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

Abigail E. Page^{1,2,*}, Matthew G. Thomas², Daniel Smith³, Mark Dyble⁴, Sylvain Viguiier², Nikhil Chaudhary⁵, Gul Deniz Salali², James Thompson², Ruth Mace², Andrea B. Migliano⁶

¹Department of Population Health, London School of Hygiene and Tropical Medicine, London, UK

²Department of Anthropology, University College London, London, UK ³Bristol Medical School,

University of Bristol, Bristol, UK ⁴Department of Zoology, University of Cambridge, Cambridge,

UK ⁵Department of Archaeology, University of Cambridge, UK ⁶Department of Anthropology,

University of Zurich, Zurich, Switzerland

Abstract

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

Women in natural fertility populations rapidly produce, on average, six to eight highly dependent offspring during their lifetime¹. This frequently entails more provisioning than mothers alone can provide, causing long-term shortfalls in childcare². The cooperative breeding hypothesis argues that such rapid reproduction is only possible due to the assistance from non-parental sources, known as alloparenting. While authors point to humans' large social networks, indicating the importance of a diverse array of alloparents,

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*Corresponding author: Abigail E. Page (abigail.page@lshtm.ac.uk; ORCID linked to account on Manuscript Tracking system).

Author contributions

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

Competing interests

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including non-kin³⁻⁷, previous literature has tended to focus on key relatives such as grandmothers⁸ and siblings (who are seen as both co-operators and competitors^{9,10}) as well as exploring the adaptive value of allocare in terms of increased child survival and maternal fertility¹¹⁻¹³ or decreases to maternal workload^{14,15}. Thus, it is well established that one type of relative (exactly which depends on ecological context¹¹) has a positive influence on child survival, wellbeing or maternal fertility. However, comparatively underexplored is a systematic exploration of the alternative hypotheses for cooperation in breeding.

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

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

Reciprocal cooperation can evolve if the cost of helping in the present is outweighed by the probability of future benefits²⁷, even if the 'transactions' are not balanced²⁸ as cooperation can be directed at 'needy' individuals²⁹. Therefore, cooperation can occur in the absence of indirect fitness benefits³⁰. However, early theorists explicitly stated that 'kinship may be involved'²⁷, indicating that kin selection and reciprocity are not competing hypotheses. Thus, cooperators can receive direct benefits regardless of whether they are related or not²³. The evidence of the importance of reciprocity is now mounting in food sharing³¹, allogrooming²⁴ and childcare³² in both human and non-human primates. Furthermore, recent work in vampire bats (*Desmodus rotundus*) demonstrated that highly related pairs engaged in more reciprocal food sharing³³, as also witnessed in humans^{5,34,35}, however this has not consistently been the case³⁶. Certainly, related reciprocal dyads will receive indirect benefits on top of direct returns, reducing the possible direct fitness losses associated with cheating³⁷. Furthermore, reciprocity may be more likely in kin due to reduced geographic distance and thus increased opportunity and lower transaction costs, prompting cooperation regardless of relatedness^{18,35}. Consequently, capturing residential proximity may reduce the importance of relatedness as they frequently co-vary^{21,35,38,39}.

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

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

Other direct benefits of alloparenting include increasing an individual's mating success and their future ability to rear offspring. Lancaster (1971) posited that young, non-reproductively active females may alloparent to learn and develop their skills, since more experienced primiparous mothers have better infant outcomes⁵³. Particularly, this should be the case if offspring are highly vulnerable and dependent on high quality care⁵⁴. Accordingly, Baker (1991) found that inexperienced, non-reproductive free-ranging golden lion tamarin (*Leontopithecus rosalia*) females carried offspring more than other allomothers. Furthermore, in Mongolian gerbils (*Meriones unguiculatus*) first-time mothers with allomothering experience had increased reproductive performance and pup condition⁵⁶. The third possible direct benefit is increased mating success, where males signal their quality to a mate by partaking in costly allocare⁵⁷. Therefore, alloparenting may develop if it increases a male's access to females, or if male alloparenting becomes a desirable trait to picky females⁵⁸. For instance, cotton-top tamarins (*Saguinus oedipus*) males were more likely to engage in successful copulation when carrying infants⁵⁹ and male mountain gorillas (*Gorilla beringei*) who affiliated with more infants sired more offspring⁶⁰. Thus, here we will explore the relative importance of both indirect benefits (kin selection) and direct benefits (reciprocity, learning-to-mother and costly signalling) in a foraging population, the Agta of Palanan, Philippines.

We hypothesise that indirect and direct benefits are important and mutually inclusive predictors of alloparenting, allowing for access to a wide-range of cooperators, including non-kin. Given the literature cited above, we developed the following predictions: *i)*

frequency of interactions between children and alloparents will increase with indirect benefits (relatedness) and direct benefits (reciprocity, costly signalling and learning-to-mother); *ii*) reciprocity will occur among kin to varying degrees, depending on relatedness; *iii*) relatedness will positively interact with need; and *iv*) childcare interactions will be influenced by costs which decrease interactions. To test these predictions, we collected high-resolution interaction data from 1,701 alloparent-child dyads (147 alloparents, 85 children in six camps) over roughly one-week in each camp using 1.5-meter spatial proximity as a proxy for childcare.

Results

All model residuals were checked for normality and zero-inflation using the DHARMA package and descriptive statistics for all variables are given in Supplementary Tables 2-4. All variables in the analysis were standardised over two standard deviations allowing easy comparison of the effect of different predictor variables. All models are two-tailed tests.

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

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

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

Interaction models

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

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

Discussion

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

Relatedness had a strong effect on the number of interactions between alloparents and children, in line with a wide array of literature on cooperation in hunter-gatherers, from childcare, economic games and food sharing^{5,20,21,46,47,66}. We have shown that, following Hamilton’s rule, benefits are important mediators in breeding cooperatively. Accordingly,

we demonstrated that close kin provided more childcare when the indirect benefits (i.e. household need) were high, a finding which has been repeated elsewhere^{36,41,42,67}. We were not so successful at capturing a measure of giver 'cost', as alloparent households with more carers interacted with children more, not less. It may be that this finding reflects the fact that when there are a lot of carers available, each of these alloparents do less. Further exploration is required to parcel out these effects.

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

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

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

Likewise, we found that reproductively aged males interacted with dependent children the least, likely because males were heavily involved in indirect childcare activities such as food production. Thus, this does not support the costly signalling hypothesis which suggests that males copiously signal their quality in direct childcare to achieve increased mating success (of course, here signalling via hunting skills has gone unmeasured). Similar results have been found in callitrichids, where males did not increase care according to mating access, receptiveness of females, state of oestrus, nor was the provisioning of care closely followed by copulation attempts^{77,78}. Motivations of paternal care have also been explored among the Tsimane horticultural-foragers of Bolivia, finding no support for the predictions of costly signalling. As males provided the most passive care (in contrast to conspicuous, ‘signalling’ childcare) when mothers were absent, it appeared that the division of labour was a more important motivator of male childcare in humans⁷⁹.

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

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

While motes cannot provide data on the nature of the interaction, they do capture a far wider range of alloparents. Yet, of course, while direct allocare requires close proximity, this does not mean that close proximity equates to allocare. For instance, some interactions may be superfluous as two individuals simply walk past one another, or even antagonistic. There is no way to separate these interactions from the motes data. However, as discussed in the methodological section, there is near perfect overlap between the motes data and the observational data which confirms that the ‘motes proximity’ is the same as observational ‘childcare proximity’. Therefore, this inability to separate interactions is not systematically biasing the data. A final consideration is that our measure of ‘allocare’ is not dependent on the absence of the child’s main caregiver. Therefore, some interactions may consist of a ten-

year old interacting with a three-year-old when the mother is present. This feature has been maintained in the data because it is reflective of reality; by entertaining and engaging with a younger child in the presence of the mother, the older child has significantly reduced the mother's workload allowing her to rest, socialise or conduct other household tasks in the presence of a dependent child. Ultimately, while the notes produce less in-depth data, due to the increased sample size and duration the amount of data allows for more complex analyses required to explore the question 'why care?'

Here, we have demonstrated that while kinship plays an important role in structuring childcare interactions in a foraging population, this is not the sole explanation. When different predictors of alternative hypotheses are examined together, alongside costs and benefits, we find that different predictors are important for different individuals. For close kin, interactions increased when the inclusive fitness returns are high. However, while both close and distant relatives share genetic material with children, their interactions appeared *also* dependent on household-level reciprocity. This household-level reciprocity may have been maintained because of the increased trust and likelihood of future interactions between relatives, however its maintenance was not *solely* dependent on indirect benefits. Thus, it is incomplete to argue that nepotistic mechanisms drive cooperation in breeding for humans without conducting multivariate analyses to weigh up different hypotheses and including adequate controls⁸². Without this intensive care from close kin and a wide childcare network of distant kind and non-kin, mothers may not be able to maintain a rapid reproductive rate, particularly in the face of unpredictable shortfalls during environmental stochasticity. In a population with minimal-to-no material wealth, social capital and cooperation from outside the household may provide a 'buffer' to energetic shortfalls⁴⁹. Ensuring cooperation from both kin and non-kin alike is likely a major behavioural adaptation to ensure individuals' reproductive success. By exploring childcare in humans from this perspective, we can offer important new insights into why both kin and non-kin alloparents care in an unpredictable foraging ecology, highlighting how ultimate explanations must be considered mutually inclusive.

Methods

The Agta

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

highly variable foraging returns, necessitating significant food distribution and cooperation, influencing the social structure of camps⁴⁷. Therefore, we expect there to be significant cooperation between a wide range of individuals.

Data collection occurred over two field seasons from April to June 2013 and February to October 2014. We stayed approximately 10-14 days in six camps for two, sometimes three visits during the fieldwork period and conducted genealogical interviews, notes data collection and focal follows. Overall the genealogies collected contained 2,953 living and dead Agta from Palanan and neighbouring municipalities. From this data, it was possible to establish the coefficient of relatedness (r) of each dyad. As a small population the sample and its ultimate size is a product of everyone who we met in each of the camps who was willing to participate in the various data collection activities. No statistical methods were used to pre-determine sample sizes but our sample sizes are larger than previously reported in childcare analyses in foragers^{20,81}.

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

Motes and childcare observations

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

Each device sent a message every two minutes that contained its unique ID, a time stamp and the signal strength. These messages are stored by any other mote within a three meter radius. Being within three meters is a common threshold applied in behavioural studies of human and non-human primates to denote dyadic exchanges⁸⁷⁻⁹⁰, however for increased robustness, here we will use a subset of the interactions which occur within 1.5 meters. This

threshold captured close interactions, such as playing, hunting, foraging and socialising as well as low-investment proximity, such as watching or simply being near to a child and intervening when required. Once these data were processed, we checked and confirmed autocorrelation was not systematically biasing our data (Supplementary Figure 3).

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

Means were produced for the proportion of time these five children spent within three-meters of various categories of kin. The differences between the two forms of data collection are minimal, and the distribution of observations is not significantly altered between the two methods. For instance, the motes recorded that the children spent on average $34 \pm 26\%$ (SD) of time with mothers, $11 \pm 5\%$ of time with fathers, $24 \pm 13\%$ of time with siblings and $6 \pm 6\%$, $7 \pm 7\%$ and $23 \pm 13\%$ for grandparents, other kin ($r = 0.25$ and 0.125) and non-kin ($r < 0.125$), respectively (note these proportions do not sum to 1 since children can be with more than one individual at any given observation). These same children were observed spending $37 \pm 26\%$ of time within three meters of their mothers, $19 \pm 19\%$ with fathers, $24 \pm 19\%$ with siblings and $2 \pm 1\%$, $7 \pm 8\%$ and $24 \pm 20\%$ of their time with grandparents, other kin and non-kin, respectively (Supplementary Figure 2). Overall, the consistency between the observational and motes data leads us to conclude motes have a high reliability (specifically, they are not systematically biasing the data with superfluous interactions) and represent a type of proximity which can be considered ‘childcare’.

It is also important to establish what kinds of interactions actually occur between individuals within three meters of one another. Using a larger sample of behavioural observations (which do not coincide with the motes data collection) of 40 children (64.5% males; 20 infants (aged less than two years) and 20 toddlers (aged two to five years)) we explored what ‘proximity’ actually means. This analysis revealed that alloparents were in proximity (i.e. not engaging in any other activities) for 61% of interactions with children and 63.6% of interactions with infants (Table 1). This includes touching, being at arms-length, or being three meters from a child. In contrast, high investment activities (play, carry, groom, etc.) only accounted for 11.8% of interactions for infants and 8.3% for children. Childcare in the

Agta, thus, is defined by low-investment, passive childcare, rather than high-investment, active childcare. We would like to reinforce the importance of proximity as a form of childcare, as if the ultimate aim of allocare is to reduce the maternal workload by ‘watching’ or being ‘proximate’ to children then our definition of childcare should not ignore these key forms of investment. Here, however, as we are using proximity data in which we do not know the nature of the interaction we have reduced the data down to interactions at 1.5 meters or closer to ensure we are not capturing too many superfluous interactions in which an older individual is simply nearby a child, but pays little attention to that child.

Motes allowed us to produce high-resolution proximity networks for a larger sample than previously possible. While a one-week snapshot of interactions may not be reflective of a typical week for all individuals, this method greatly increases the sample size and observational time compared to traditional methods. Given the labour-intensive nature of behavioural observations, many previous studies have been limited by small sample sizes. For instance, in previous studies using focal follow techniques, sample sizes are often limited to 15 to 25 children^{20,81}, who are only observed for a total of 9 hours^{91,92}. Thus, while not only increasing the number individuals observed, the motes also greatly increase the duration of these observations. This substantially increases the representativeness of the sample and the statistical power of any analysis, allowing more complex methods. This issue of sample size is perhaps one reason why the study of cooperation in breeding within anthropology has not systematically explored alternative hypotheses; more elaborate methods which systematically control for the interrelationships between relatedness, proximity and reciprocity require significantly more statistical power. Furthermore, while the motes offer less detail than traditional approaches, they do consist of a less intrusive form of data collection, and therefore the fieldworker does not risk biasing the results due to their presence in following and recording all activities of a focal child.

Variables

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

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

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

This variable was created as follows: for the 'giving household' (household *i*) a composite value was created which captures all *observed* childcare events each dependent child in *i* had received from all carers in the 'receiving household' (household *j*, visualised in Supplementary Figure 1). As reciprocity is a household-level predictor, it was only used in analyses *between* households (i.e. it is not used to predict co-residing sibling care, and therefore the sample is reduced from $n = 1,701$ to $n = 1,615$). As the reciprocity variable was created from the observed childcare interactions between a carer and a child, this measure only contains actual childcare interactions which includes playing, holding, cleaning, feeding, talking to, or watching and/or being in close proximity to a child.

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

dependent children (0-11 years) in the child's household by the number of carers in that household.

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

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

Statistical analysis

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

In each analysis we controlled for child age and sex (0 = male) as well as the age difference between alloparent and child, to capture the fact that children closer in age were more likely to be playing together. Age difference was run in an interaction with carer age (grouped into child (aged 10 or less), adult (aged 10 to 40) and older adult (aged 40 plus) for the sake of the interaction) as the effect of age difference varies between age groups, Supplementary Table 8). As household-level reciprocity and our measures of giver 'cost' (number of household dependents and carers) are only measured for dyads residing in different households the sample size was reduced to $n = 1,615$ for four models. Consequently, two sets of 'full' models are presented in Table 3, predicting allocare between and within

households in which cost and reciprocity are not included ($n = 1,701$), and between households which includes all variables but co-residing alloparents are now excluded ($n = 1615$).

Data availability

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

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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References

1. Campbell, KL, Wood, JW. Fertility in traditional societies *Natural Human Fertility*. Diggory, P, Teper, S, Potts, M, editors. Macmillan Publishing; 1988. 39–69.
2. Hill K, Hurtado AM. Cooperative breeding in South American hunter-gatherers. *Proc Biol Sci*. 2009; 276:3863–3870. [PubMed: 19692401]
3. Meehan, CL, Helfrecht, C, Malcom, CD. Implications of length development and maternal life history: allomaternal investment, peer relationships and social networks *Childhood: Origins, evolution and implications*. Meehan, CL, Crittenden, AN, editors. SAR Press; 2016. 199–220.
4. Bogin B, Bragg J, Kuzawa C. Humans are not cooperative breeders but practice biocultural reproduction. *Ann Hum Biol*. 2014; 41:368–380. [PubMed: 24932750]
5. Meehan CL. Allomaternal investment and relational uncertainty among Ngandu farmers of the Central African Republic. *Hum Nat*. 2008; 19:211–226. [PubMed: 26181465]
6. Meehan, CL, Hawks, S. Maternal and allomaternal responsiveness: the significance of cooperative caregiving in attachment theory *Different faces of attachment: Cultural variations on a universal human need*. Otto, H, Keller, H, editors. Cambridge University Press; 2014. 113–140.
7. Meehan, CL, Hawks, S. Cooperative breeding and attachment among the Aka foragers *Attachment reconsidered: Cultural perspectives on a western theory*. Quinn, N, Mageo, JM, editors. Palgrave macmillan; 2013. 85–113.
8. Hawkes K, O'Connell J. Grandmothering, menopause, and the evolution of human life histories. *Proc Natl Acad Sci*. 1998; 95:1336–1339. [PubMed: 9448332]
9. Helfrecht C, Meehan CL. Sibling effects on nutritional status: Intersections of cooperation and competition across development. *Am J Hum Biol*. 2016; 28:159–170. [PubMed: 26179564]
10. Lawson DW, Mace R. Trade-offs in modern parenting: a longitudinal study of sibling competition for parental care. *Evol Hum Behav*. 2009; doi: 10.1016/j.evolhumbehav.2008.12.001
11. Sear R, Mace R. Who keeps children alive? A review of the effects of kin on child survival. *Evol Hum Behav*. 2008; 29:1–18.
12. Snopkowski K, Sear R. Kin influences on fertility in Thailand: Effects and mechanisms. *Evol Hum Behav*. 2013; 34:130–138.

13. Meehan CL, Helfrecht C, Quinlan RJ. Cooperative breeding and Aka children's nutritional status: Is flexibility key? *Am J Phys Anthropol.* 2014; 153:513–525. [PubMed: 24452414]
14. Kramer KL, Veile A. Infant allocare in traditional societies. *Physiol Behav.* 2018; 193:117–126. [PubMed: 29730035]
15. Meehan CL, Quinlan R, Malcom CD. Cooperative breeding and maternal energy expenditure among aka foragers. *Am J Hum Biol.* 2013; 25:42–57. [PubMed: 23203600]
16. Foster KR, Wenseleers T, Ratnieks FLW. Kin selection is the key to altruism. *Trends Ecol Evol.* 2006; 21:57–60. [PubMed: 16701471]
17. Rand DG, Nowak MA. Human cooperation. *Trends Cogn Sci.* 2013; 17:413–425. [PubMed: 23856025]
18. Clutton-Brock T. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science.* 2002; 296:69–72. [PubMed: 11935014]
19. Hamilton WD. The genetical evolution of social behaviour. I. *J Theor Biol.* 1964; 7:1–16. [PubMed: 5875341]
20. Ivey PK. Cooperative reproduction in Ituri forest Hunter-Gatherers: Who cares for Efe infants? *Curr Anthropol.* 2000; 41:856–866.
21. Crittenden AN, Marlowe FW. Allomaternal care among the Hadza of Tanzania. *Hum Nat.* 2008; 19:249–262. [PubMed: 26181616]
22. Apicella, CL, Crittenden, AN. Hunter-Gatherer Families and Parenting *The Handbook of Evolutionary Psychology.* Buss, DM, editor. Vol. IV. Wiley; 2013. 1–20.
23. Chapais, B. Kinship, competence and cooperation in primates *Cooperation in Primates and Humans.* Kappeler, PM, Van Schaik, CP, editors. Springer; 2006. 47–61.
24. Schino G, Aureli F. The relative roles of kinship and reciprocity in explaining primate altruism. *Ecol Lett.* 2010; 13:45–50. [PubMed: 19840082]
25. Crittenden AN, Zes DA. Food Sharing among Hadza Hunter-Gatherer Children. *PLoS One.* 2015; 10:e0131996. [PubMed: 26151637]
26. Lukas D, Clutton-Brock T. Cooperative breeding and monogamy in mammalian societies. *Proc R Soc B Biol Sci.* 2012; 279:2151–2156.
27. Axelrod R, Hamilton WD. The Evolution of Cooperation. *Science (80-).* 1981; 211:1390–1396.
28. Gurven M. The Evolution of Contingent Cooperation. *Curr Anthropol.* 2006; 47:185–192.
29. Smith D, et al. A friend in need is a friend indeed: Need-based sharing, rather than cooperative assortment, predicts experimental resource transfers among Agta hunter-gatherers. *Evol Hum Behav.* 2018; 577
30. Trivers RL. The evolution of reciprocal altruism. *Chicago Journals.* 1971; 46:35–57.
31. Jaeggi AV, Gurven M. Reciprocity explains food sharing in humans and other primates independent of kin selection and tolerated scrounging: a phylogenetic meta-analysis. *Proc R Soc B Biol Sci.* 2013; 280:1–8.
32. Jaeggi AV, Hooper PL, Beheim BA, Kaplan H, Gurven M. Reciprocal Exchange Patterned by Market Forces Helps Explain Cooperation in a Small-Scale Society. *Curr Biol.* 2016; 26:2180–2187. [PubMed: 27451903]
33. Carter GG, Wilkinson GS, Carter GG. Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. 2013
34. Allen-Arave W, Gurven M, Hill K. Reciprocal altruism, rather than kin selection, maintains nepotistic food transfers on an Ache reservation. *Evol Hum Behav.* 2008; 29:305–318.
35. Nolin DA. Food-Sharing Networks in Lamalera, Indonesia: Reciprocity, Kinship, and Distance. *Hum Nat.* 2010; 21:243–268. [PubMed: 21218145]
36. Koster J. Interhousehold Meat Sharing among Mayangna and Miskito Horticulturalists in Nicaragua. *Hum Nat.* 2011; 22:394–415. [PubMed: 22388945]
37. Wilkinson GS. Reciprocal food sharing in the vampire bat. *Nature.* 1984; 308:181–184.
38. Gurven M. Reciprocal altruism and food sharing decisions among Hiwi and Ache hunter-gatherers. *Behav Ecol Sociobiol.* 2004; 56:366–380.
39. Koster JM, Leckie G. Food sharing networks in lowland Nicaragua: An application of the social relations model to count data. *Soc Networks.* 2014; 38:100–110.

40. Snopkowski K, Sear R. Grandparental help in Indonesia is directed preferentially towards needier descendants: a potential confounder when exploring grandparental influences on child health. *Soc Sci Med.* 2015; 128:105–114. [PubMed: 25603472]
41. Hames R. Garden labour exchange among the Yekwana. *Ethol Sociobiol.* 1987; 8:259–284.
42. Thomas MG, et al. Kinship underlies costly cooperation in mosuo villages. *R Soc Open Sci.* 2018; 5
43. Hawkes K. Hunting income patterns among the Hadza: big game, common goods, foraging goals and the evolution of the human diet. *Philos Trans Biol Sci.* 1991; 334:243–250.
44. Gurven M, Allen-Arave W, Hill K, Hurtado M. 'It's a Wonderful Life'. signaling generosity among the Ache of Paraguay. *Evol Hum Behav.* 2000; 21:263–282. [PubMed: 10899478]
45. Sugiyama LS. Illness, injury, and disability among Shiwiar forager-horticulturalists: Implications of health-risk buffering for the evolution of human life history. *Am J Phys Anthropol.* 2004; 123:371–389. [PubMed: 15022365]
46. Jaeggi AV, Gurven M. Natural cooperators: Food sharing in humans and other primates. *Evol Anthropol.* 2013; 22:186–195. [PubMed: 23943272]
47. Dyble M, et al. Networks of Food Sharing Reveal the Functional Significance of Multilevel Sociality in Two Hunter-Gatherer Groups. *Curr Biol.* 2016; 26:2017–2021. [PubMed: 27451900]
48. Carter GG, Wilkinson GS. Social benefits of non-kin food sharing by female vampire bats. *Proc Natl Acad Sci B.* 2015; 282
49. Page AE, et al. Hunter-Gatherer Social Networks and Reproductive Success. *Sci Rep.* 2017; 7:1153. [PubMed: 28442785]
50. Dyble M, et al. Sex equality can explain the unique social structure of hunter-gatherer bands. *Science (80-.).* 2015; 348:796–798.
51. Hill KR, et al. Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science.* 2011; 331:1286–1289. [PubMed: 21393537]
52. Lancaster JB. Play-mothering: the relations between juvenile females and young infants among free-ranging vervet monkeys (*Cercopithecus aethiops*). *Folia Primatol (Basel).* 1971; 15:161–182.
53. Baker AJ, Woods F. Reproduction of the emperor tamarin (*Saguinus imperator*) in captivity, with comparisons to cotton-top and golden lion tamarins. *Am J Primatol.* 1992; 26:1–10.
54. Solomon, NG, Hayes, LD. The Biological Basis of Alloparental Behaviour in Mammals Substitute Parents: Biological and Social perspective on alloparenting across human societies. Bentley, G, Mace, R, editors. Berghahn Books; 2009. 13–49.
55. Baker, AJ. Evolution of the social system of the golden lion tamarin (*Leontopithecus rosalia*). University of Maryland: 1991.
56. Salo AL, French JA. Early experience, reproductive success and development of parental behaviour in mongolian gerbils. *Anim Behav.* 1989; 38:693–702.
57. Zahavi A. Arabian babblers: the quest for social status in a cooperative breeder. *Cooperative breeding in birds: long term studies of ecology and behaviour.* 1990; :103–130. DOI: 10.1017/CBO9780511752452.005
58. Tardif, SD. The Bioenergetics of Parental Behaviour and the Evolution of Alloparent Care in Marmosets and Tamarins Cooperative Breeding in Mammals. Solomon, NG, French, JA, editors. Cambridge University Press; 1997. 11–33.
59. Price EC, McGrew WC. Cotton-top tamarins (*Saguinus oedipus*) in a semi-naturalistic captive colony. *Am J Primatol.* 1990; 20:1–12.
60. Rosenbaum S, Vigilant L, Kuzawa CW, Stoinski TS. Caring for infants is associated with increased reproductive success for male mountain gorillas. *Sci Rep.* 2018; 8
61. Kramer KL. Cooperative Breeding and its Significance to the Demographic Success of Humans. *Annu Rev Anthropol.* 2010; 39:417–436.
62. Sear R, Coall D. How Much Does Family Matter? Cooperative Breeding and the Demographic Transition. *Popul Dev Rev.* 2011; 37:81–112. [PubMed: 21280366]
63. Jetz W, Rubenstein DR. Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Curr Biol.* 2011; 21:72–78. [PubMed: 21185192]

64. Baden AL, Wright PC, Louis EE, Bradley BJ. Communal nesting, kinship, and maternal success in a social primate. *Behav Ecol Sociobiol.* 2013; 67:1939–1950.
65. Kokko H, Johnstone Ra, Clutton-Brock TH. The evolution of cooperative breeding through group augmentation. *Proc Biol Sci.* 2001; 268:187–196. [PubMed: 11209890]
66. Smith D, et al. Camp stability predicts patterns of hunter-gatherer cooperation. *R Soc Open Sci.* 2016; 3
67. Snopkowski K, Sear R. Grandparental help in Indonesia is directed preferentially towards needier descendants: a potential confounder when exploring grandparental influences on child health. *Soc Sci Med.* 2015; 128:105–14. [PubMed: 25603472]
68. Dyble M, Gardner A, Vinicius L, Migliano AB. Inclusive fitness for in-laws. *Biol Lett.* 2018; 14
69. Carter GG, Wilkinson GS, Page RA. Food-sharing vampire bats are more nepotistic under conditions of perceived risk. *Behav Ecol.* 2017; 280
70. Barclay P. Strategies for cooperation in biological markets, especially for humans. *Evolution and Human Behavior.* 2013; 34:164–175.
71. Davies, NB, Krebs, JR, West, S. *An Introduction to Behavioural Ecology.* Wiley-Blackwell; 2012.
72. Fried, JJ. *The role of juvenile pine voles (Microtus pinetorum) in the caretaking of their younger siblings.* North Carolina State University; 1987.
73. Silk JB. Kidnapping and female competition among captive bonnet macaques. *Primates.* 1980; 21:100–110.
74. Hrdy, SB. *Mothers and Others: The evolutionary origins of mutual understanding.* Harvard University Press; 2009.
75. Tardif SD, Carson RL, Gangaware BL. Infant-care Behavior of Non-reproductive Helpers in a Communal-care Primate, the Cotton-top Tamarin (*Saguinus oedipus*). *Ethology.* 1992; 92:155–167.
76. Kramer KL, Veile A, Otárola-Castillo E. Sibling competition & growth tradeoffs. Biological vs. statistical significance. *PLoS One.* 2016; 11:1–17.
77. Davies NB, Hatchwell BJ, Robson T, Burke T. Paternity and parental effort in dunnocks *Prunella modularis*: how good are male chick-feeding rules? *Anim Behav.* 1992; 43:729–745.
78. Baker AJ, Dietz JM, Kleiman DG. Behavioural evidence for monopolization of paternity in multi-male groups of golden lion tamarins. *Anim Behav.* 1993; 46:1091–1103.
79. Winking J, Gurven M, Kaplan H, Stieglitz J. The goals of direct paternal care among a south Amerindian population. *Am J Phys Anthropol.* 2009; 139:295–304. [PubMed: 19140194]
80. Scelza BA. The grandmaternal niche: Critical caretaking among Martu Aborigines. *Am J Hum Biol.* 2009; 21:448–454. [PubMed: 19402034]
81. Meehan CL. The effects of residential locality on parental and alloparental investment among the Aka foragers of the central African Republic. *Hum Nat.* 2005; 16:58–80. [PubMed: 26189516]
82. Barclay P, Reeve HK. The varying relationship between helping and individual quality. *Behav Ecol.* 2012; 23:693–698.
83. Minter, T. *The Agta of the Northern Sierra Madre: Livelihood strategies and resilience among Philippine hunter-gatherers.* Leiden University; 2010.
84. Page AE, et al. Reproductive trade-offs in extant hunter-gatherers suggest adaptive mechanism for the Neolithic expansion. *Proc Natl Acad Sci.* 2016; 113:4694–4699. [PubMed: 27071109]
85. Page AE, Minter T, Viguier S, Migliano AB. Hunter-gatherer health and development policy: How the promotion of sedentism worsens the Agta's health outcomes. *Soc Sci Med.* 2018; 197:39–48. [PubMed: 29220707]
86. Migliano AB, et al. Characterization of hunter-gatherer networks and implications for cumulative culture. *Nat Hum Behav.* 2017; 1:1–6.
87. Meehan CL, Quinlan R, Malcom CD. Cooperative breeding and maternal energy expenditure among aka foragers. *Am J Hum Biol.* 2013; 25:42–57. [PubMed: 23203600]
88. Flack JC, Girvan M, de Waal FBM, Krakauer DC. Policing stabilizes construction of social niches in primates. *Nature.* 2006; 439:426–429. [PubMed: 16437106]

89. Brent LJN, Semple S, Dubuc C, Heistermann M, Maclarnon A. Social capital and physiological stress levels in free-ranging adult female rhesus macaques. *Physiol Behav.* 2011; 102:76–83. [PubMed: 20933532]
90. Isella L, et al. What's in a crowd? Analysis of face-to-face behavioral networks. *J Theor Biol.* 2011; 271:166–180. [PubMed: 21130777]
91. Hewlett BS, Lamb ME, Leyendecker B, Schölmerich A. Parental investment strategies among Aka foragers, Ngandu farmers and Euro-American urban-industrialists. *Adaptation and Human Behaviour: an Anthropological Perspective.* 2000:155–177.
92. Fouts HN, Hewlett BS, Lamb ME. Parent-Offspring Weaning Conflicts among the Bofi Farmers and Foragers of Central Africa. *Curr Anthropol.* 2005; 46:29–50.
93. Lee RD, Kramer KL. Children's Economic Roles in the Maya Family Life Cycle: Cain, Caldwell, and Chayanov Revisited. *Popul Dev Rev.* 2002; 28:475–499.
94. Crittenden AN, Conklin-Brittain NL, Zes DA, Schoeninger MJ, Marlowe FW. Juvenile foraging among the Hadza: Implications for human life history. *Evol Hum Behav.* 2013; 34:299–304.
95. Kramer KL. The evolution of human parental care and recruitment of juvenile help. *Trends Ecol Evol.* 2011; 26:533–540. [PubMed: 21784548]
96. Konner, M. Hunter-Gatherer Infancy and Childhood: The !Kung and Others Hunter-Gatherer Childhoods: Cultural, Developmental, & Evolutionary Perspectives. Hewlett, BS, Lamb, ME, editors. Aldine Transaction; 2005. 19–64.
97. Koster J, Leckie G, Miller A, Hames R. Multilevel modeling analysis of dyadic network data with an application to Ye'kwana food sharing. *Am J Phys Anthropol.* 2015; 157:507–512. [PubMed: 25773376]
98. Gurven M. To give and to give not: The behavioral ecology of human food transfers. *Behavioral and Brain Sciences.* 2004; 27:543–583.

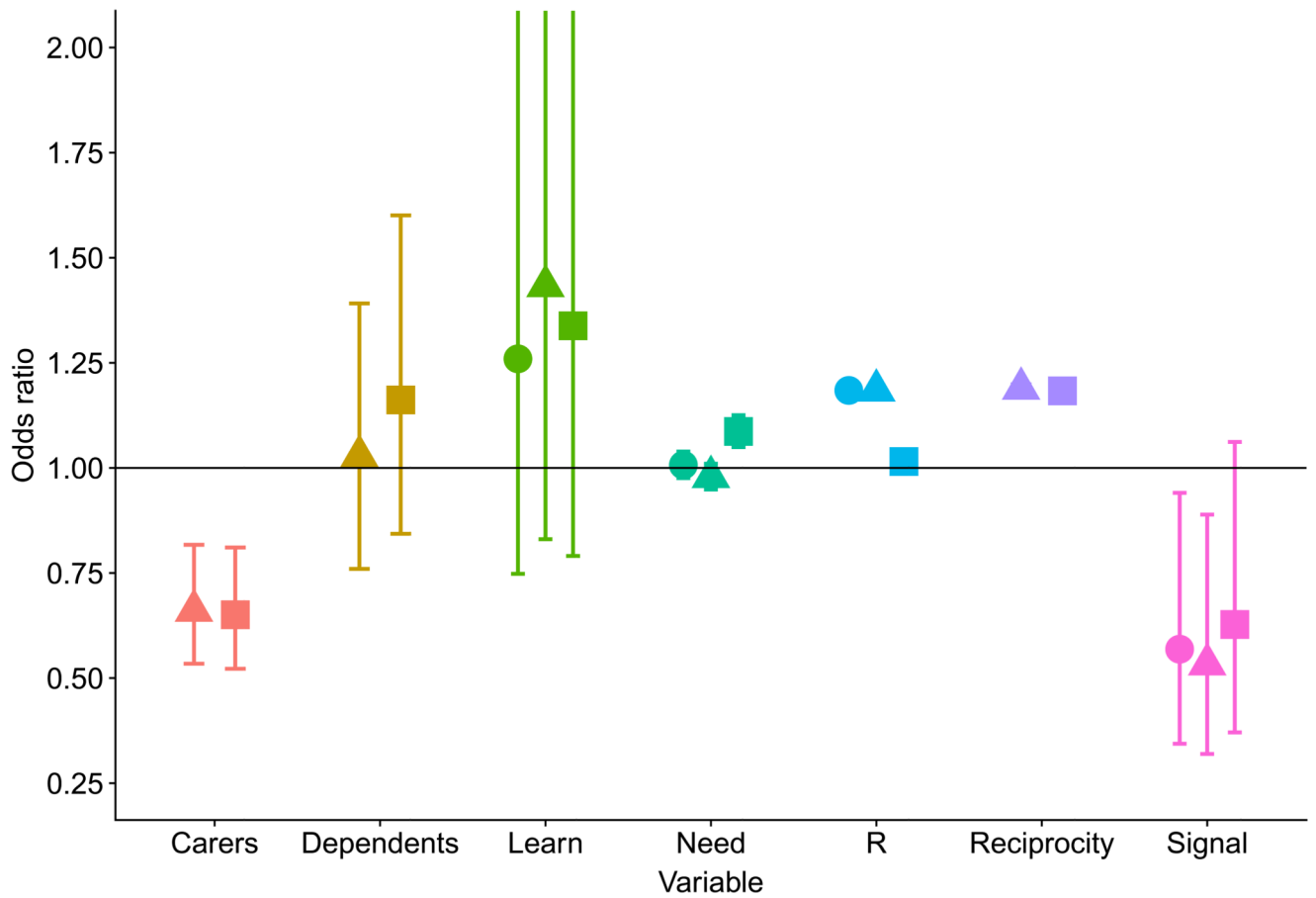


Figure 1. Predictors of carer-child interactions.

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

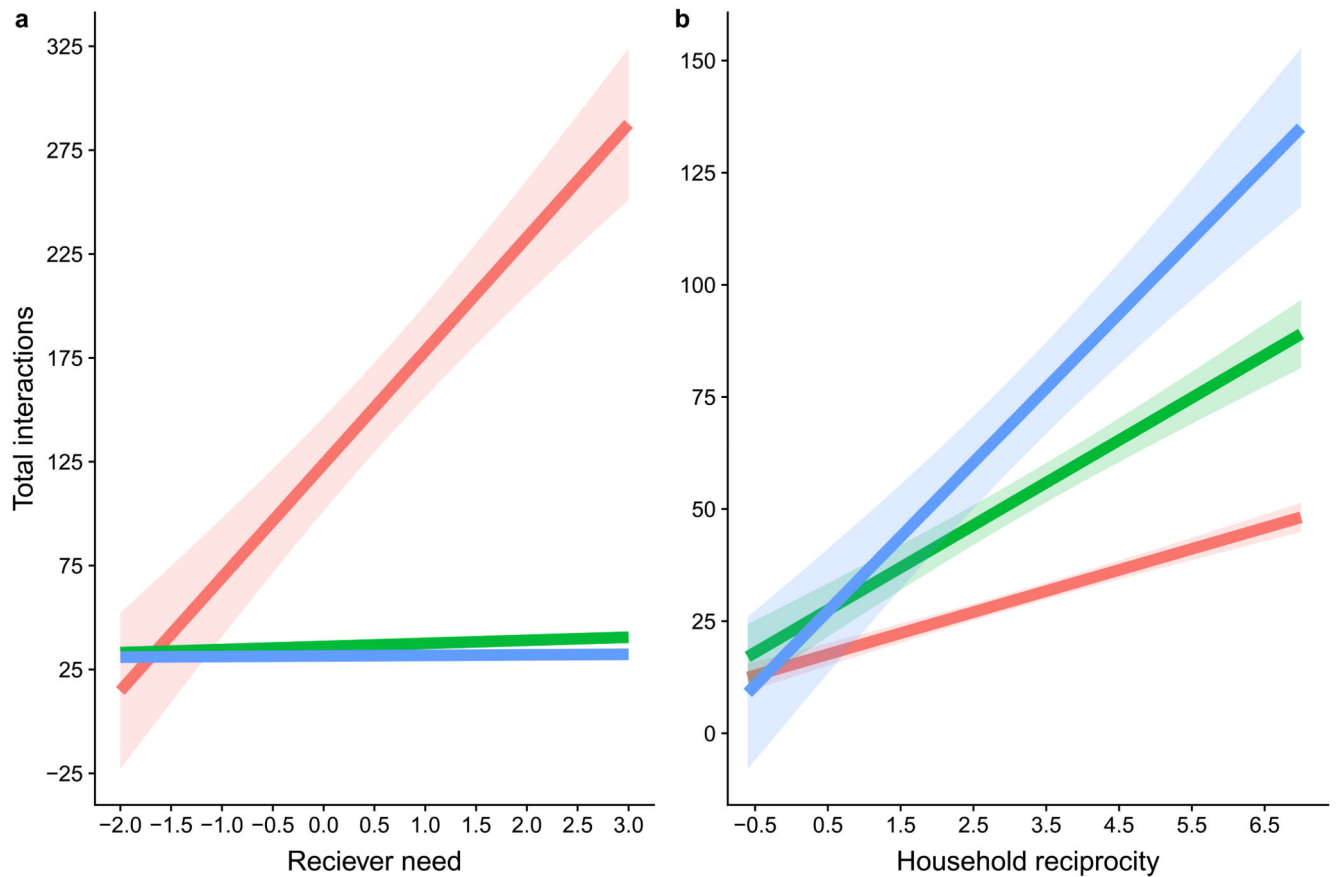


Figure 2. Relatedness, need and reciprocity and carer-child interactions.

Model predicted number of contacts based on interactions between kin type and a) receiver household need; b) household reciprocity. Red lines are close kin ($r=0.5$), green lines distant kin ($0 < r < 0.25$) and non-kin ($r=0$) are represented by blue lines. Shaded zones represent 95% confidence intervals

Table 1

Breakdown of the proportion of allocare activities received by infants and children. Being ‘talked to’ is when a caregiver may be talking to the focal child within the specified 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

Table 2

Results from multi-level models examining different predictors for the number of dyadic interactions between and within households ($n = 1,701$). Standardised odds ratios (OR) are reported alongside 95% confidence intervals. 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 groups is juvenile (6 – 16 years), the reference for 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%)	

Table 3

Results from the multi-level models examining different predictors for the number of dyadic interactions between households only as the three predictors are household level variables ($n = 1,615$). Standardised odds ratios (OR) are reported alongside 95% confidence intervals. 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 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%)		

Table 4

Full models with all variables for model (A) between and within households ($n = 1,701$) and model (B) between households only ($n = 1615$). Standardised odds ratios (OR) are reported alongside 95% confidence intervals. Random effect variances are presented for each specified 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%)		

Table 5

Model predicted relationship between need and reciprocity interacting with kin type. In each model, the reference group is close kin ($r = 0.5$). The predictor is relevant to the model (need in model 1 and reciprocity in model 2). The beta values given for the interactions (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. The ORs given in text represent the effect of need or reciprocity in each kin group, presented alongside 95% confidence intervals. The reference 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