

Testing adaptive hypotheses of alloparenting in Agta foragers

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43 **Abstract**

44 Human children are frequently cared for by non-parental caregivers (alloparents), yet few
45 studies have conducted systematic alternative hypothesis tests of *why* alloparents help. Here,
46 we explore whether predictions from kin selection, reciprocity, learning-to-mother and costly
47 signalling hypotheses explain non-parental childcare among Agta hunter-gatherers from the
48 Philippines. To test these hypotheses, we use high-resolution proximity data from 1,701 child-
49 alloparent dyads. Our results indicate that reciprocity and relatedness were positively
50 associated with number of interactions with a child (our proxy for childcare). Need appeared
51 more influential in close kin, suggesting indirect benefits, while reciprocity proved to be a
52 stronger influence in non-kin, pointing to direct benefits. However, despite shared genes,
53 close and distant kin interactions were also contingent on reciprocity. Compared to other
54 apes, humans are unique in rapidly producing energetically demanding offspring. Our results
55 suggest that the support that mothers require is met through support based on kinship and
56 reciprocity.

57

58 **Main**

59 Women in natural fertility populations rapidly produce, on average, six to eight highly
60 dependent offspring during their lifetime¹. This frequently entails more provisioning than
61 mothers alone can provide, causing long-term shortfalls in childcare². The cooperative
62 breeding hypothesis argues that such rapid reproduction is only possible due to the assistance
63 from non-parental sources, known as alloparenting. While authors point to humans' large
64 social networks, indicating the importance of a diverse array of alloparents, including non-
65 kin³⁻⁷, previous literature has tended to focus on key relatives such as grandmothers⁸ and
66 siblings (who are seen as both co-operators and competitors^{9,10}) as well as exploring the
67 adaptive value of allocare in terms of increased child survival and maternal fertility¹¹⁻¹³ or
68 decreases to maternal workload^{14,15}. Thus, it is well established that one type of relative
69 (exactly which depends on ecological context¹¹) has a positive influence on child survival,
70 wellbeing or maternal fertility. However, comparatively underexplored is a systematic
71 exploration of the alternative hypotheses for cooperation in breeding.

72

73 True altruism is not an evolutionary stable strategy as individuals who choose to help will
74 ultimately suffer from reduced fitness^{16,17}. Consequently, a major question in the evolution
75 of cooperation explores what individuals gain from helping. The answer for cooperatively
76 breeding species has often fallen to indirect fitness¹⁸. Hamilton's (1964) theory of kin
77 selection states that a behaviour that benefits another may be selectively advantageous if the
78 costs (c) to the actor are outweighed by the benefits to the recipient (b), weighted by the
79 probability of shared genes due to common descent (r).

80

81 In the hunter-gatherer/subsistence farming literature, several studies have demonstrated
82 that more closely related individuals provide more childcare^{5,20,21}, meeting the expectations
83 of kin selection. For instance, Meehan (2008) demonstrates that in Ngandu infants (aged 8-
84 12 months) genetically related individuals were more likely to participate in investment
85 behaviours than non-kin. Similarly, Crittenden and Marlowe (2008) found that the carrying of
86 children (aged under 4 years) was positively predicted by relatedness. While the literature
87 suggests that non-kin provide a significant proportion of childcare²², it has not yet
88 systematically explored what direct fitness benefits (such as future cooperation, mating
89 access or additional parenting skills) non-kin may gain. Furthermore, simply because two
90 individuals are related does not mean that kin selection is the *only* ultimate explanation for
91 cooperation²³⁻²⁶. It would be erroneous to conclude that kinship is *the* major predictor of
92 childcare without testing it against alternative hypotheses.

93

94 Reciprocal cooperation can evolve if the cost of helping in the present is outweighed by the
95 probability of future benefits²⁷, even if the 'transactions' are not balanced²⁸ as cooperation
96 can be directed at 'needy' individuals²⁹. Therefore, cooperation can occur in the absence of
97 indirect fitness benefits³⁰. However, early theorists explicitly stated that 'kinship may be
98 involved'²⁷, indicating that kin selection and reciprocity are not competing hypotheses. Thus,
99 cooperators can receive direct benefits regardless of whether they are related or not²³. The
100 evidence of the importance of reciprocity is now mounting in food sharing³¹, allogrooming²⁴
101 and childcare³² in both human and non-human primates. Furthermore, recent work in
102 vampire bats (*Desmodus rotundus*) demonstrated that highly related pairs engaged in more
103 reciprocal food sharing³³, as also witnessed in humans^{5,34,35}, however this has not consistently
104 been the case³⁶. Certainly, related reciprocal dyads will receive indirect benefits on top of

105 direct returns, reducing the possible direct fitness losses associated with cheating³⁷.
106 Furthermore, reciprocity may be more likely in kin due to reduced geographic distance and
107 thus increased opportunity and lower transaction costs, prompting cooperation regardless of
108 relatedness^{18,35}. Consequently, capturing residential proximity may reduce the importance of
109 relatedness as they frequently co-vary^{21,35,38,39}.

110

111 Nonetheless, given key predictions from kin selection, while reciprocity can occur among kin,
112 it may be far less important given that the most indirect benefits may be achieved by helping
113 households most 'in need' of this assistance^{36,40}. In this case, aid will be significantly
114 unbalanced, or unidirectional⁴¹. For instance, Thomas *et al.* (2018) found among the Mosuo
115 from southwest China that households helped (in terms of farm labour) kin in need, but not
116 needy non-kin⁴². Therefore, theoretically we should expect interactions between nepotism
117 and 'need', reciprocity and 'need', as well as between reciprocity and relatedness to be
118 important predictors of behaviour. This is particularly so in hunter-gatherers who reside in
119 high-risk foraging niches, increasing the importance of reciprocity and wider social networks
120 comprised of kin and non-kin³².

121

122 Many hunter-gatherers face unpredictability in foraging returns⁴³, as well as longer-term
123 sickness and disability^{44,45}. Wide-ranging reciprocal cooperation is a key strategy for
124 smoothing over environmental stochasticity⁴⁶. Human foragers must deal with the extremes
125 of a complete failure of a hunt on some days compared to the bounty of returns on others.
126 Here, cooperating with *only* kin may not be sufficient to balance out shortfalls in returns⁴⁷.
127 Thus, helping non-kin extends an individual's cooperative network^{32,48,49}. This stochasticity in
128 foraging can result in acute childcare shortages as energy is invested away from childcare into
129 food production; thus both kin and non-kin may be important childcare providers. Given that
130 all human societies are comprised of social ties with unrelated individuals²², and hunter-
131 gatherers reside in camps with a significant proportion of unrelated individuals^{50,51} it seems a
132 large oversight to ignore their role in childcare. Accordingly, we expect wide, reciprocal
133 childcare networks including kin and non-kin to be important.

134

135 Other direct benefits of alloparenting include increasing an individual's mating success and
136 their future ability to rear offspring. Lancaster (1971) posited that young, non-reproductively

137 active females may alloparent to learn and develop their skills, since more experienced
138 primiparous mothers have better infant outcomes⁵³. Particularly, this should be the case if
139 offspring are highly vulnerable and dependent on high quality care⁵⁴. Accordingly, Baker
140 (1991) found that inexperienced, non-reproductive free-ranging golden lion tamarin
141 (*Leontopithecus rosalia*) females carried offspring more than other allomothers. Furthermore,
142 in Mongolian gerbils (*Meriones unguiculatus*) first-time mothers with allomothering
143 experience had increased reproductive performance and pup condition⁵⁶. The third possible
144 direct benefit is increased mating success, where males signal their quality to a mate by
145 partaking in costly allocare⁵⁷. Therefore, alloparenting may develop if it increases a male's
146 access to females, or if male alloparenting becomes a desirable trait to picky females⁵⁸. For
147 instance, cotton-top tamarins (*Saguinus oedipus*) males were more likely to engage in
148 successful copulation when carrying infants⁵⁹ and male mountain gorillas (*Gorilla beringei*)
149 who affiliated with more infants sired more offspring⁶⁰. Thus, here we will explore the relative
150 importance of both indirect benefits (kin selection) and direct benefits (reciprocity, learning-
151 to-mother and costly signalling) in a foraging population, the Agta of Palanan, Philippines.

152

153 We hypothesise that indirect and direct benefits are important and mutually inclusive
154 predictors of alloparenting, allowing for access to a wide-range of cooperators, including non-
155 kin. Given the literature cited above, we developed the following predictions: *i*) frequency of
156 interactions between children and alloparents will increase with indirect benefits
157 (relatedness) and direct benefits (reciprocity, costly signalling and learning-to-mother); *ii*)
158 reciprocity will occur among kin to varying degrees, depending on relatedness; *iii*) relatedness
159 will positively interact with need; and *iv*) childcare interactions will be influenced by costs
160 which decrease interactions. To test these predictions, we collected high-resolution
161 interaction data from 1,701 alloparent-child dyads (147 alloparents, 85 children in six camps)
162 over roughly one-week in each camp using 1.5-meter spatial proximity as a proxy for
163 childcare.

164

165 **Results**

166 All model residuals were checked for normality and zero-inflation using the DHARMA package
167 and descriptive statistics for all variables are given in Supplementary Tables 2-4. All variables

168 in the analysis were standardised over two standard deviations allowing easy comparison of
169 the effect of different predictor variables. All models are two-tailed tests.

170

171 Both household-level reciprocity (OR = 1.189, $p < 0.001$, 95% CI [1.17, 1.20]) and relatedness
172 (OR = 1.184, $p < 0.001$, 95% CI [1.80, 1.20]) were positive predictors of the number of
173 interactions between alloparents and dependent children in the univariable models, (Tables
174 2 & 3, Figure 1). The number of dependents in the giver's household did not predict
175 interactions (OR = 0.734, $p = 0.286$, 95% CI [0.42, 1.30]); however, contra expectations, the
176 number of carers available negatively predicted interactions (OR = 0.661, $p = <0.001$, 95% CI
177 [0.53, 0.82]). Therefore, if alloparents had more carers in their household they were less likely
178 to interact with another's child, not more (Table 3). Receiver household need (i.e. there were
179 more children than providers within the receiving household) was not significantly correlated
180 with the number of interactions between alloparents and children (OR = 0.979, $p = 0.177$, 95%
181 CI [0.95, 1.01], Table 2). Likewise, the learning-to-mother variable was a non-significant
182 predictor of interactions (OR = 1.433, $p = 0.196$, 95% CI [0.83, 2.47]), indicating that pre-
183 reproductive females were not significantly more likely to interact with dependent children.
184 While the variable for costly signalling (operationalised as reproductively active males) was
185 significant, contra to predictions, the relationship was negative (OR = 0.533, $p = 0.016$, 95%
186 CI [0.32, 0.89]), as reproductively aged males were associated with fewer interactions.

187

188 All variables were entered into two full models (Table 4) to control for confounding effects.
189 The first was the 'between and within households' model ($n = 1,701$) which contained all
190 variables except household reciprocity, giver's dependents and giver's carers. In this model,
191 all the previously statistically significant variables retained their significance and the non-
192 significant terms remained non-significant. Relatedness remained a strong predictor of future
193 interactions (OR = 1.185, $p < 0.001$, 95% CI [1.18, 1.20]). In the second full model ($n = 1,615$)
194 which included all predictions but removed alloparents from the same household (primarily
195 siblings), household reciprocity remains an equally strong predictor of future interactions (OR
196 = 1.183, $p < 0.001$, 95% CI [1.17, 1.20]), equal in size to relatedness within and between
197 households. However, once co-residing siblings are removed from the model which looks at
198 between household interactions only, the effect of relatedness, while statistically significant,
199 has a very small effect (OR = 1.015, $p = 0.010$, 95% CI [1.00, 1.03]). This suggests that while

200 relatedness is a strong predictor of allocare for close, co-residing kin, it was perhaps less
201 important for more distant kin. Likewise, when looking at between household alloparenting
202 only, receiver need becomes a significant predictor of interactions but again with a very small
203 effect size (OR = 1.087, $p < 0.001$, 95% CI [1.05, 1.13]). Overall, these relationships remained
204 despite the presence of residential proximity in all models, demonstrating that even when
205 households were spatially close, related individuals and cooperative partners still interacted
206 more than unrelated or non-reciprocal dyads.

207

208 Interaction models

209 A second set of analyses were performed to explore the interaction between relatedness,
210 household-level reciprocity and receiver need. Interactions were run with each of the three
211 kin categories: close kin, distant kin and non-kin, with close kin acting as the reference group.
212 As these models do not explore the relative roles of the alternative hypotheses (and there
213 was little difference between the full and univariable models), these models were run with
214 controls for child age and sex (0 = male) but without the other predictors.

215

216 Model one (Table 5, Figure 2a) reveals that the effect of need on interactions was different
217 dependent on kin type. The relationship between receiver need and total interactions is
218 strongest in close kin (OR = 1.485, $p < 0.001$, 95% CI [1.43, 1.54]), and has a much smaller, and
219 non-significant, influence on interactions with distant kin (OR = 1.041, 95% CI [0.97, 1.11])
220 and non-kin (OR = 1.01, 95% CI [0.94, 1.08]). The interpretation of these findings may be aided
221 by the relationship between kin group and household-level reciprocity. In model two,
222 interactions with close kin, distant kin and non-kin *all increased* with increasing household
223 reciprocal interactions (Figure 2b), however the effect is strongest in non-kin (OR = 1.290,
224 95% CI [1.21, 1.38]) as compared to distant kin (OR = 1.208, 95% CI [1.14, 1.29]) and close kin
225 OR = 1.176, 95% CI [1.14, 1.21]). Thus, if non-kin are influenced more by household reciprocal
226 interactions, they may be avoiding 'needy' households because they are poor reciprocators,
227 while close kin receive more inclusive fitness benefits from aiding the same 'needy'
228 households.

229

230 Discussion

231 Formalised alternative hypotheses testing of why alloparents provide childcare is rare in the
232 cooperative breeding literature in humans. The focus of the literature in general has been on
233 which kin provide the most childcare and the indirect fitness benefits of this care^{3,9,11,61,62},
234 rather than the broader question of why would *anyone* cooperate in childcare. This is in
235 opposition to the broader behavioural ecology literature, which has provided a theoretical
236 framework for the evolution and function of cooperative breeding^{52,63–65}. In humans, little
237 exploration has occurred to understand the ultimate motivations of non-kin alloparents, for
238 example via alternative hypotheses such as reciprocity. Here, we sought to fill this gap and
239 explore the relative roles of indirect and direct benefits regardless of kinship or lack thereof.

240

241 Relatedness had a strong effect on the number of interactions between alloparents and
242 children, in line with a wide array of literature on cooperation in hunter-gatherers, from
243 childcare, economic games and food sharing^{5,20,21,46,47,66}. We have shown that, following
244 Hamilton's rule, benefits are important mediators in breeding cooperatively. Accordingly, we
245 demonstrated that close kin provided more childcare when the indirect benefits (i.e.
246 household need) were high, a finding which has been repeated elsewhere^{36,41,42,67}. We were
247 not so successful at capturing a measure of giver 'cost', as alloparent households with more
248 carers interacted with children more, not less. It may be that this finding reflects the fact that
249 when there are a lot of carers available, each of these alloparents do less. Further exploration
250 is required to parcel out these effects.

251

252 Our measure of reciprocal household interactions also positively predicted interactions with
253 dependent children, indicating the importance of bi-directional exchanges and direct fitness
254 benefits since the effect of reciprocity was comparable to relatedness. The influence of
255 household-level reciprocity was strongest in non-kin; however, as predicted, reciprocal
256 cooperation was not limited to non-kin; household-level reciprocity was also associated with
257 increased interactions in both close and distant kin, but to a lesser degree than non-kin.
258 Similar results have been found elsewhere, as the effects of kinship quickly evaporate as r
259 decreases³⁹ and distantly related individuals may receive higher fitness returns from following
260 reciprocal exchanges²⁷. Reciprocity is expected when $Bp > C$ (p = the probability of future
261 interactions); thus, even if cooperating individuals are related, the potential of reciprocity will
262 influence behaviour, encouraging cooperation.

263 Kin are not only tied by relatedness, but share multiple social bonds as they often reside at
264 close proximity and experience increased trust and familiarity^{48,68}. As a result, while
265 cooperative dyads may be formed due to relatedness, this cooperation is maintained and
266 stabilised by direct benefits^{32,69}, as found in food transfers in the Ache horticultural-
267 foragers³⁴. Partner choice was originally posited as a form of reciprocity, as individuals can
268 avoid 'cheaters' by switching to a more 'safe-bet' partners, who may often be relatives³⁰. In
269 concordance with partner choice models of reciprocity, the small effect of need on alloparent-
270 child interactions with distant kin and non-kin may have been the consequence of avoiding
271 'labour poor' households as childcare assistance may not occur readily in return⁷⁰. Too many
272 children relative to providers within a household may signal an inability to reciprocate
273 childcare⁷¹, and thus these households were avoided as cooperative partners.

274

275 The proxy for the learning-to-mother hypothesis was non-significant in the full model, which
276 was perhaps not altogether surprising as there are significant shortcomings in this
277 hypothesis⁷². Primarily, it is unclear why, if infants are so vulnerable, mothers would allow
278 inexperienced, inept juveniles to provide childcare. There is evidence that allomothers
279 present a significant danger to offspring in non-human primates⁷³: a potential reason for the
280 lack of alloparenting in non-human apes or baboons⁷⁴. Furthermore, this hypothesis assumes
281 that time spent in allocare directly equates to future reproductive success, while in
282 cooperatively breeding primates, juveniles are often inept and intolerant carers who do not
283 seem to improve their skills by conducting these caring activities⁷⁵. Longitudinal data on
284 juvenile involvement in childcare and later child outcomes would be necessary to test this
285 hypothesis more fully. However, an analysis in the Maya found that girls who spent more time
286 in allocare did not have more surviving offspring⁷⁶. Therefore, currently there seems little
287 support for this hypothesis.

288

289 Likewise, we found that reproductively aged males interacted with dependent children the
290 least, likely because males were heavily involved in indirect childcare activities such as food
291 production. Thus, this does not support the costly signalling hypothesis which suggests that
292 males copiously signal their quality in direct childcare to achieve increased mating success (of
293 course, here signalling via hunting skills has gone unmeasured). Similar results have been
294 found in callitrichids, where males did not increase care according to mating access,

295 receptiveness of females, state of oestrus, nor was the provisioning of care closely followed
296 by copulation attempts^{77,78}. Motivations of paternal care have also been explored among the
297 Tsimane horticultural-foragers of Bolivia, finding no support for the predictions of costly
298 signalling. As males provided the most passive care (in contrast to conspicuous, ‘signalling’
299 childcare) when mothers were absent, it appeared that the division of labour was a more
300 important motivator of male childcare in humans⁷⁹.

301

302 Overall, these findings highlight how the benefits (be they direct or indirect) of cooperation
303 can influence interactions with dependent children differently based on who the alloparent
304 is; indirect and direct benefits are not competing explanations of behaviour. Carter and
305 colleagues (2017), based on their work on food sharing in vampire bats, suggest that
306 cooperation should be considered to exist on a continuous spectrum from 100% direct fitness
307 benefits to 100% indirect benefits. While we fully agree this avoids behaviours being labelled
308 as *only* nepotistic or *only* reciprocal, this still implies that increases in direct benefit requires
309 a *decrease* in indirect benefits, which need not to be the case. A layered analogy may be far
310 more suitable, indicating that individuals are built up of different interacting ‘motivational
311 layers’.

312

313 A limitation of this work is the use of proximity at 1.5 meters as a measure of ‘childcare’, as it
314 is not possible to uncover who initiated the interaction, or separate high-investment activities
315 (carrying, feeding, grooming etc.) from low-investment activities (proximate observation,
316 touching etc.). Previous studies, particularly in small-scale societies, have focused on high-
317 investment childcare^{21,61,80}. However, as the function of childcare is to reduce maternal
318 workload, then the definition of childcare should not only be limited to high-quality
319 investment. Sole focus on high-investing caretakers effectively ignores alloparents who
320 engage in passive childcare. While these activities do not take significant effort or attention,
321 individuals who are proximate to children are those who intervene and respond when specific
322 situations arise⁸¹. This is reinforced here, as we have argued that passive proximity is an
323 important form of childcare for the Agta.

324

325 While notes cannot provide data on the nature of the interaction, they do capture a far wider
326 range of alloparents. Yet, of course, while direct allocare requires close proximity, this does

327 not mean that close proximity equates to allocare. For instance, some interactions maybe be
328 superfluous as two individuals simply walk pass one another, or even antagonistic. There is
329 no way to separate these interactions from the motes data. However, as discussed in the
330 methodological section, there is near perfect overlap between the motes data and the
331 observational data which confirms that the 'motes proximity' is the same as observational
332 'childcare proximity'. Therefore, this inability to separate interactions is not systematically
333 biasing the data. A final consideration is that our measure of 'allocare' is not dependent on
334 the absence of the child's main caregiver. Therefore, some interactions may consist of a ten-
335 year old interacting with a three-year-old when the mother is present. This feature has been
336 maintained in the data because it is reflective of reality; by entertaining and engaging with a
337 younger child in the presence of the mother, the older child has significantly reduced the
338 mother's workload allowing her to rest, socialise or conduct other household tasks in the
339 presence of a dependent child. Ultimately, while the motes produce less in-depth data, due
340 to the increased sample size and duration the amount of data allows for more complex
341 analyses required to explore the question 'why care?'

342

343 Here, we have demonstrated that while kinship plays an important role in structuring
344 childcare interactions in a foraging population, this is not the sole explanation. When different
345 predictors of alternative hypotheses are examined together, alongside costs and benefits, we
346 find that different predictors are important for different individuals. For close kin, interactions
347 increased when the inclusive fitness returns are high. However, while both close and distant
348 relatives share genetic material with children, their interactions appeared *also* dependent on
349 household-level reciprocity. This household-level reciprocity may have been maintained
350 because of the increased trust and likelihood of future interactions between relatives,
351 however its maintenance was not *solely* dependent on indirect benefits. Thus, it is incomplete
352 to argue that nepotistic mechanisms drive cooperation in breeding for humans without
353 conducting multivariate analyses to weigh up different hypotheses and including adequate
354 controls⁸². Without this intensive care from close kin and a wide childcare network of distant
355 kind and non-kin, mothers may not be able to maintain a rapid reproductive rate, particularly
356 in the face of unpredictable shortfalls during environmental stochasticity. In a population with
357 minimal-to-no material wealth, social capital and cooperation from outside the household
358 may provide a 'buffer' to energetic shortfalls⁴⁹. Ensuring cooperation from both kin and non-

359 kin alike is likely a major behavioural adaptation to ensure individuals' reproductive success.
360 By exploring childcare in humans from this perspective, we can offer important new insights
361 into why both kin and non-kin alloparents care in an unpredictable foraging ecology,
362 highlighting how ultimate explanations must be considered mutually inclusive.

363

364 **Methods**

365 The Agta

366 There are around 1,000 Agta living in Palanan municipality in north-eastern Luzon. Riverine
367 and marine spearfishing provides the primary source of animal protein, supplemented by
368 inter-tidal foraging and the gathering of wild foods as well as low-intensity cultivation, wage
369 labour and trade^{83,84}. The Agta are, like any group, a diverse population with some individuals
370 engaging in more cultivation and living in permanent camps while others are highly mobile
371 and spend more time foraging^{84,85}. Full ethnographic details about modes of subsistence,
372 mobility and diet can be found in the SI. The Agta, as a small-scale population, are ideal for
373 the following analyses because their social networks are predominantly contained within
374 their camps, which are not large (range 6-119 individuals), enabling us to capture the majority
375 of interactions during data collection. Furthermore, like many similar hunter-gatherer
376 populations, the Agta live in camps of fluid membership containing a large proportion of
377 unrelated individuals⁵⁰, as well as being highly cooperative⁶⁶. This stems from highly variable
378 foraging returns, necessitating significant food distribution and cooperation, influencing the
379 social structure of camps⁴⁷. Therefore, we expect there to be significant cooperation between
380 a wide range of individuals.

381

382 Data collection occurred over two field seasons from April to June 2013 and February to
383 October 2014. We stayed approximately 10-14 days in six camps for two, sometimes three
384 visits during the fieldwork period and conducted genealogical interviews, notes data
385 collection and focal follows. Overall the genealogies collected contained 2,953 living and dead
386 Agta from Palanan and neighbouring municipalities. From this data, it was possible to
387 establish the coefficient of relatedness (r) of each dyad. As a small population the sample
388 and its ultimate size is a product of everyone who we met in each of the camps who was

389 willing to participant in the various data collection activities. No statistical methods were used
390 to pre-determine sample sizes but our sample sizes are larger than previously reported in
391 childcare analyses in foragers^{20,81}.

392

393 This research was approved by UCL Ethics Committee (UCL Ethics code 3086/003) and carried
394 out with permission from local government and tribal leaders. Informed consent was
395 obtained from all participants, after group and individual consultation and explanation of the
396 research objectives in the indigenous language. A small compensation (usually a thermal
397 bottle or cooking utensils) was given to each participant.

398

399 Motes and childcare observations

400 Motes are wireless sensing devices which store all between-device communications within a
401 specified distance^{49,86}. The device we utilised was the UCMote Mini (with a TinyOS operating
402 system). The motes were sealed into wristbands and belts (depending on size and
403 preference⁸⁶) and labelled with a unique number and identified with coloured string to avoid
404 accidental swaps. All individuals within a camp wore the motes from a period ranging from
405 five to seven days. The motes create ad hoc networks and require no grounded infrastructure.
406 Therefore, they have the advantage of collecting interactions even when a group of
407 individuals were far from camp foraging. Data was only selected from between 05:00 and
408 20:00 to avoid long hours of recording who slept in the same shelter. If individuals arrived at
409 a camp during data collection, they were promptly given a mote and entry time was recorded.
410 Similarly, if an individual left a camp at any time before the end of data collection, the time
411 they returned the mote was recorded. To ensure swaps did not occur, individuals were asked
412 twice daily to check they were wearing the correct armband. All mote numbers were also
413 checked when they were returned. Any swaps were recorded during data collection and
414 adjusted in the final data processing by associating the individual with the correct mote at
415 any given point during data collection. The total number of interactions became the
416 dependent variable in the analyses, and a term was entered into all models to control for the
417 number of hours each dyad was present in camp and wearing a mote.

418

419 Each device sent a message every two minutes that contained its unique ID, a time stamp and
420 the signal strength. These messages are stored by any other mote within a three meter radius.
421 Being within three meters is a common threshold applied in behavioural studies of human
422 and non-human primates to denote dyadic exchanges^{87–90}, however for increased robustness,
423 here we will use a subset of the interactions which occur within 1.5 meters. This threshold
424 captured close interactions, such as playing, hunting, foraging and socialising as well as low-
425 investment proximity, such as watching or simply being near to a child and intervening when
426 required. Once these data were processed, we checked and confirmed autocorrelation was
427 not systematically biasing our data (Supplementary Figure 3).

428

429 In order to verify that proximity is associated with actual helping behaviours, we compared
430 the motes proximity with an observational measure of proximity. The observational measure
431 is acquired from two researchers (AEP and SV), following the same focal sampling techniques
432 and protocols^{81,91,92}, observing a child for a 9-hour period and recording who came within
433 three-meter proximity of that child (i.e. sitting within the same shelter as well as directly
434 interacting with that child) and the exact nature of their interaction (i.e. playing, grooming,
435 carrying, watching). These observations are broken into three 4-hour intervals (6:00 – 10:00,
436 10:00 – 14:00 and 14:00 – 18:00), in which the researcher records the activities of the focal
437 child and carers each 20 seconds, stopping for a 15-minute break each hour. These 4-hour
438 intervals were conducted on non-consecutive days to reduce any sampling bias (e.g. if a father
439 was out of camp for those two days). Focal follows were conducted on all children within the
440 sample whose parents were willing to participate in the study. Where there were more
441 children than possible to observe within the timeframe in one camp, we observed at least
442 one child from each household (Supplementary Table 1). This data was compared to the
443 motes data for five children who were observed at exactly the same time as the motes data
444 collection.

445

446 Means were produced for the proportion of time these five children spent within three-
447 meters of various categories of kin. The differences between the two forms of data collection
448 are minimal, and the distribution of observations is not significantly altered between the two
449 methods. For instance, the motes recorded that the children spent on average $34 \pm 26\%$ (SD)
450 of time with mothers, $11 \pm 5\%$ of time with fathers, $24 \pm 13\%$ of time with siblings and $6 \pm 6\%$,

451 7 ± 7% and 23 ± 13% for grandparents, other kin ($r \leq 0.25$ and ≥ 0.125) and non-kin ($r < 0.125$),
452 respectively (note these proportions do not sum to 1 since children can be with more than
453 one individual at any given observation). These same children were observed spending 37 ±
454 26% of time within three meters of their mothers, 19 ± 19% with fathers, 24 ± 19 % with
455 siblings and 2 ± 1%, 7 ± 8% and 24 ± 20% of their time with grandparents, other kin and non-
456 kin, respectively (Supplementary Figure 2). Overall, the consistency between the
457 observational and motes data leads us to conclude motes have a high reliability (specifically,
458 they are not systematically biasing the data with superfluous interactions) and represent a
459 type of proximity which can be considered 'childcare'.

460

461 It is also important to establish what kinds of interactions actually occur between individuals
462 within three meters of one another. Using a larger sample of behavioural observations (which
463 do not coincide with the motes data collection) of 40 children (64.5% males; 20 infants (aged
464 less than two years) and 20 toddlers (aged two to five years)) we explored what 'proximity'
465 actually means. This analysis revealed that alloparents were in proximity (i.e. not engaging in
466 any other activities) for 61% of interactions with children and 63.6% of interactions with
467 infants (Table 1). This includes touching, being at arms-length, or being three meters from a
468 child. In contrast, high investment activities (play, carry, groom, etc.) only accounted for
469 11.8% of interactions for infants and 8.3% for children. Childcare in the Agta, thus, is defined
470 by low-investment, passive childcare, rather than high-investment, active childcare. We
471 would like to reinforce the importance of proximity as a form of childcare, as if the ultimate
472 aim of allocare is to reduce the maternal workload by 'watching' or being 'proximate' to
473 children then our definition of childcare should not ignore these key forms of investment.
474 Here, however, as we are using proximity data in which we do not know the nature of the
475 interaction we have reduced the data down to interactions at 1.5 meters or closer to ensure
476 we are not capturing too many superfluous interactions in which an older individual is simply
477 nearby a child, but pays little attention to that child.

478

479 Motes allowed us to produce high-resolution proximity networks for a larger sample than
480 previously possible. While a one-week snapshot of interactions may not be reflective of a
481 typical week for all individuals, this method greatly increases the sample size and
482 observational time compared to traditional methods. Given the labour-intensive nature of

483 behavioural observations, many previous studies have been limited by small sample sizes. For
484 instance, in previous studies using focal follow techniques, sample sizes are often limited to
485 15 to 25 children^{20,81}, who are only observed for a total of 9 hours^{91,92}. Thus, while not only
486 increasing the number individuals observed, the notes also greatly increase the duration of
487 these observations. This substantially increases the representativeness of the sample and the
488 statistical power of any analysis, allowing more complex methods. This issue of sample size
489 is perhaps one reason why the study of cooperation in breeding within anthropology has not
490 systematically explored alternative hypotheses; more elaborate methods which
491 systematically control for the interrelationships between relatedness, proximity and
492 reciprocity require significantly more statistical power. Furthermore, while the notes offer
493 less detail than traditional approaches, they do consist of a less intrusive form of data
494 collection, and therefore the fieldworker does not risk biasing the results due to their
495 presence in following and recording all activities of a focal child.

496

497 Variables

498 ***Alloparents and dependent children***

499 Individuals aged six or over were defined as alloparents following our observations and the
500 wider literature which demonstrates increased production and economic activities after the
501 age of five⁹³⁻⁹⁵. As dependent children are all those under the age of 11 years there is overlap
502 between the child and alloparent categories (for 33 alloparents or 22.3% of the sample). To
503 avoid this circularity, children could only be 'cared' for by individuals who were at least five
504 years older than themselves. For instance, a child of five years could be 'cared' for by an
505 individual aged ten years, a situation not uncommon from our observations and within the
506 childcare literature in hunter-gatherers^{61,96}. However, a child of nine years could not be
507 'cared' for by the same ten-year-old. As a result, the youngest child in a camp could not be
508 considered to be alloparent, regardless of whether they were aged six or over. This allowed
509 us to capture the crossover of juveniles as both dependents and carers. To confirm the five-
510 year age difference exerted no undue influence on our results we ran sensitivity analysis
511 (Supplementary Tables 5-7) exploring the effect of age difference thresholds of two, five and
512 ten years. These analyses demonstrate the results are robust regardless of the age difference.

513 ***Residential proximity***

514 To capture the effects of residential proximity we captured a measure of geographic
515 proximity. Camp clusters were created based on household proximity in camps; lean-tos and
516 shelters are clustered together in twos and threes, which structure within-camp interactions.
517 For instance, food sharing commonly occurs between these two or three nearby households.
518 Therefore, as a measure of repeated interactions due to shared space, these clusters were
519 used to capture association effects. If a child's parents and alloparent(s) belonged to the same
520 camp cluster they were coded as one, otherwise zero.

521 ***Household-level reciprocity***

522 To test the influence of reciprocity, a reciprocity variable was created for each household
523 dyad based on the observational data to avoid issues of statistical endogeneity⁹⁷. As discussed
524 above, the key prediction of reciprocity can be understood as 'contingency', defined as the
525 relationship between what A gives B and what B gives A⁹⁸. Capturing contingent cooperation
526 'on the ground', however, is difficult, particularly as it is frequently not perfectly balanced,
527 nor expected to be^{34,38}. This is especially the case in childcare as dependent children cannot
528 immediately reciprocate care. Furthermore, while tit-for-tat models of cooperation²⁷ include
529 a temporal dimension (i.e. if A helps B in interaction 1, B will help A in interaction 2), this need
530 not be the case as reciprocity in the real-world is often far more complex than score-keeping,
531 especially when we understand that imbalance in transactions is to be expected to mitigate
532 risks²⁸. Therefore, taking these considerations into account, we created a continuous measure
533 of contingency which captures the help from household B to household A when a member of
534 household A is the 'alloparent'. We are not capturing individual-level dyadic reciprocity, but
535 rather *household-level reciprocity* in which the original 'help' from household A to household
536 B may be returned from a different person in household B. For example, mother *i* in
537 household A may help child *j* in household B, then in return mother *i* in household B may look
538 after child *j* in household A.

539

540 This variable was created as follows: for the 'giving household' (household *i*) a composite
541 value was created which captures all *observed* childcare events each dependent child in *i* had
542 received from all carers in the 'receiving household' (household *j*, visualised in Supplementary
543 Figure 1). As reciprocity is a household-level predictor, it was only used in analyses *between*
544 households (i.e. it is not used to predict co-residing sibling care, and therefore the sample is

545 reduced from $n = 1,701$ to $n = 1,615$). As the reciprocity variable was created from the
546 observed childcare interactions between a carer and a child, this measure only contains actual
547 childcare interactions which includes playing, holding, cleaning, feeding, talking to, or
548 watching and/or being in close proximity to a child.

549 ***Giver household cost and receiver need***

550 Cost was denoted by two variables at the giver's household level. Firstly, high cost is captured
551 by the giver having many dependents in the household (individuals aged 0-11 years, discrete
552 variable, range: 0-7). Secondly, high cost is measured as having few carers available in the
553 giver's household (individual age six years and above, discrete variable, range: 0-5). Similar to
554 the measure of reciprocity, these cost measures are household-level measures, thus, they are
555 only used in analyses between households ($n = 1,615$). Receiver household need was
556 produced by dividing the number of dependent children (0-11 years) in the child's household
557 by the number of carers in that household.

558

559 ***Relatedness and individual categories***

560 In the first set of analyses, relatedness was measured by the coefficient of relatedness (r) and
561 ranged from 0 to 0.5. The second set of analyses (focusing on the interaction between
562 relatedness, household-level reciprocity and need), kin was separated into three categories
563 to ease interpretation: close kin, distant kin and non-kin. Close kin referred to all individuals
564 who are related $r = 0.5$, thus only included siblings (as parents are removed from this sample).
565 Distant kin ($r = 0.0 - 0.25$) included grandparents, half siblings, aunts and uncles and first and
566 second and third cousins. Non-kin ($r = 0$) included individuals who were completely unrelated
567 or were so distantly related we were unable to track this relationship with the genealogies.

568

569 To explore the hypothesis that allocare was a form of learning-to-mother, we examined the
570 prediction that pre-reproductive females would be more likely to provide allocare. Therefore,
571 we coded allocarers as either pre-reproductive (aged under 16 years) females as one,
572 everyone else zero. Likewise, the costly signalling hypothesis was explored by examining the
573 prediction that reproductively aged males would be more likely to provide allocare.
574 Therefore, we coded reproductively (aged 16 years or over) aged males as one, everyone else
575 zero.

576 Statistical analysis

577 We ran zero-inflated Poisson mixed-effect models (also known as multilevel models) in R
578 version 3.2.2 using the glmmTMB package to explore the effects of the predictor variables on
579 the total number of interactions a carer had with a child during the data collection period.
580 Some individuals started or stopped data collection at different times, therefore the models
581 were offset with an 'hours' term to adjust for the number of hours both individuals within a
582 dyad were involved in data collection at the same time. All interactions between parents and
583 children were removed from the dataset, thus all remaining interactions reflect alloparents.
584 The unit of analysis in the model was the dyadic relationship ($n = 1,701$) between a child ($n =$
585 85 , 41.9% female, age range: 0.08 – 11 years) and alloparent ($n = 147$, 50.9% female, age
586 range: 6.22-75 years). Random effects captured clustering at the household (alloparent
587 household $n = 42$; child household $n = 33$) and camp ($n = 6$) levels, as well as the repeated
588 observations from children and alloparents in different dyads. All random-effect variances are
589 presented at the bottom of Tables 2, 3 and 4.

590

591 In each analysis we controlled for child age and sex (0 = male) as well as the age difference
592 between alloparent and child, to capture the fact that children closer in age were more likely
593 to be playing together. Age difference was run in an interaction with carer age (grouped into
594 child (aged 10 or less), adult (aged 10 to 40) and older adult (aged 40 plus) for the sake of the
595 interaction) as the effect of age difference varies between age groups, Supplementary Table
596 8). As household-level reciprocity and our measures of giver 'cost' (number of household
597 dependents and carers) are only measured for dyads residing in different households the
598 sample size was reduced to $n = 1,615$ for four models. Consequently, two sets of 'full' models
599 are presented in Table 3, predicting allocare between and within households in which cost
600 and reciprocity are not included ($n = 1,701$), and between households which includes all
601 variables but co-residing alloparents are now excluded ($n = 1615$).

602

603 **Data availability**

604 The data that support the findings of this study are available from the corresponding author
605 upon request.

606

607 **References**

- 608 1. Campbell, K. L. & Wood, J. W. Fertility in traditional societies. in *Natural Human*
609 *Fertility* (eds. Diggory, P., Teper, S. & Potts, M.) 39–69 (Macmillan Publishing, 1988).
- 610 2. Hill, K. & Hurtado, A. M. Cooperative breeding in South American hunter-gatherers.
611 *Proc. Biol. Sci.* **276**, 3863–3870 (2009).
- 612 3. Meehan, C. L., Helfrecht, C. & Malcom, C. D. Implications of length development and
613 maternal life history: allomaternal investment, peer relationships and social
614 networks. in *Childhood: Origins, evolution and implications* (eds. Meehan, C. L. &
615 Crittenden, A. N.) 199–220 (SAR Press, 2016).
- 616 4. Bogin, B., Bragg, J. & Kuzawa, C. Humans are not cooperative breeders but practice
617 biocultural reproduction. *Ann. Hum. Biol.* **41**, 368–380 (2014).
- 618 5. Meehan, C. L. Allomaternal investment and relational uncertainty among Ngandu
619 farmers of the Central African Republic. *Hum. Nat.* **19**, 211–226 (2008).
- 620 6. Meehan, C. L. & Hawks, S. Maternal and allomaternal responsiveness: the significance
621 of cooperative caregiving in attachment theory. in *Different faces of attachment:*
622 *Cultural variations on a universal human need* (eds. Otto, H. & Keller, H.) 113–140
623 (Cambridge University Press, 2014).
- 624 7. Meehan, C. L. & Hawks, S. Cooperative breeding and attachment among the Aka
625 foragers. in *Attachment reconsidered: Cultural perspectives on a western theory* (eds.
626 Quinn, N. & Mageo, J. M.) 85–113 (Palgrave macmillan, 2013).
- 627 8. Hawkes, K. & O’Connell, J. Grandmothering, menopause, and the evolution of human
628 life histories. *Proc. Natl. Acad. Sci.* **95**, 1336–1339 (1998).
- 629 9. Helfrecht, C. & Meehan, C. L. Sibling effects on nutritional status: Intersections of
630 cooperation and competition across development. *Am. J. Hum. Biol.* **28**, 159–170
631 (2016).
- 632 10. Lawson, D. W. & Mace, R. Trade-offs in modern parenting: a longitudinal study of
633 sibling competition for parental care. *Evol. Hum. Behav.* (2009).
634 doi:10.1016/j.evolhumbehav.2008.12.001
- 635 11. Sear, R. & Mace, R. Who keeps children alive? A review of the effects of kin on child
636 survival. *Evol. Hum. Behav.* **29**, 1–18 (2008).
- 637 12. Snopkowski, K. & Sear, R. Kin influences on fertility in Thailand: Effects and
638 mechanisms. *Evol. Hum. Behav.* **34**, 130–138 (2013).
- 639 13. Meehan, C. L., Helfrecht, C. & Quinlan, R. J. Cooperative breeding and Aka children’s
640 nutritional status: Is flexibility key? *Am. J. Phys. Anthropol.* **153**, 513–525 (2014).
- 641 14. Kramer, K. L. & Veile, A. Infant allocare in traditional societies. *Physiol. Behav.* **193**,
642 117–126 (2018).
- 643 15. Meehan, C. L., Quinlan, R. & Malcom, C. D. Cooperative breeding and maternal
644 energy expenditure among aka foragers. *Am. J. Hum. Biol.* **25**, 42–57 (2013).
- 645 16. Foster, K. R., Wenseleers, T. & Ratnieks, F. L. W. Kin selection is the key to altruism.
646 *Trends Ecol. Evol.* **21**, 57–60 (2006).
- 647 17. Rand, D. G. & Nowak, M. A. Human cooperation. *Trends Cogn. Sci.* **17**, 413–425
648 (2013).
- 649 18. Clutton-Brock, T. Breeding together: kin selection and mutualism in cooperative
650 vertebrates. *Science* **296**, 69–72 (2002).
- 651 19. Hamilton, W. D. The genetical evolution of social behaviour. I. *J. Theor. Biol.* **7**, 1–16
652 (1964).

- 653 20. Ivey, P. K. Cooperative reproduction in Ituri forest Hunter-Gatherers: Who cares for
654 Efe infants? *Curr. Anthropol.* **41**, 856–866 (2000).
- 655 21. Crittenden, A. N. & Marlowe, F. W. Allomaternal care among the Hadza of Tanzania.
656 *Hum. Nat.* **19**, 249–262 (2008).
- 657 22. Apicella, C. L. & Crittenden, A. N. Hunter-Gatherer Families and Parenting. in *The*
658 *Handbook of Evolutionary Psychology* (ed. Buss, D. M.) **IV**, 1–20 (Wiley, 2013).
- 659 23. Chapais, B. Kinship, competence and cooperation in primates. in *Cooperation in*
660 *Primates and Humans* (eds. Kappeler, P. M. & Van Schaik, C. P.) 47–61 (Springer,
661 2006).
- 662 24. Schino, G. & Aureli, F. The relative roles of kinship and reciprocity in explaining
663 primate altruism. *Ecol. Lett.* **13**, 45–50 (2010).
- 664 25. Crittenden, A. N. & Zes, D. A. Food Sharing among Hadza Hunter-Gatherer Children.
665 *PLoS One* **10**, e0131996 (2015).
- 666 26. Lukas, D. & Clutton-Brock, T. Cooperative breeding and monogamy in mammalian
667 societies. *Proc. R. Soc. B Biol. Sci.* **279**, 2151–2156 (2012).
- 668 27. Axelrod, R. & Hamilton, W. D. The Evolution of Cooperation. *Science (80-)*. **211**,
669 1390–1396 (1981).
- 670 28. Gurven, M. The Evolution of Contingent Cooperation. *Curr. Anthropol.* **47**, 185–192
671 (2006).
- 672 29. Smith, D. *et al.* A friend in need is a friend indeed: Need-based sharing, rather than
673 cooperative assortment, predicts experimental resource transfers among Agta
674 hunter-gatherers. *Evol. Hum. Behav.* **577**, (2018).
- 675 30. Trivers, R. L. The evolution of reciprocal altruism. *Chicago Journals* **46**, 35–57 (1971).
- 676 31. Jaeggi, A. V & Gurven, M. Reciprocity explains food sharing in humans and other
677 primates independent of kin selection and tolerated scrounging: a phylogenetic meta-
678 analysis. *Proc. R. Soc. B Biol. Sci.* **280**, 1–8 (2013).
- 679 32. Jaeggi, A. V, Hooper, P. L., Beheim, B. A., Kaplan, H. & Gurven, M. Reciprocal
680 Exchange Patterned by Market Forces Helps Explain Cooperation in a Small-Scale
681 Society. *Curr. Biol.* **26**, 2180–2187 (2016).
- 682 33. Carter, G. G., Wilkinson, G. S. & Carter, G. G. Food sharing in vampire bats : reciprocal
683 help predicts donations more than relatedness or harassment. (2013).
- 684 34. Allen-Arave, W., Gurven, M. & Hill, K. Reciprocal altruism, rather than kin selection,
685 maintains nepotistic food transfers on an Ache reservation. *Evol. Hum. Behav.* **29**,
686 305–318 (2008).
- 687 35. Nolin, D. A. Food-Sharing Networks in Lamalera, Indonesia: Reciprocity, Kinship, and
688 Distance. *Hum. Nat.* **21**, 243–268 (2010).
- 689 36. Koster, J. Interhousehold Meat Sharing among Mayangna and Miskito
690 Horticulturalists in Nicaragua. *Hum. Nat.* **22**, 394–415 (2011).
- 691 37. Wilkinson, G. S. Reciprocal food sharing in the vampire bat. *Nature* **308**, 181–184
692 (1984).
- 693 38. Gurven, M. Reciprocal altruism and food sharing decisions among Hiwi and Ache
694 hunter-gatherers. *Behav. Ecol. Sociobiol.* **56**, 366–380 (2004).
- 695 39. Koster, J. M. & Leckie, G. Food sharing networks in lowland Nicaragua: An application
696 of the social relations model to count data. *Soc. Networks* **38**, 100–110 (2014).
- 697 40. Snopkowski, K. & Sear, R. Grandparental help in Indonesia is directed preferentially
698 towards needier descendants: a potential confounder when exploring grandparental
699 influences on child health. *Soc. Sci. Med.* **128**, 105–114 (2015).

- 700 41. Hames, R. Garden labour exchange among the Yekwana. *Ethol. Sociobiol.* **8**, 259–284
701 (1987).
- 702 42. Thomas, M. G. *et al.* Kinship underlies costly cooperation in mosuo villages. *R. Soc.*
703 *Open Sci.* **5**, (2018).
- 704 43. Hawkes, K. Hunting income patterns among the Hadza: big game, common goods,
705 foraging goals and the evolution of the human diet. *Philos. Trans. Biol. Sci.* **334**, 243–
706 250 (1991).
- 707 44. Gurven, M., Allen-Arave, W., Hill, K. & Hurtado, M. ‘It’s a Wonderful Life’. signaling
708 generosity among the Ache of Paraguay. *Evol. Hum. Behav.* **21**, 263–282 (2000).
- 709 45. Sugiyama, L. S. Illness, injury, and disability among Shiwiar forager-horticulturalists:
710 Implications of health-risk buffering for the evolution of human life history. *Am. J.*
711 *Phys. Anthropol.* **123**, 371–389 (2004).
- 712 46. Jaeggi, A. V & Gurven, M. Natural cooperators: Food sharing in humans and other
713 primates. *Evol. Anthropol.* **22**, 186–195 (2013).
- 714 47. Dyble, M. *et al.* Networks of Food Sharing Reveal the Functional Significance of
715 Multilevel Sociality in Two Hunter-Gatherer Groups. *Curr. Biol.* **26**, 2017–2021 (2016).
- 716 48. Carter, G. G. & Wilkinson, G. S. Social benefits of non-kin food sharing by female
717 vampire bats. *Proc. Natl. Acad. Sci. B* **282**, 20152524 (2015).
- 718 49. Page, A. E. *et al.* Hunter-Gatherer Social Networks and Reproductive Success. *Sci. Rep.*
719 **7**, 1153 (2017).
- 720 50. Dyble, M. *et al.* Sex equality can explain the unique social structure of hunter-
721 gatherer bands. *Science (80-)*. **348**, 796–798 (2015).
- 722 51. Hill, K. R. *et al.* Co-residence patterns in hunter-gatherer societies show unique
723 human social structure. *Science* **331**, 1286–1289 (2011).
- 724 52. Lancaster, J. B. Play-mothering: the relations between juvenile females and young
725 infants among free-ranging vervet monkeys (*Cercopithecus aethiops*). *Folia Primatol.*
726 (*Basel*). **15**, 161–182 (1971).
- 727 53. Baker, A. J. & Woods, F. Reproduction of the emperor tamarin (*Saguinus imperator*)
728 in captivity, with comparisons to cotton-top and golden lion tamarins. *Am. J.*
729 *Primatol.* **26**, 1–10 (1992).
- 730 54. Solomon, N. G. & Hayes, L. D. The Biological Basis of Alloparental Behaviour in
731 Mammals. in *Substitute Parents: Biological and Social perspective on alloparenting*
732 *across human societies* (eds. Bentley, G. & Mace, R.) 13–49 (Berghahn Books, 2009).
- 733 55. Baker, A. J. Evolution of the social system of the golden lion tamarin (*Leontopithecus*
734 *rosalia*). (University of Maryland, 1991).
- 735 56. Salo, A. L. & French, J. A. Early experience, reproductive success and development of
736 parental behaviour in mongolian gerbils. *Anim. Behav.* **38**, 693–702 (1989).
- 737 57. Zahavi, A. Arabian babblers: the quest for social status in a cooperative breeder. in
738 *Cooperative breeding in birds: long term studies of ecology and behaviour* 103–130
739 (1990). doi:10.1017/CBO9780511752452.005
- 740 58. Tardif, S. D. The Bioenergetics of Parental Behaviour and the Evolution of Alloparent
741 Care in Marmosets and Tamarins. in *Cooperative Breeding in Mammals* (eds.
742 Solomon, N. G. & French, J. A.) 11–33 (Cambridge University Press, 1997).
- 743 59. Price, E. C. & McGrew, W. C. Cotton-top tamarins (*Saguinus oedipus*) in a semi-
744 naturalistic captive colony. *Am. J. Primatol.* **20**, 1–12 (1990).
- 745 60. Rosenbaum, S., Vigilant, L., Kuzawa, C. W. & Stoinski, T. S. Caring for infants is
746 associated with increased reproductive success for male mountain gorillas. *Sci. Rep.*

- 747 **8**, 15223 (2018).
- 748 61. Kramer, K. L. Cooperative Breeding and its Significance to the Demographic Success of
749 Humans. *Annu. Rev. Anthropol.* **39**, 417–436 (2010).
- 750 62. Sear, R. & Coall, D. How Much Does Family Matter? Cooperative Breeding and the
751 Demographic Transition. *Popul. Dev. Rev.* **37**, 81–112 (2011).
- 752 63. Jetz, W. & Rubenstein, D. R. Environmental uncertainty and the global biogeography
753 of cooperative breeding in birds. *Curr. Biol.* **21**, 72–78 (2011).
- 754 64. Baden, A. L., Wright, P. C., Louis, E. E. & Bradley, B. J. Communal nesting, kinship, and
755 maternal success in a social primate. *Behav. Ecol. Sociobiol.* **67**, 1939–1950 (2013).
- 756 65. Kokko, H., Johnstone, R. a & Clutton-Brock, T. H. The evolution of cooperative
757 breeding through group augmentation. *Proc. Biol. Sci.* **268**, 187–196 (2001).
- 758 66. Smith, D. *et al.* Camp stability predicts patterns of hunter-gatherer cooperation. *R.*
759 *Soc. Open Sci.* **3**, 160131 (2016).
- 760 67. Snopkowski, K. & Sear, R. Grandparental help in Indonesia is directed preferentially
761 towards needier descendants: a potential confounder when exploring grandparental
762 influences on child health. *Soc. Sci. Med.* **128**, 105–14 (2015).
- 763 68. Dyble, M., Gardner, A., Vinicius, L. & Migliano, A. B. Inclusive fitness for in-laws. *Biol.*
764 *Letts.* **14**, 20180515 (2018).
- 765 69. Carter, G. G., Wilkinson, G. S. & Page, R. A. Food-sharing vampire bats are more
766 nepotistic under conditions of perceived risk. *Behav. Ecol.* **280**, 20122573 (2017).
- 767 70. Barclay, P. Strategies for cooperation in biological markets, especially for humans.
768 *Evolution and Human Behavior* **34**, 164–175 (2013).
- 769 71. Davies, N. B., Krebs, J. R. & West, S. *An Introduction to Behavioural Ecology.* (Wiley-
770 Blackwell, 2012). doi:10.1037/026600
- 771 72. Fried, J. J. The role of juvenile pine voles (*Microtus pinetorum*) in the caretaking of
772 their younger siblings. (North Carolina State University, 1987).
- 773 73. Silk, J. B. Kidnapping and female competition among captive bonnet macaques.
774 *Primates* **21**, 100–110 (1980).
- 775 74. Hrdy, S. B. *Mothers and Others: The evolutionary origins of mutual understanding.*
776 (Harvard University Press, 2009).
- 777 75. Tardif, S. D., Carson, R. L. & Gangaware, B. L. Infant-care Behavior of Non-
778 reproductive Helpers in a Communal-care Primate, the Cotton-top Tamarin (*Saguinus*
779 *oedipus*). *Ethology* **92**, 155–167 (1992).
- 780 76. Kramer, K. L., Veile, A. & Otárola-Castillo, E. Sibling competition & growth tradeoffs.
781 Biological vs. statistical significance. *PLoS One* **11**, 1–17 (2016).
- 782 77. Davies, N. B., Hatchwell, B. J., Robson, T. & Burke, T. Paternity and parental effort in
783 dunnocks *Prunella modularis*: how good are male chick-feeding rules? *Anim. Behav.*
784 **43**, 729–745 (1992).
- 785 78. Baker, A. J., Dietz, J. M. & Kleiman, D. G. Behavioural evidence for monopolization of
786 paternity in multi-male groups of golden lion tamarins. *Anim. Behav.* **46**, 1091–1103
787 (1993).
- 788 79. Winking, J., Gurven, M., Kaplan, H. & Stieglitz, J. The goals of direct paternal care
789 among a south Amerindian population. *Am. J. Phys. Anthropol.* **139**, 295–304 (2009).
- 790 80. Scelza, B. A. The grandmaternal niche: Critical caretaking among Martu Aborigines.
791 *Am. J. Hum. Biol.* **21**, 448–454 (2009).
- 792 81. Meehan, C. L. The effects of residential locality on parental and alloparental
793 investment among the Aka foragers of the central African Republic. *Hum. Nat.* **16**,

- 794 58–80 (2005).
- 795 82. Barclay, P. & Reeve, H. K. The varying relationship between helping and individual
796 quality. *Behav. Ecol.* **23**, 693–698 (2012).
- 797 83. Minter, T. *The Agta of the Northern Sierra Madre: Livelihood strategies and resilience*
798 *among Philippine hunter-gatherers.* (Leiden University, 2010).
- 799 84. Page, A. E. *et al.* Reproductive trade-offs in extant hunter-gatherers suggest adaptive
800 mechanism for the Neolithic expansion. *Proc. Natl. Acad. Sci.* **113**, 4694–4699. (2016).
- 801 85. Page, A. E., Minter, T., Viguier, S. & Migliano, A. B. Hunter-gatherer health and
802 development policy: How the promotion of sedentism worsens the Agta’s health
803 outcomes. *Soc. Sci. Med.* **197**, 39–48 (2018).
- 804 86. Migliano, A. B. *et al.* Characterization of hunter-gatherer networks and implications
805 for cumulative culture. *Nat. Hum. Behav.* **1**, 1–6 (2017).
- 806 87. Meehan, C. L., Quinlan, R. & Malcom, C. D. Cooperative breeding and maternal
807 energy expenditure among aka foragers. *Am. J. Hum. Biol.* **25**, 42–57 (2013).
- 808 88. Flack, J. C., Girvan, M., de Waal, F. B. M. & Krakauer, D. C. Policing stabilizes
809 construction of social niches in primates. *Nature* **439**, 426–429 (2006).
- 810 89. Brent, L. J. N., Semple, S., Dubuc, C., Heistermann, M. & Maclarnon, A. Social capital
811 and physiological stress levels in free-ranging adult female rhesus macaques. *Physiol.*
812 *Behav.* **102**, 76–83 (2011).
- 813 90. Isella, L. *et al.* What’s in a crowd? Analysis of face-to-face behavioral networks. *J.*
814 *Theor. Biol.* **271**, 166–180 (2011).
- 815 91. Hewlett, B. S., Lamb, M. E., Leyendecker, B. & Schölmerich, A. Parental investment
816 strategies among Aka foragers, Ngandu farmers and Euro-American urban-
817 industrialists. in *Adaptation and Human Behaviour: an Anthropological Perspective*
818 155–177 (2000).
- 819 92. Fouts, H. N., Hewlett, B. S. & Lamb, M. E. Parent-Offspring Weaning Conflicts among
820 the Bofi Farmers and Foragers of Central Africa. *Curr. Anthropol.* **46**, 29–50 (2005).
- 821 93. Lee, R. D. & Kramer, K. L. Children’s Economic Roles in the Maya Family Life Cycle:
822 Cain, Caldwell, and Chayanov Revisited. *Popul. Dev. Rev.* **28**, 475–499 (2002).
- 823 94. Crittenden, A. N., Conklin-Brittain, N. L., Zes, D. A., Schoeninger, M. J. & Marlowe, F.
824 W. Juvenile foraging among the Hadza: Implications for human life history. *Evol. Hum.*
825 *Behav.* **34**, 299–304 (2013).
- 826 95. Kramer, K. L. The evolution of human parental care and recruitment of juvenile help.
827 *Trends Ecol. Evol.* **26**, 533–540 (2011).
- 828 96. Konner, M. Hunter-Gatherer Infancy and Childhood: The !Kung and Others. in *Hunter-*
829 *Gatherer Childhoods: Cultural, Developmental, & Evolutionary Perspectives* (eds.
830 Hewlett, B. S. & Lamb, M. E.) 19–64 (Aldine Transaction, 2005).
- 831 97. Koster, J., Leckie, G., Miller, A. & Hames, R. Multilevel modeling analysis of dyadic
832 network data with an application to Ye’kwana food sharing. *Am. J. Phys. Anthropol.*
833 **157**, 507–512 (2015).
- 834 98. Gurven, M. To give and to give not: The behavioral ecology of human food transfers.
835 *Behavioral and Brain Sciences* **27**, 543–583 (2004).
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841 **Acknowledgements**

842 We thank the Human Evolutionary Ecology Group for their comments on earlier drafts, our
843 assistants in the Philippines, and most importantly, the Agta. We would also like to thank
844 Louise Barrett, Gillian Bentley and Rebecca Sear for their guidance and useful suggestions to
845 improve this work. This project was funded by Leverhulme Trust Grant RP2011-R 045 (to
846 A.B.M. and R.M.). R.M. received funding from European Research Council Advanced Grant
847 AdG 249347. A.E.P received funding from the MRC & DFID (grant number MR/P014216/1).
848 The funders had no role in study design, data collection and analysis, decision to publish or
849 preparation of the manuscript.

850

851 **Author contributions**

852 A.E.P conceived and designed this study, A.B.M led the research project and supervised the
853 study. S.V and A.E.P designed the notes, A.E.P analysed the data with M.G.T and wrote the
854 manuscript with A.B.M. A.E.P, M.D, S.V and D.S collected data. M.G.T, M.D, S.V, D.S, N.C, J.T,
855 G.S, R.M and A.B.M all assisted in writing the manuscript.

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857 **Competing interests**

858 The authors declare no competing interests.

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876 **Figures legends**

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879 **Figure 1: Predictors of carer-child interactions.** Odd ratios with 95% CI for each of the
880 predictor variables in the univariable mixed-effect models (triangles) and the full mixed-effect
881 models between and within households (circles; $n = 1,701$) and the full mixed-effect models
882 between households only (squares; $n = 1,615$). Bars represent 95% confidence intervals, bars
883 spanning the 0 line are non-significant.

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885 **Figure 2: Relatedness, need and reciprocity and carer-child interactions.** Model predicted
886 number of contacts based on interactions between kin type and a) receiver household need;
887 b) household reciprocity. Red lines are close kin ($r = 0.5$), green lines distant kin ($0 \leq r \leq 0.25$)
888 and non-kin ($r = 0$) are represented by blue lines. Shaded zones represent 95% confidence
889 intervals

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892 **Tables**

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894 **Table 1:** Breakdown of the proportion of allocare activities received by infants and children.
895 Being 'talked to' is when a caregiver may be talking to the focal child within the specified
896 levels of proximity.

	Infants	Children
Carried	0.056	0.007
Care for (fed and cleaned)	0.028	0.012
Played with	0.034	0.064
Talked to	0.208	0.189
In a playgroup	0.038	0.119
Touched	0.105	0.057
Arms-length	0.349	0.350
3-meters	0.182	0.203

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901 **Table 2:** Results from multi-level models examining different predictors for the number of dyadic interactions between and within households
 902 ($n = 1,701$). Standardised odds ratios (OR) are reported alongside 95% confidence intervals. Random effect variances are presented for each
 903 specified effect in the model at the bottom of the table. Reference for the adult and old age groups is juvenile (6 – 16 years), the reference for
 904 child sex is male (female = 1).

Parameter	Relatedness				Household need				Learning to mother				Costly signalling			
	OR	<i>p</i>	95% CI		OR	<i>p</i>	95% CI		OR	<i>p</i>	95% CI		OR	<i>p</i>	95% CI	
Intercept	0.004	<0.001	0.002	0.01	0.002	<0.001	0.001	0.004	0.002	<0.001	0.001	0.004	0.002	<0.001	0.001	0.004
Child age	0.995	0.958	0.837	1.184	0.985	0.863	0.831	1.168	0.983	0.845	0.829	1.166	0.964	0.678	0.812	1.145
Child sex	1.336	0.085	0.961	1.859	1.325	0.089	0.958	1.833	1.332	0.084	0.962	1.844	1.332	0.084	0.962	1.844
Adult	3.338	<0.001	1.693	6.579	5.227	<0.001	2.643	10.337	6.004	<0.001	2.896	12.447	6.096	<0.001	3.09	12.027
Old age	3.484	0.004	1.485	8.176	6.983	<0.001	2.969	16.424	8.884	<0.001	3.382	23.341	10.105	<0.001	4.126	24.746
Age diff	0.172	<0.001	0.105	0.284	0.08	<0.001	0.048	0.131	0.08	<0.001	0.048	0.131	0.072	<0.001	0.043	0.118
Proximity	1.51	<0.001	1.478	1.543	1.961	<0.001	1.926	1.995	1.957	<0.001	1.924	1.992	1.957	<0.001	1.924	1.992
<i>r</i>	1.184	<0.001	1.175	1.194	-	-	-	-	-	-	-	-	-	-	-	-
Need	-	-	-	-	0.979	0.177	0.948	1.01	-	-	-	-	-	-	-	-
Learn	-	-	-	-	-	-	-	-	1.433	0.196	0.83	2.473	-	-	-	-
Signal	-	-	-	-	-	-	-	-	-	-	-	-	0.533	0.016	0.32	0.889
Adult*age diff	9.472	<0.001	6.497	13.809	14.597	<0.001	10.029	21.246	14.528	<0.001	9.981	21.148	14.537	<0.001	9.988	21.158
Old*age diff	6.44	<0.001	4.418	9.386	13.738	<0.001	9.454	19.964	13.683	<0.001	9.415	19.887	13.683	<0.001	9.416	19.883
<i>Giver</i>			1.242 (56.30%)				1.278 (59.7%)				1.221 (56.91%)				1.199 (57.25%)	
<i>Child</i>			0.508 (23.02%)				0.485 (22.67%)				0.484 (22.55%)				0.484 (23.09%)	
<i>Give-house</i>			0.159 (7.22%)				0.144 (6.72%)				0.20 (9.31%)				0.172 (8.19%)	
<i>Child-house</i>			0.049 (2.22%)				0.052 (2.44%)				0.059 (2.73%)				0.059 (2.82%)	
<i>Camp</i>			0.248 (11.25%)				0.182 (8.47%)				0.182 (8.50%)				0.181 (8.65%)	

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908 **Table 3:** Results from the multi-level models examining different predictors for the number of dyadic interactions between households only as
 909 the three predictors are household level variables ($n = 1,615$). Standardised odds ratios (OR) are reported alongside 95% confidence intervals.
 910 Random effect variances are presented for each specified effect in the model at the bottom of the table. Reference for the adult and old age
 911 groups is juvenile (6 – 16 years), the reference for child sex is male (female = 1).

Parameter	Household Reciprocity				Givers dependents				Givers carers			
	OR	<i>p</i>	95% CI		OR	<i>p</i>	95% CI		OR	<i>p</i>	95% CI	
Intercept	0.010	<0.001	0.004	0.025	0.013	<0.001	0.005	0.033	0.017	<0.001	0.007	0.041
Child age	1.039	0.686	0.863	1.252	1.010	0.914	0.841	1.214	1.042	0.663	0.866	1.253
Child sex	1.425	0.054	0.995	2.043	1.421	0.051	0.998	2.023	1.420	0.052	0.998	2.022
Adult	1.076	0.846	0.513	2.256	0.657	0.271	0.311	1.387	0.632	0.225	0.301	1.326
Old age	1.397	0.475	0.558	3.494	1.050	0.917	0.419	2.632	0.707	0.468	0.278	1.801
Age difference	0.540	0.034	0.306	0.953	0.734	0.286	0.417	1.295	0.867	0.625	0.489	1.537
Proximity	1.063	<0.001	1.037	1.090	1.326	<0.001	1.298	1.356	1.326	<0.001	1.298	1.356
Reciprocity	1.189	<0.001	1.179	1.199	-	-	-	-	-	-	-	-
Givers depends	-	-	-	-	0.734	0.286	0.417	1.295	-	-	-	-
Givers carers	-	-	-	-	-	-	-	-	0.661	0.000	0.534	0.817
Adult*age diff	2.686	0.000	1.686	4.281	1.532	0.070	0.966	2.431	1.523	0.074	0.960	2.417
Old age*agediff	2.043	0.002	1.287	3.244	1.503	0.082	0.950	2.377	1.497	0.085	0.946	2.367
<i>Giver</i>			1.260 (48.67%)				1.264 (51.81%)				1.317 (54.4%)	
<i>Child</i>			0.540 (20.88%)				0.546 (22.37%)				0.549 (22.66%)	
<i>Giver house</i>			0.228 (8.80%)				0.236 (9.7%)				0.217 (8.95%)	
<i>Child house</i>			0.152 (5.89%)				0.095 (3.9%)				0.091 (3.75%)	
<i>Camp</i>			0.408 (15.76%)				0.298 (12.2%)				0.248 (10.24%)	

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915 **Table 4:** Full models with all variables for model (A) between and within households ($n = 1,701$) and model (B) between households only ($n =$
916 1615). Standardised odds ratios (OR) are reported alongside 95% confidence intervals. Random effect variances are presented for each specified
917 effect in the model. Reference for the adult and old age groups is juvenile (6 – 16 years), the reference for child sex is male (female = 1).

Parameter	(A) Full model between and within households				(B) Full model between households			
	OR	<i>p</i>	95% CI		OR	<i>p</i>	95% CI	
Intercept	0.003	<0.001	0.001	0.008	0.009	<0.001	0.003	0.025
Child age	0.976	0.783	0.820	1.161	1.052	0.599	0.871	1.271
Child sex	1.338	0.085	0.961	1.863	1.455	0.043	1.012	2.091
Adult	4.177	<0.001	2.075	8.412	1.342	0.446	0.630	2.857
Old age	5.713	<0.001	2.208	14.784	1.561	0.390	0.566	4.305
Age difference	0.156	<0.001	0.094	0.257	0.576	0.064	0.322	1.032
Proximity	1.510	<0.001	1.477	1.542	1.048	<0.001	1.021	1.075
R	1.185	<0.001	1.175	1.194	1.015	0.010	1.004	1.027
Receivers need	1.007	0.673	0.976	1.039	1.087	<0.001	1.050	1.126
Learn to mother	1.260	0.386	0.748	2.121	1.338	0.278	0.790	2.265
Costly signalling	0.569	0.028	0.344	0.941	0.628	0.083	0.371	1.062
Reciprocity	-	-	-	-	1.183	<0.001	1.172	1.195
Givers depends	-	-	-	-	1.162	0.359	0.843	1.601
Givers carers	-	-	-	-	0.651	<0.001	0.522	0.811
Adult*age diff	9.457	<0.001	6.486	13.789	2.721	<0.001	1.706	4.340
Old age*agediff	6.424	<0.001	4.407	9.365	2.070	0.002	1.302	3.290
<i>Giver</i>			1.140 (52.68%)				1.232(48.54%)	
<i>Child</i>			0.506 (23.38%)				0.543 (21.39%)	
<i>Giver house</i>			0.214 (9.86%)				0.2261 (10.29%)	
<i>Child house</i>			0.052 (2.44%)				0.171 (6.74%)	
<i>Camp</i>			0.252 (11.64%)				0.331 (13.05%)	

918 **Table 5:** Model predicted relationship between need and reciprocity interacting with kin type. In each model, the reference group is close kin (r
 919 = 0.5). The predictor is relevant to the model (need in model 1 and reciprocity in model 2). The beta values given for the interactions
 920 (predictor*distant or non-kin) denotes the change in the odds ratio (OR) within each kin group compared to the reference group of close kin.
 921 The ORs given in text represent the effect of need or reciprocity in each kin group, presented alongside 95% confidence intervals. The reference
 922 for child sex is male (female = 1).

Parameter	Model 1: Need ($n = 1701$)				Model 2: Reciprocity ($n = 1610$)			
	OR	p	2.5% CI	97.5% CI	OR	p	2.5% CI	97.5% CI
Intercept	0.048	<0.001	0.031	0.076	0.008	<0.001	0.004	0.015
Child age	0.963	0.663	0.814	1.140	1.021	0.815	0.857	1.217
Child sex	1.363	0.077	0.967	1.921	1.431	0.051	0.998	2.051
Predictor	1.485	<0.001	1.428	1.544	1.176	<0.001	1.140	1.212
Distant kin	0.368	<0.001	0.357	0.379	1.551	<0.001	1.437	1.674
Non-kin	0.322	<0.001	0.312	0.332	1.544	<0.001	1.430	1.667
Predictor*distant kin	0.701	<0.001	0.681	0.722	1.028	0.095	0.995	1.061
Predictor*non-kin	0.679	<0.001	0.660	0.699	1.097	<0.001	1.061	1.135

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