well the model predicts the dependent variable), with a lower value indicating increased model fit, with appropriate penalties for increased model complexity to prevent over-fitting (Burnham & Anderson, 2002).

Use of these metrics permits comparison of multiple hypotheses in parallel, rather than stepwise selection of terms based on arbitrary p -value thresholds, as with frequentist approaches (Garamszegi, 2011). A distinct advantage of this IT approach is that model uncertainty can be quantified and utilized in downstream analysis (Grueber, Nakagawa, Laws, & Jamieson, 2011). Based on the information criterion used, Akaike weights can then be quantified for each of the candidate models. This is a value between 0 and 1 which can be interpreted as the probability that a given model is the best fit to the data (Symonds & Moussalli, 2011). Therefore, a model

with an Akaike weight of 0.95 means that, of all models compared, there is a 95% chance that this is the best-fitting model. As this weight decreases there is less certainty that a given model is the best model, such that other models may be a better model fit (or that multiple models provide a similar fit).

If there is uncertainty over which is the 'best' model, model averaging over a set of these 'top models' can be used to obtain parameter estimates which take this model uncertainty into consideration (Grueber et al., 2011). This procedure uses weighted parameter estimates, in that terms from weakly-predictive models (i.e., lower Akaike weights) are given lower weights than terms from models with greater predictive power (i.e., higher Akaike weights). We define the 'top model set' as any models within two information criterion values (i.e., two QIC values) of the best-fitting model (Grueber et al., 2011). We utilize a 'zero method' of model averaging, in which parameters absent in a subset of the top models are substituted with a value of '0'. This 'zero method' of model averaging is a more stringent method than the alternative 'conditional method' which only averages parameters over the models they appear in, while ignoring these parameters in top models in which they are absent. This 'zero method' therefore reduces the effect sizes of weakly predictive variables, meaning that the remaining predictive variables are those possessing the strongest association with the response variable, reducing the possibility of type I errors (false positives; Barton, 2015; Grueber et al., 2011).

IT approaches are likely to be most useful in multivariate analyses where several variables may be associated with a specific response (Symonds & Moussalli, 2011), as is the case here with multiple hypotheses derived from several different theories examined in tandem to explore the evolutionary factors which influence human cooperation.

Table S1: Number (and percentage) of individuals in each kinship category in the analysis ($n=272$, dyads=1,312).

Kinship Category	Number of camp-mates (%)
Primary kin (PK)	172 (13%)
Distant kin (DK)	152 (12%)
Spouse	84 (6%)
Spouse's primary kin/Primary kin's spouse (SPK/PKS)	176 (13%)
Spouse's distant kin/Other affines (SDK/OA)	526 (40%)
Non-relatives (NR)	202 (15%)

Table S2: Results of the model averaging procedure for sharing resources with camp-mates, displaying standardized and unstandardized coefficients ($n=272$, dyads=1,312). Coefficients are log-odd estimates, with 95% confidence intervals displayed in brackets. Variables in which confidence intervals do not pass through '0' are highlighted in bold. Relative importance denotes the summed Akaike weight (w_i) of each parameter in the top models used in model averaging, with a '1' indicating that this term occurred in all top models. Proximity does not appear here as no top model contained this variable. All models contain an 'ego cooperative score' variable (not displayed) to control for differences in amount given between individuals.

Variable	Std. Parameter Estimate (95% CI)	Unstd. Parameter Estimate (95% CI)	Relative Import. (w_i)
Kinship (Baseline: Non-kin)			
Primary Kin	1.39 [0.85; 1.92]	1.39 [0.85; 1.92]	1
Distant Kin	0.58 [0.04; 1.11]	0.58 [0.04; 1.11]	1
Spouse's Primary Kin/ Primary Kin's Spouse	0.19 [-0.31; 0.68]	0.19 [-0.31; 0.68]	1
Spouse's Distant Kin/ Other Affines	0.06 [-0.34; 0.45]	0.06 [-0.34; 0.45]	1
Spouse	0.17 [-0.47; 0.8]	0.17 [-0.47; 0.8]	1
Reciprocity (1=Yes)	0.52 [0.21; 0.83]	0.52 [0.21; 0.83]	1
Alter Cooperativeness	-0.46 [-0.16; -0.75]	-0.011 [-0.004; -0.018]	1
Cooperative Homophily	0.03 [-0.16; 0.22]	0.001 [-0.004; 0.005]	0.28
Ego Age	-0.08 [-0.36; 0.19]	-0.003 [-0.012; 0.007]	N/A
Alter Age	0.4 [0.11; 0.68]	0.014 [0.004; 0.024]	N/A
Age Difference	0.09 [-0.2; 0.38]	0.004 [-0.008; 0.016]	N/A
Ego Sex (1=Male)	0.01 [-0.27; 0.28]	0.01 [-0.27; 0.28]	N/A
Alter Sex (1=Male)	-0.17 [-0.44; 0.1]	-0.17 [-0.44; 0.1]	N/A
Same Sex (1=No)	-0.64 [-0.35; -0.92]	-0.64 [-0.35; -0.92]	N/A
Intercept	-1.27 [-0.92; -1.61]	2.36 [1.64; 3.09]	N/A

Table S3: Results of the model averaging procedure for sharing resources with camp-mates, using a logistic mixed-effects model with both givers and receivers as random effects ($n=272$, dyads=1,312). Coefficients are standardized log-odd estimates, with 95% confidence intervals displayed in brackets. Variables in which confidence intervals do not pass through '0' (or do so only marginally) are highlighted in bold. Relative importance denotes the summed Akaike weight (w_i) of each parameter in the top models used in model averaging, with a '1' indicating that this term occurred in all top models. All models contain an 'ego cooperative score' variable (not displayed) to control for differences in amount given between individuals. The parameter estimates in this model are qualitatively identical to those in the GEE model (Table S2), demonstrating the robustness of these findings.

Variable	Standardized Parameter Estimate (95% CI)	Relative Import. (w_i)
Kinship (Baseline: Non-kin)		
Primary Kin	1.41 [0.74; 2.08]	1
Distant Kin	0.64 [-0.02; 1.29]	1
Spouse's Primary Kin/ Primary Kin's Spouse	0.23 [-0.4; 0.86]	1
Spouse's Distant Kin/ Other Affines	0.08 [-0.41; 0.57]	1
Spouse	0.15 [-0.67; 0.97]	1
Reciprocity (1=Yes)	0.58 [0.21; 0.95]	1
Alter Cooperativeness	-0.53 [-0.14; -0.91]	1
Proximity	-0.05 [-0.32; 0.22]	0.26
Cooperative Homophily	0.04 [-0.2; 0.28]	0.25
Ego Age	-0.11 [-0.43; 0.22]	N/A
Alter Age	0.43 [0.06; 0.8]	N/A
Age Difference	0.07 [-0.27; 0.41]	N/A
Ego Sex (1=Male)	-0.01 [-0.33; 0.31]	N/A
Alter Sex (1=Male)	-0.15 [-0.51; 0.21]	N/A
Same Sex (1=No)	-0.68 [-0.35; -1.01]	N/A
Intercept	-1.35 [-0.9; -1.8]	N/A

Table S4: Frequency and percentage of answers given as to why individuals gave resources to others (answers=1,001). Note that some answers included two categories (e.g., 'Father' and 'has a kind heart'), in which case half a point was coded as 'Genetic Kin' and the other half as 'Personal Qualities'.

Category	Example Answers	Frequency (%)
Genetic Kin	Father, Mother, Son	279 (27.9%)
Affinal Kin and Spouse	Father-in-law, Brother-in-law, Spouse	163 (16.3%)
Non-Kin Relationship	Friend, Neighbor, Companion	55.5 (5.5%)
Need-based/ Helping	Alter is/has; Old, Pregnant, Many children, Cannot work, No food. To help them.	258.5 (25.8%)
Reciprocity	When ego needs something alter is there, Alter shares with ego, If ego asks alter gives	94 (9.4%)
Personal Qualities	Alter is/has; Good, A kind heart, Good in sharing, Chief	84.5 (8.4%)
Fairness/ Equality	Need to share, So everybody has some, So they have the same	12.5 (1.3%)
Other	Varied, including; guilt, reasons related to the game, and 'don't know why'	54 (5.4%)

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