

1 Why care for someone else's child? Testing
2 adaptive hypotheses in Agta foragers

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42 **Abstract**

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

56

57 **Main**

58 Women in natural fertility populations rapidly produce, on average, six to eight highly
59 dependent offspring during their lifetime¹. This frequently entails more provisioning than
60 mothers alone can provide, causing long-term shortfalls in childcare². The cooperative
61 breeding hypothesis argues that such rapid reproduction is only possible due to the assistance
62 from non-parental sources, known as alloparenting. While authors point to humans' large
63 social networks, indicating the importance of a diverse array of alloparents, including non-
64 kin^{3–7}, previous literature has tended to focus on key relatives such as grandmothers⁸ and
65 siblings (who are seen as both co-operators and competitors^{9,10}) as well as exploring the
66 adaptive value of allocare in terms of increased child survival and maternal fertility^{11–13} or
67 decreases to maternal workload^{14,15}. Thus, it is well established that one type of relative
68 (exactly which depends on ecological context¹¹) has a positive influence on child survival,
69 wellbeing or maternal fertility. However, comparatively underexplored is a systematic
70 exploration of the alternative hypotheses for cooperation in breeding.

71

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

79

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

92

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

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

109

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

120

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

133

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

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

151

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

163

164 **Results**

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

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

169

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

186

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

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

206

207 Interaction models

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

214

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

228

229 Discussion

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

239

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

250

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

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

273

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

287

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

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

300

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

311

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

323

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

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

341

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

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

362

363 **Methods**

364 **The Agta**

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

380

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

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

391

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

397

398 Motes and childcare observations

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

417

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

427

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

444

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

450 7 ± 7% and 23 ± 13% for grandparents, other kin ($r \leq 0.25$ and ≥ 0.125) and non-kin ($r < 0.125$),
451 respectively (note these proportions do not sum to 1 since children can be with more than
452 one individual at any given observation). These same children were observed spending 37 ±
453 26% of time within three meters of their mothers, 19 ± 19% with fathers, 24 ± 19 % with
454 siblings and 2 ± 1%, 7 ± 8% and 24 ± 20% of their time with grandparents, other kin and non-
455 kin, respectively (Supplementary Figure 2). Overall, the consistency between the
456 observational and motes data leads us to conclude motes have a high reliability (specifically,
457 they are not systematically biasing the data with superfluous interactions) and represent a
458 type of proximity which can be considered ‘childcare’.

459

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

477

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

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

495

496 Variables

497 ***Alloparents and dependent children***

498 Individuals aged six or over were defined as alloparents following our observations and the
499 wider literature which demonstrates increased production and economic activities after the
500 age of five^{93–95}. As dependent children are all those under the age of 11 years there is overlap
501 between the child and allopARENT categories (for 33 alloparents or 22.3% of the sample). To
502 avoid this circularity, children could only be ‘cared’ for by individuals who were at least five
503 years older than themselves. For instance, a child of five years could be ‘cared’ for by an
504 individual aged ten years, a situation not uncommon from our observations and within the
505 childcare literature in hunter-gatherers^{61,96}. However, a child of nine years could not be
506 ‘cared’ for by the same ten-year-old. As a result, the youngest child in a camp could not be
507 considered to be allopARENT, regardless of whether they were aged six or over. This allowed
508 us to capture the crossover of juveniles as both dependents and carers. To confirm the five-
509 year age difference exerted no undue influence on our results we ran sensitivity analysis
510 (Supplementary Tables 5-7) exploring the effect of age difference thresholds of two, five and
511 ten years. These analyses demonstrate the results are robust regardless of the age difference.

512 ***Residential proximity***

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

520 ***Household-level reciprocity***

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

538

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

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

548 ***Giver household cost and receiver need***

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

557

558 ***Relatedness and individual categories***

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

567

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

575 Statistical analysis

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

589

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

601

602 **Data availability**

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

605

606 **References**

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

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

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

- 746 **8**, 15223 (2018).
- 747 61. Kramer, K. L. Cooperative Breeding and its Significance to the Demographic Success of
748 Humans. *Annu. Rev. Anthropol.* **39**, 417–436 (2010).
- 749 62. Sear, R. & Coall, D. How Much Does Family Matter? Cooperative Breeding and the
750 Demographic Transition. *Popul. Dev. Rev.* **37**, 81–112 (2011).
- 751 63. Jetz, W. & Rubenstein, D. R. Environmental uncertainty and the global biogeography
752 of cooperative breeding in birds. *Curr. Biol.* **21**, 72–78 (2011).
- 753 64. Baden, A. L., Wright, P. C., Louis, E. E. & Bradley, B. J. Communal nesting, kinship, and
754 maternal success in a social primate. *Behav. Ecol. Sociobiol.* **67**, 1939–1950 (2013).
- 755 65. Kokko, H., Johnstone, R. a & Clutton-Brock, T. H. The evolution of cooperative
756 breeding through group augmentation. *Proc. Biol. Sci.* **268**, 187–196 (2001).
- 757 66. Smith, D. *et al.* Camp stability predicts patterns of hunter-gatherer cooperation. *R. Soc. Open Sci.* **3**, 160131 (2016).
- 758 67. Snopkowski, K. & Sear, R. Grandparental help in Indonesia is directed preferentially
759 towards needier descendants: a potential confounder when exploring grandparental
760 influences on child health. *Soc. Sci. Med.* **128**, 105–14 (2015).
- 761 68. Dyble, M., Gardner, A., Vinicius, L. & Migliano, A. B. Inclusive fitness for in-laws. *Biol. Lett.* **14**, 20180515 (2018).
- 762 69. Carter, G. G., Wilkinson, G. S. & Page, R. A. Food-sharing vampire bats are more
763 nepotistic under conditions of perceived risk. *Behav. Ecol.* **280**, 20122573 (2017).
- 764 70. Barclay, P. Strategies for cooperation in biological markets, especially for humans.
765 *Evolution and Human Behavior* **34**, 164–175 (2013).
- 766 71. Davies, N. B., Krebs, J. R. & West, S. *An Introduction to Behavioural Ecology*. (Wiley-
767 Blackwell, 2012). doi:10.1037/026600
- 768 72. Fried, J. J. The role of juvenile pine voles (*Microtus pinetorum*) in the caretaking of
769 their younger siblings. (North Carolina State University, 1987).
- 770 73. Silk, J. B. Kidnapping and female competition among captive bonnet macaques.
771 *Primates* **21**, 100–110 (1980).
- 772 74. Hrdy, S. B. *Mothers and Others: The evolutionary origins of mutual understanding*.
773 (Harvard University Press, 2009).
- 774 75. Tardif, S. D., Carson, R. L. & Gangaware, B. L. Infant-care Behavior of Non-
775 reproductive Helpers in a Communal-care Primate, the Cotton-top Tamarin (*Saguinus*
776 *oedipus*). *Ethology* **92**, 155–167 (1992).
- 777 76. Kramer, K. L., Veile, A. & Otárola-Castillo, E. Sibling competition & growth tradeoffs.
778 Biological vs. statistical significance. *PLoS One* **11**, 1–17 (2016).
- 779 77. Davies, N. B., Hatchwell, B. J., Robson, T. & Burke, T. Paternity and parental effort in
780 dunnocks *Prunella modularis*: how good are male chick-feeding rules? *Anim. Behav.*
781 **43**, 729–745 (1992).
- 782 78. Baker, A. J., Dietz, J. M. & Kleiman, D. G. Behavioural evidence for monopolization of
783 paternity in multi-male groups of golden lion tamarins. *Anim. Behav.* **46**, 1091–1103
784 (1993).
- 785 79. Winking, J., Gurven, M., Kaplan, H. & Stieglitz, J. The goals of direct paternal care
786 among a south Amerindian population. *Am. J. Phys. Anthropol.* **139**, 295–304 (2009).
- 787 80. Scelza, B. A. The maternal niche: Critical caretaking among Martu Aborigines.
788 *Am. J. Hum. Biol.* **21**, 448–454 (2009).
- 789 81. Meehan, C. L. The effects of residential locality on parental and alloparental
790 investment among the Aka foragers of the central African Republic. *Hum. Nat.* **16**,
- 791
- 792

- 793 58–80 (2005).
- 794 82. Barclay, P. & Reeve, H. K. The varying relationship between helping and individual
795 quality. *Behav. Ecol.* **23**, 693–698 (2012).
- 796 83. Minter, T. The Agta of the Northern Sierra Madre: Livelihood strategies and resilience
797 among Philippine hunter-gatherers. (Leiden University, 2010).
- 798 84. Page, A. E. *et al.* Reproductive trade-offs in extant hunter-gatherers suggest adaptive
799 mechanism for the Neolithic expansion. *Proc. Natl. Acad. Sci.* **113**, 4694–4699. (2016).
- 800 85. Page, A. E., Minter, T., Viguier, S. & Migliano, A. B. Hunter-gatherer health and
801 development policy: How the promotion of sedentism worsens the Agta's health
802 outcomes. *Soc. Sci. Med.* **197**, 39–48 (2018).
- 803 86. Migliano, A. B. *et al.* Characterization of hunter-gatherer networks and implications
804 for cumulative culture. *Nat. Hum. Behav.* **1**, 1–6 (2017).
- 805 87. Meehan, C. L., Quinlan, R. & Malcom, C. D. Cooperative breeding and maternal
806 energy expenditure among aka foragers. *Am. J. Hum. Biol.* **25**, 42–57 (2013).
- 807 88. Flack, J. C., Girvan, M., de Waal, F. B. M. & Krakauer, D. C. Policing stabilizes
808 construction of social niches in primates. *Nature* **439**, 426–429 (2006).
- 809 89. Brent, L. J. N., Semple, S., Dubuc, C., Heistermann, M. & Maclarnon, A. Social capital
810 and physiological stress levels in free-ranging adult female rhesus macaques. *Physiol.*
811 *Behav.* **102**, 76–83 (2011).
- 812 90. Isella, L. *et al.* What's in a crowd? Analysis of face-to-face behavioral networks. *J.*
813 *Theor. Biol.* **271**, 166–180 (2011).
- 814 91. Hewlett, B. S., Lamb, M. E., Leyendecker, B. & Schölmerich, A. Parental investment
815 strategies among Aka foragers, Ngandu farmers and Euro-American urban-
816 industrialists. in *Adaptation and Human Behaviour: an Anthropological Perspective*
817 155–177 (2000).
- 818 92. Fouts, H. N., Hewlett, B. S. & Lamb, M. E. Parent-Offspring Weaning Conflicts among
819 the Bofi Farmers and Foragers of Central Africa. *Curr. Anthropol.* **46**, 29–50 (2005).
- 820 93. Lee, R. D. & Kramer, K. L. Children's Economic Roles in the Maya Family Life Cycle:
821 Cain, Caldwell, and Chayanov Revisited. *Popul. Dev. Rev.* **28**, 475–499 (2002).
- 822 94. Crittenden, A. N., Conklin-Brittain, N. L., Zes, D. A., Schoeninger, M. J. & Marlowe, F.
823 W. Juvenile foraging among the Hadza: Implications for human life history. *Evol. Hum.*
824 *Behav.* **34**, 299–304 (2013).
- 825 95. Kramer, K. L. The evolution of human parental care and recruitment of juvenile help.
826 *Trends Ecol. Evol.* **26**, 533–540 (2011).
- 827 96. Konner, M. Hunter-Gatherer Infancy and Childhood: The !Kung and Others. in *Hunter-*
828 *Gatherer Childhoods: Cultural, Developmental, & Evolutionary Perspectives* (eds.
829 Hewlett, B. S. & Lamb, M. E.) 19–64 (Aldine Transaction, 2005).
- 830 97. Koster, J., Leckie, G., Miller, A. & Hames, R. Multilevel modeling analysis of dyadic
831 network data with an application to Ye'kwana food sharing. *Am. J. Phys. Anthropol.*
832 **157**, 507–512 (2015).
- 833 98. Gurven, M. To give and to give not: The behavioral ecology of human food transfers.
834 *Behavioral and Brain Sciences* **27**, 543–583 (2004).
- 835
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849

850 **Author contributions**

851 A.E.P conceived and designed this study, A.B.M led the research project and supervised the
852 study. S.V and A.E.P designed the motes, A.E.P analysed the data with M.G.T and wrote the
853 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,
854 G.S, R.M and A.B.M all assisted in writing the manuscript.

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856 **Competing interests**

857 The authors declare no competing interests.

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875 **Figures legends**

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

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

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891 **Tables**

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893 **Table 1:** Breakdown of the proportion of allocare activities received by infants and children.
894 Being 'talked to' is when a caregiver may be talking to the focal child within the specified
895 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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900 **Table 2:** Results from multi-level models examining different predictors for the number of dyadic interactions between and within households
 901 ($n = 1,701$). Standardised odds ratios (OR) are reported alongside 95% confidence intervals. Random effect variances are presented for each
 902 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
 903 child sex is male (female = 1).

Parameter	Relatedness				Household need				Learning to mother				Costly signalling			
	OR	p	95% CI		OR	p	95% CI		OR	p	95% CI		OR	p	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
r	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
Giver	1.242 (56.30%)				1.278 (59.7%)				1.221 (56.91%)				1.199 (57.25%)			
Child	0.508 (23.02%)				0.485 (22.67%)				0.484 (22.55%)				0.484 (23.09%)			
Give-house	0.159 (7.22%)				0.144 (6.72%)				0.20 (9.31%)				0.172 (8.19%)			
Child-house	0.049 (2.22%)				0.052 (2.44%)				0.059 (2.73%)				0.059 (2.82%)			
Camp	0.248 (11.25%)				0.182 (8.47%)				0.182 (8.50%)				0.181 (8.65%)			

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907 **Table 3:** Results from the multi-level models examining different predictors for the number of dyadic interactions between households only as
 908 the three predictors are household level variables ($n = 1,615$). Standardised odds ratios (OR) are reported alongside 95% confidence intervals.
 909 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
 910 groups is juvenile (6 – 16 years), the reference for child sex is male (female = 1).

Parameter	Household Reciprocity				Givers dependents				Givers carers			
	OR	p	95% CI		OR	p	95% CI		OR	p	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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914 **Table 4:** Full models with all variables for model (A) between and within households ($n = 1,701$) and model (B) between households only ($n =$
 915 1615). Standardised odds ratios (OR) are reported alongside 95% confidence intervals. Random effect variances are presented for each specified
 916 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	p	95% CI		OR	p	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%)	

917 **Table 5:** Model predicted relationship between need and reciprocity interacting with kin type. In each model, the reference group is close kin (r
 918 = 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
 919 (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.
 920 The ORs given in text represent the effect of need or reciprocity in each kin group, presented alongside 95% confidence intervals. The reference
 921 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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