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Author-supplied statements

Relevant information will appear here if provided.

Ethics

Does your article include research that required ethical approval or permits?:
Yes

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

Data

It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:
Yes

Statement (if applicable):
The datasets and analysis script supporting this article have been uploaded as part of the supplementary material. As the Agta are a small and vulnerable population and the data of a personal nature every effort has been made to anonymise this data and all personal information has been removed.

Conflict of interest

I/We declare we have no competing interests

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Authors' contributions

This paper has multiple authors and our individual contributions were as below

Statement (if applicable):
AEP conceptualised this study, designed the field methodology, and conducted focal follows with SV. AEP conducted data processing and analysis, while the analysis process was continually reviewed by EE, MD and DS. AEP drafted and refined the manuscript which was critically revised with by EE. MD, DS, NC, SV and ABM helped draft the manuscript. ABM oversaw and ran the project.

Children are important too: juvenile playgroups and maternal childcare in a foraging population, the Agta

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Abstract

Non-maternal caregivers (allomothers) are hypothesised to lighten the mother's workload, allowing for the specialised human life history including relatively short interbirth intervals and multiple dependent offspring. Here, using in-depth observational data on childcare provided to 78 Agta children (a foraging population in northern Philippines; aged 0-6 years), we explore whether allomaternal childcare substitutes and decreases maternal childcare. We found that allomother caregiving was associated with reduced maternal childcare, but the substitutive effect varied depending on the source and type of care. Children-only playgroups consistently predicted a decrease in maternal childcare. While grandmothers were rarely available, their presence was negatively associated with maternal presence and childcare, and grandmothers performed similar childcare activities to mothers. These results underscore the importance of allomothering in reducing maternal childcare in the Agta. Our findings suggest that flexibility in childcare sources, including children-only playgroups, may have been the key to human life history evolution. Overall, our results reinforce the necessity of a broad conceptualisation of social support in human childcare.

Keywords

Childcare; playgroups; grandmothers; allomothering; support; hunter-gatherers

Primates, compared to other mammals, are known for their "slow" life history; taking a longer time to reach maturity, having relatively fewer dependent offspring and longer interbirth intervals [1]. As primates, humans clearly share some of these characteristics. However, we are unusual in our ability to "speed-up" reproduction [2]. Humans, compared to other great apes wean infants relatively early, meaning mothers are physically able to resume reproduction quicker, leading to shorter interbirth intervals with multiple highly dependent offspring [3]. Compared to other primates, humans produce and invest in a larger number of highly costly offspring. It has been theorised that such "stacking" of offspring is only possible due to high levels of allomothering, which is unseen in other great apes [3].

Allomothering refers to investments of time and/or energy in childrearing from any individual who is not the child's mother. These transfers of time/energy can include childcare, such as holding or playing with a child (i.e., direct caregiving/care; the focus of this paper), as well as provisioning food and other resources (i.e., indirect caregiving/provisioning)[4]. To date, evolutionary anthropology's approach to understanding allomothering has largely (but not exclusively) investigated the ultimate explanations of allomothering (i.e., why it evolved) by examining allomother effects on maternal reproductive success (measured by fertility, child health and/or development and child survival)[5,6]. From this perspective, allomothers are assumed to reduce maternal energetic burden, freeing up the mother, allowing her to "stack" offspring[3]. Humans arguably evolved an obligate system of cooperative childrearing (also referred to as cooperative breeding *sensu lato*) in which allomothers facilitate the more rapid production of children *and* offspring survival[5,7,8].

For a holistic understanding of cooperative childrearing, however, ultimate reasons must be complemented with an understanding of *how* allomothering translates to increased reproductive success[6,9]. Conceptually, this is dependent on how mothers reinvest time/energy "freed up" by allomothering. For example, mothers could reallocate their "freed up" time/energy back into the existing child by, for instance, playing with the child at the same time as an allomother [10]. This is expected where mothers opt to increase child quality, as children then receive higher levels of care overall, leading to better outcomes, as demonstrated in a range of studies [11,12]. Alternatively, mothers may reduce childcare and provisioning, and re-invest elsewhere (known as *substitutive* investments[8]). In this case, allomaternal help may be associated with increased

fertility rather than child quality, as 'saved' energy is re-invested into reproductive effort. Therefore, the 'ultimate' outcome of allomothering depends on the mechanism: child condition and survivorship may even be *reduced* in some instances due to increasing fertility rates [8]- yet these pathways are frequently overlooked (but see [13,14] for notable exceptions).

This paper focuses on the mechanism behind how allomaternal caregiving influence maternal and child outcomes. We ask whether allomaternal childcare (i.e., not provisioning) substitutes maternal childcare, and whether this is influenced by the type of allomother. By substitution, we mean whether *any form of childcare* by an allomother which is associated with reductions in *any form of childcare* by the mother. By exploring these mechanisms, we are better able to hypothesise about the mechanism behind the evolution of cooperative childrearing and gain insights into human life history.

Who helps?

There is a wealth of literature on cooperative childrearing in small-scale societies, especially hunter-gatherers, exploring its consequences for maternal and child outcomes. Hunter-gatherers are populations which rely heavily (but not necessarily exclusively) on hunted, fished or foraged resources. These groups tend to be highly cooperative, widely sharing resources and labour [15]. Mothers in small-scale societies provide a high proportion of childcare [16,17], due to on-demand breastfeeding and close physical contact to mitigate early mortality risks [11,12]. As children age and become more independent maternal childcare decreases [11,16,18,19], suggesting that after weaning the opportunity for allomaternal care increases.

Some of the earliest research explored paternal care (a form of allomaternal care), hypothesising that male provisioning allowed mothers to redirect their energy from production activities to fertility and childcare, increasing maternal reproduction and child survivorship [20,21]. For instance, among Agta foragers, males generally provide the majority of calories, while females spend more time in domestic tasks and childcare [22]. While male childcare is high in some populations (e.g. the Aka [23]), fathers typically specialise in provisioning [18], and as such, studies have found that father absence is associated with greater child mortality in a range of pre-industrial societies [24]. However, this does not seem to be universal: only 47% of statistically controlled studies (n = 15) reviewed by Sear and Mace [12] found a positive relationship between

father presence and child survival, which may be because contributions from fathers can be replaced by other allomothers [11].

Beyond fathers, studies have investigated grandmothers as key allomothers given their close genetic relationship with grandchildren and reduced caring responsibilities[25]. In support, Sear and Mace [12] found that maternal grandmother presence was most consistently positively correlated with child survival (64% of 11 statistically controlled studies in natural fertility populations). However, a number of studies, particularly in hunter-gatherer/subsistence farming populations, have indicated that grandmothers have little allomaternal involvement, both in terms of direct childcare [18,26] and provisioning [27]. For example, among Aché foragers, only ~10% of females in their 30s co-resided with their mothers [27]. For most mothers, grandmothers were not available as allomothers.

Overall, fathers and grandmothers are sometimes, but not always, available as important allomothers. Interestingly, there is increasing cross-cultural evidence that children become 'helpful' in terms of household tasks, food production and childcare after 6-7 years of age [3,28,29]. Demographic studies highlight considerable levels of juvenile contributions [30,31], particularly in high-fertility societies with large siblings cohorts and few educational commitments [32]. Children provide significant help to their siblings and mothers, ensuring positive energy balances, and ultimately, household survival [26,33,34]. As a result, we expect siblings to be important allomothers in high-fertility populations.

It is important to note that, under cooperative childrearing, mothers are not restricted to receive help from kin, but may receive help from *anyone* [35]. In fact, the best cooperative strategy for successful reproduction is likely to be a flexible one, depending on which allomothers are present, willing and able [5,32]. Meehan, Helfrecht and Malcom [36] indicate that mothers and children's social networks are composed of a wide range of individuals and households are rarely dependent on a single type of allomother. Evidence suggests that non-relatives gain direct benefits from allomaternal childcare, such as having someone available to help your own children in return [37] or learning key parenting skills to improve child survival [38]. Indeed, several studies have indirectly shown that a considerable amount of allomaternal caregiving is provided by non-relatives [11,18,27].

A common feature of social life across hunter-gatherer societies is the formation of mixed-age mixed-sex playgroups, where children and young teens from different households play. The literature on playgroups in hunter-gatherers is extensive, with surprisingly similar descriptions of children collectively roaming, with freedom, around the camp and the surrounding areas [19,39–41]. These playgroups comprise of children aged ≥2 years, often without adult supervision [40]. Studies have often focused on the function of play behaviours from a developmental perspective [42]. However, playgroups also provide protection, care, teaching and stimulation to younger children [17,39]. Despite this, playgroups have not been empirically explored as a form of childcare in the cooperative childrearing literature. If playgroups allow mothers to reduce their caregiving, then playgroups may be an important facilitator for multiple, overlapping dependant offspring.

Current Aims

This paper aims to move beyond the focus on kin as allomothers and explores allomaternal care from the entirety of a child's social network. In doing so, it offers important insights into the dynamics of cooperative childrearing in humans. In particular, we investigate whether direct caregiving by non-kin, juvenile playgroups, as well as relatives (fathers, siblings, grandparents, aunts and uncles and cousins) reduces maternal childcare in a hunter-gatherer population, the Agta. Using in-depth observations of 78 children, we test the degree to which all allomaternal childcare is substitutive of maternal childcare, implicitly allowing her to re-invest energy into other domains. Once the overall substitutive role of allomaternal care is established, we then compare the importance of fathers, siblings, grandparents, distant and non-kin as well as playgroups.

As observed in other hunter-gatherer societies, we hypothesise that childcare is provided by a wide range of individuals among the Agta, but that siblings and non-related juveniles in playgroups will be particularly important caregivers. In contrast, we expect fathers to have a small role in caregiving given their focus on food production [22]. Further, we hypothesise that the effect of grandmothers will be limited due to their high mortality and high residential mobility within the population (meaning grandmothers are likely to live elsewhere) [43,44]. Specifically, we predict that: 1) allomaternal childcare from fathers and grandmothers will have no relationship with maternal childcare; 2) childcare from individual siblings will have a negative

relationship with maternal childcare, indicating substitution; and 3) allomaternal care from playgroups (including siblings, distant and non-kin juveniles) will be negatively associated with maternal childcare, also indicating substitution.

Methods

The Agta

There are around 1,000 Agta living in the Palanan municipality of north-eastern Luzon, Philippines. Riverine and marine spearfishing provides their primary source of animal protein, supplemented by hunting and gathering, as well as low-intensity cultivation, wage labour and trade [22,45]. The Agta are bilocal [46], meaning children are equally likely to reside with either their mother's or father's family [47]. As the Agta frequently change residential camp, children will likely spend time with a wide range of kin and non-kin over the course of their childhood. Previous research has highlighted their extensive cooperation, between kin and non-kin, in the domains of food sharing and childcare [37,47–49]. The Agta practice serial monogamy and have a total fertility rate of 7.7 [43] and a short average interbirth interval of 2.8 years. Infant and childhood mortality rates are high, with an estimated 38.9% of offspring dying before the age of 16 years [43]. Mortality is higher for males throughout childhood and early adulthood; however, the high costs of reproduction mean that females are increasingly underrepresented in older cohorts [44].

The Agta style of childcare, like most other hunter-gatherers, has been labelled as indulgent, affectionate and intensive where infants are permanently held, cuddled or played-with [16,45]. Children are breastfed on-demand for approximately two years (as observed during our fieldwork and reported approximately by mothers). Young children aged 0-2 years are frequently carried by mothers, usually in fabric slings [50]. As children are weaned they are carried less frequently, watched less intensively, and have significant freedom within camp as they start to participate in mixed-age, mixed-sex playgroups [16,45,51]. As documented in other populations [3,28,29], while younger children spend the time as they like, children after the age of six become increasingly involved in the household economy and provide childcare to younger siblings [16,45,50].

Data collection

Data collection occurred over two field seasons from April-June 2013 and February-October 2014. In the first season we censused 915 Agta individuals (54.7% which were male) across 20 camps. Following relative aging protocols [52], accurate ages were established for all individuals post data collection. Relatedness was established from household genealogies (involving both mothers and fathers; see [44,47]). In the second season we stayed approximately 10-14 days in ten camps to conduct focal follows of children.

Focal follows were conducted with 78 children across 10 study camps: 34 children aged 0-1.9 and 44 children aged 2 – 5.9. These two age groupings we made based on the observation that children are still intensively breastfed up until the age of two, while we considered children over the age of 6 to be providing more allomaternal care than he/she received (a decision we made during our fieldwork, prior to any analyses). No formal sampling techniques were used due to the small population size, as we were able to observe the majority of children within the study camps (Table S1). Where we were unable to observe all children in a camp, we observed at least one child per household. Although our total sample contains more boys than girls (48 males, 61.54%), this is in line with the male-biased sex ratio seen in the 0-5 year cohort in this population[44].

Recording allomothering

Two researchers (A.E.P and S.V), observed a focal child for a 9-hour period (see [13] for protocol). These observations were broken into 3x 4-hour intervals (6:00 – 10:00, 10:00 – 14:00 and 14:00 – 18:00) with a 15-minute break at each hour, and each 4-hr observation was conducted on non-consecutive days to reduce any sampling bias. During observation, researchers recorded the activities of the focal child every 20 seconds, including who came within 3m of the focal child, and the nature of their interaction.

Information on mothers was recorded regardless of the 3m proximity to the focal child. Where observable (common due to the open nature of camps), activities of the mother were recorded (which included: providing high-investment childcare for the focal child such as carrying/holding, playing; engaging in childcare of another child; household tasks; leisure; being present but not actively engaging in a task and; food production). If the mother was absent, but the observer

knew the maternal activity based on reports from family members or neighbours (i.e. individual x has gone to collect water), then this activity was recorded for the mother until she returned. Otherwise, if the mother was absent, she was recorded as 'not present'.

For allomothers, their presence and information on their activities were recorded if they were within three meters of the focal child. During data collection, only individuals estimated to be 6 years+ were recorded as allomothers. Once accurate ages had been produced, records of 'allomothers' aged below 6 years were removed from the analysis. If a focal child was involved in a playgroup (defined as when three or more children (adults could also be involved) engaged collectively in a play activity or roamed around the camp [39]) then the observer recorded the playgroup as a binary event (yes or no), for each of the individuals involved in the playgroup, during each observation interval.

Prior to the main data collection, both researchers piloted the methodology and were in close agreement about childcare/activity categories. In the following analyses, childcare by mothers and allomothers has been categorised into low-investment childcare (passive engagement; being within three-meter proximity and watching a child) or high-investment childcare (carrying/holding, playing, grooming, cleaning or providing medical attention, feeding/breastfeeding, teaching or otherwise stimulating a child; see Table S2). Throughout this paper, *childcare* refers to both low- and high-investment activities, unless otherwise specified.

Data analysis

Chi-squared analysis

To test whether allomaternal childcare was substitutive overall, we explored whether maternal activity budgets were correlated with allomaternal caregiving (regardless of type or source). Chi-squared proportion tests compared the proportion of time allocated to different tasks between 1) mothers looking after a child alone, and 2) mothers with allomaternal help.

Logistic multilevel models

The association between allomothers and maternal childcare according to the type of allomother was explored with multilevel logistic regression models, with two outcomes. The first outcome

was *maternal absence*, coded as 1 for presence and 0 for absence at the point of observation. If a mother is absent, she is not providing childcare to the focal child, thus the allocare is substitutive. The second outcome was *intensity of maternal childcare* (contingent on their presence), coded as 1 if mothers were engaged in active or high-investment childcare or 0 if they were engaged in passive or low-investment childcare. This second outcome explores partially substitutive allocare, where mothers are present (potentially supervising) but can engage in other activities.

The unit of analysis was each individual instance of childcare between an allomother and the focal child, resulting in a total observational sample size of 202,351 observations from 78 children in 84,240 observational intervals (removing those intervals in which children were alone or only with their mother). To account for the temporal sequencing in the data (i.e. that the first observation will likely predict the second, and third observations etc. with decreasing likelihood over time) the time of the observation is included as a fixed effect to adjust for the non-independence [53]. For children aged 0-1.9 years (n=34 children from 33 households), there were 82,322 dyadic interactions between 622 dyads, involving 301 allomothers from 94 households. For children aged >2 years (n=44 children from 36 households), there were 120,029 dyadic interactions between 901 dyads, involving 335 allomothers from 95 households.

Logistic mixed effect models were carried out in R v 3.2.2 using package Lme4 (function glmer [54]). To take account of clustering, random effects were added at the dyadic level (since each dyad had multiple interactions), the allomother level, the allomother's household, the child's household, and at camp level. Originally, we intended to add the child as a random effect. However, since the majority (88.46**%**) of households only contributed one child to the sample, we encountered convergence issues. The random effect variance attributed the child level was nil, thus its removal had no impact on the model.

The main predictor of kin type was modelled as 10 binary dummy variables (0 = no, 1 = yes). Individuals were established as either a: father, brother, sister, maternal grandmother, paternal grandmother, maternal grandfather, paternal grandfather, extended kin ($r = 0.25$, but excluding grandparents as named above), distant kin ($r \geq 0.03125$ & $r < 0.25$) and non-kin ($r < 0.0325$). Therefore, a sister would be recorded as 0 for the father, brother, maternal grandmother,

paternal grandmother, paternal grandfather, maternal grandfather, extended, distant and non-kin variables and 1 for the sister variable.

As playgroups were hypothesised to be of importance (in and of themselves, as well as altering the effect of specific allomothers within playgroups) an additional set of models were run. These models include a predictor term for playgroup (0 = allomother not in a playgroup, 1 = allomother in a playgroup), as well as interactions for the different types of participants in playgroups (sisters, brothers, distant, extended and non-kin, defined based on descriptive analysis of the composition of playgroups). These interactions test whether the substitutive effect of care from a particular allomother was altered by being in a playgroup. Due to the lack of playgroups in the 0-1.9 sample, the playgroup analysis was only run in the 2-5.9 sample.

All models contained controls for child age in years (as children receive less care from their mother as they age) and sex (0 = male). The distant kin, extended kin and non-kin models controlled for the allomother's age and sex. Beyond what is presented below, all model outputs are presented in the SI Tables 7-62 for transparency, and results in text are given alongside 95% confidence intervals of the odds ratios (OR). Multiple comparisons were adjusted for using Hochberg correction, and adjusted p-values are given in Table S5.

Post-hoc analyses

We conducted post-hoc exploratory analyses on the type of care provided by the three allomother types who were negatively associated with maternal childcare. This post-hoc analysis sought to test whether different allomothers engaged in different types of childcare. Looking at the mean proportion of interactions grandmothers (n= 19), grandfathers (n=18) and playgroups (n=190) spent in either: a) proximity/watching; b) playing; c) caring for; and d) holding a child, permutation tests were run to explore if the means significantly differed between the groups; 100,000 simulations shuffled the existing data randomly to produce 100,000 simulated mean differences. The p-value is then produced based on the number of times out of 100,000 that the simulated mean difference was either higher or lower than (or equal to) the mean difference of the actual sample.

Results

Descriptive statistics

Who cares?

Across the 78 children, 75 received childcare from their mothers (96%), 69 from fathers (88%), 22 and 8 from their maternal and paternal grandmothers, respectively (28% and 10%), and 23 and 13 from their maternal and paternal grandfathers, respectively (29% and 17%, Table S3). In total, children interacted with 75 sisters (per child: mean = 0.962, SD = 1.167) and 75 brothers (per child: mean = 0.915, SD = 1.200), as well as 366 distant kin (per child: mean = 4.690, SD = 3.447), 173 extended kin (per child: mean = 2.218, SD = 2.049) and 703 non-kin (per child: mean = 8.949, SD = 5.748).

Figure 1 outlines the patterns of childcare children received from mothers and allomothers (See Figures S1 and S2 for the caregiver's perspective). For children aged 0-1.9 years, mothers provided the majority of childcare (25.9% of all caregiver-child interactions), followed by non-kin, distant kin and extended kin. Siblings and fathers were involved in 7.23-8.4% of caregiver-child interactions, and grandparents in 0.3-3%. For children aged 2-5.9 years, non-kin (23.81%) rather than mothers (18.98%) provided the most childcare. Fathers, brothers and sisters had higher levels of childcare involvement (ranging from 7.7-12.8%). Maternal grandparents (1-1.9%) as well as other extended family members were less involved in childcare. Paternal grandparents' involvement was notably low at 0.3-0.6%.

Grandmothers' availability and participation

Averaged across the population, grandmothers provided little childcare because they were frequently not present (Figure S3). Only 43 (55.13%) and 34 (43.59%) of children had a maternal and paternal grandmother alive, respectively. Across 78 children, 25 co-resided (in the same camp) with a maternal grandmother (32.05% of all children; 58.14% of children with maternal grandmothers alive), and 11 with paternal grandmothers (14.10% of all children; 32.35% of children with paternal grandmothers alive). Overall, only 22 (28.21%) and 8 (10.26%) children ever received low-investment care from their maternal or paternal grandmother, respectively. For grandmothers who co-resided with focal children, 88.0% of maternal grandmothers and 72.73% of paternal grandmothers were ever observed to provide low-investment childcare. A

comparable result was found for high-investment activities (17 children received high-investment care from maternal grandmothers, equating to 21.8% of all children, or 68% with maternal grandmothers co-residing; 7 children received high-investment care from paternal grandmothers, equating to 8.97% of all children, or 63.64% with paternal grandmothers co-resident). While maternal grandmothers were more likely to be alive, present and provide childcare compared to paternal grandmothers (Table S4), our results indicate that, overall, both grandmother types were frequently *not* present in camp, and when they were, they did not necessarily provided care to grandchildren.

Playgroups

In playgroups, the average age of the focal children was 3.94 (SD = 1.28), while the average age of the allomothers was 9.85 (SD = 5.16). Only 1.8% of total observations in the 0-1.9 age group were in playgroups (which occurs mainly from children aged 1.5 – 2 years), while a total of 12.9% (observations n = 19,130) of the 2-5.9 sample's observations were in playgroups. The majority of focal children's interactions in playgroups were with children aged 6-11 years (n = 16,548, 78.3%), while interactions with adolescents aged 11-16 years comprised of 17.3% (n = 3,655) followed by interactions with individuals aged 16 + years (n = 934, 4.3%). The majority of individuals in the playgroup came from kin categories with a higher proportion of juveniles: sisters (23.5%); brothers (14.22%); distant kin (25.35%); extended kin (4.34%) and non-kin (31.49%). Adults had very little, if any, involvement in playgroups: collectively, parents and grandparents consisted of less than 1% of playgroup members. To summarise, this suggests that playgroups can be considered as *en masse* play/childcare for children aged 2-6 years by children aged 6-11 years, with some lesser involvement of adolescents, without direct adult supervision.

Chi-square results

Mothers whose children received allomaternal care, compared to mothers looking after children alone, spent 15.14 percentage points (χ^2 = 240.3, p < 0.001, 95% CI [13.37, 16.90]) less time providing childcare in the 0-1.9 sample, and 61.11 percentage points in the 2-5.9 sample (χ^2 = 1493.4, p < 0.001, 95% CI [58.19, 63.94]). Instead, mothers receiving allomaternal care spent significantly more time in food production, childcare of other children, leisure time and in

domestic tasks (SI Tables S6A and S6B). Therefore, overall allomaternal care was substitutive rather than additive in the Agta.

Logistic multilevel models results

Model set A: predicting mother presence

In the following models, an odds ratio (OR) above 1 represents an increase in maternal childcare, while an OR under 1 reflects a decrease in maternal childcare (Table 1 and 2, also see Figure S4A and S5A). In the 0-1.9 years sample, child age was negatively correlated with maternal presence (OR = 0.027, 95% CI [0.004, 0.1837], $p < 0.001$); a trend which was less strong in the 2-5.9 cohort OR = 0.562, 95% CI [0.413, 0.7651], $p < 0.001$). Overall, fathers did not provide substitutive care for mothers. In contrast, care from grandmothers and playgroups were associated with a decreased likelihood of maternal presence. For children 0-1.9yrs, childcare by paternal grandmothers was negatively associated with maternal presence (OR = 0.011, 95% CI [0.0002, 0.598], $p = 0.027$). Note, the 95% CI is wide due to the small number of paternal grandmothers, thus the point estimates may be unreliable. For children 2-5.9yrs, maternal presence was negatively predicted by maternal grandmothers (OR = 0.105, 95% CI [0.023, 0.471], $p = 0.003$) and playgroup participation (OR = 0.154, 95% CI [0.145, 0.164], $p < 0.001$). While other allomothers were not independently associated with maternal presence, this association changed when the allomothers were part of a playgroup: brothers *within playgroups* were associated with a lower odds of maternal presence (OR = 0.120, 95% CI [0.104, 0.138], $p < 0.001$), as were sisters (OR = 0.125, 95% CI [0.119, 0.140], $p < 0.001$), extended kin (OR = 0.198, 95% CI [0.158, 0.247], $p < 0.001$), distant kin (OR = 0.264, 95% CI [0.232, 0.301], $p < 0.001$) and non-kin (OR = 0.140, 95% CI [0.124, 0.159], $p < 0.001$) (Interaction models; Table 2). Therefore, within playgroups, all previously non-substitutive kin categories were negatively correlated with maternal presence.

Model set B: predicting maternal high-investment childcare

As with the maternal presence models, child age was negatively correlated with maternal childcare (0-1.9 years OR = 0.470, 95% CI [0.230, 0.962], $p = 0.039$; 2-5.9 years OR = 0.282, 95% CI [0.215, 0.371], $p < 0.001$). Overall, grandmothers did not predict a reduction in maternal childcare in either age group, nor did fathers (Table 1 and 2, also see Figure S4B & S5B). As before, in the 2-5.9yrs age group, individuals *within playgroups* were significantly associated with

reduced likelihoods of maternal childcare. Brothers in playgroups were associated with a lower odds of maternal childcare (OR = 0.118, 95% CI [0.070, 0.201], p < 0.001), as were sisters (OR = 0.532, 95% CI [0.361, 0.784], p < 0.001), extended kin (OR = 0.113, 95% CI [0.044, 0.284], p < 0.001), distant kin (OR = 0.492, 95% CI [0.342, 0.709], p < 0.001) and non-kin (OR = 0.457, 95% CI [0.317, 0.657], p < 0.001)(Interaction models; Table 2). Furthermore, in the over-twos, paternal grandfather care was associated with a reduction of maternal childcare when mothers were present (OR = 0.073, 95% CI [0.010, 0.522], p = 0.009). The opposite is true of non-kin allomothers in the under-twos (OR = 1.616, 95% CI [1.158, 2.253], p = 0.005) suggesting that mothers did not allow non-kin to provide solo-childcare to younger children.

Post-hoc analyses

From the above analysis, three categories of alloparents were negatively associated with maternal childcare: grandmothers, grandfathers and playgroups. Further explorative permutation tests demonstrated different patterns of childcare (Figure 2; see Table S6A and S6B). Grandmothers, compared to individuals in playgroups, held children more (0.113 vs. 0.019, p = 0.002), suggesting a pattern of care similar to mothers (Figure 2C and D). Unsurprisingly, individuals in playgroups played with children significantly more than grandmothers (0.172 vs. 0.014, p < 0.001) and grandfathers (0.172 vs. 0.023, p = 0.001). In contrast, the only activity grandfathers did more of was low-investment proximity/watching, compared to playgroups (0.922 vs. 0.948, p < 0.001) and grandmothers (0.867 vs. 0.948, p = 0.044). Thus, grandfathers provided extremely little 'intensive' childcare compared to all other categories.

Discussion

In the Agta, a large number of individuals were involved in providing childcare, coming from a range of kin and age categories. Overall, allomaternal childcare was associated with a reduction in maternal childcare. These results demonstrate that mothers who received help spent less time caring for that particular child and more time in other activities, such as economic tasks, caring for other children and leisure time. Thus, allomaternal care in the Agta can be considered substitutive rather than additive. While we have yet to explore why care is substitutive, such trends are likely influenced by ecological context, dependent on which strategies have the highest fitness payoffs [8]. For instance, allomaternal care in the Agta *may* be substitutive since

mothers, in general, appeared to invest in high fertility due to ecological risks [43,44] limiting the fitness payoff of the increased childcare associated with additive care. Further investigation should explore the relationship between allomothering, environmental pressures, activity budgets and fertility trends. The source of the childcare is important to consider since different allomothers were associated with different effects on maternal childcare, and childcare from grandmothers and playgroups appeared to be most consistently associated with reductions in maternal childcare.

Absent, but helpful, grandmothers

Much attention has been paid to grandmothers as important allomothers[55]. In terms of inclusive fitness, grandmothers arguably have much to gain and little to lose by allomothering due to their reproductive cessation. Studies about *how* grandmothers help across populations have highlighted their roles in food production[25], domestic tasks[56], informational and emotional support [57], as well as financial help [58] and increased maternal labour force participation [59]. Our results support these findings, where grandmothers provided care and substituted maternal childcare. Complementary results have been reported in the Aka hunter-gatherers, where grandmaternal care was associated with a 150 kcal decrease in mother's daily energetic expenditure [13]. One reason why grandmaternal care may readily replace maternal care is that maternal and grandmaternal childcare patterns are similar, focusing on holding and caring. Among the Martu, Scelza [60] found that grandmothers performed more demanding childcare tasks. However, among the Martu, grandmothers were the second most important caregivers (after mothers); a finding not replicated among the Agta. In the Agta, grandmothers were beneficial *when available*, but they rarely were.

Similar to Hill and Hurtado's [27] findings in the Ache and Hiwi (South American hunter-gatherers), we found that many children did not having a living grandmother. In the Agta, on average, grandmothers were only alive for 15-19 years after last reproduction. Furthermore, even if children had a living grandmother this did not guarantee co-residence, or that the grandmother would provide childcare due to fertility schedules: Fifty-four children had living grandmothers at time of data collection, aged between 38-74 years. Younger grandmothers aged ≤51 years (n = 18) had an average of 6.34 (SD = 2.08) children, of which 2.44 (SD = 1.75) were aged ≤11 years. As such, many grandmothers experienced reproductive conflict with their

daughters, as demonstrated elsewhere[9,61]. For older grandmothers aged ≥52 years (n = 12), while none had children aged under 11, they had on average 20.38 (SD = 11.93) grandchildren, of which 13.25 (SD = 3.96) were aged under 11. Therefore, older grandmothers certainly could not care for all of their grandchildren.

High fertility and mortality trends combined may explain why many Agta children were not co-resident with grandmothers and did not receive grandmaternal care. Grandmothers cannot be assumed to experience zero- or low-opportunity costs (i.e. they provide care because they do not have their own children) when providing allomaternal care because of overlapping reproductive careers, and their importance may be dependent on the demographic regime leading to contrasting results among different populations [27].

The duality of play and the allomaternal playgroup

These results demonstrate that playgroups collectively provided childcare which did not require adult involvement, and were negatively correlated with maternal childcare. While Konner [39] proposed that one possible function of playgroups was childcare, we know of no research empirically testing this hypothesis. By doing so, our results highlight the potential of playgroups as 'collective allomothers'. Given the ubiquitous presence of playgroups across foraging societies [62], the need of such an investigation is apparent. Playgroups may have been understudied in this domain previous due to 'play' being defined by its lack of current purpose [42], and assumed 'function' in the form of longer-term skills development [42,63–65]. Certainly, children gain much from play, however, this does not exclude the duality of 'work-play', where children also make economic contributions [66].

An interesting question is why the collective effect of playgroups had a negative relationship with maternal childcare, when the individual allomothers had no such effect. Perhaps mothers trusted the 'collective' to provide the type and quality of childcare required to keep younger children out of danger. Our results suggest that the increased play may have meant increased 'active' attention by allomothers, highlighted by playgroups providing the least amount of low investment childcare. Allomothers may be more likely to provide childcare in the playgroup because the costs of childcare are shared among five or ten other individuals [39]. In the diffused form of playgroups, childcare may have little net cost to individual allomothers, particularly if

older members of the playgroup gain key physical, social, emotional and behavioural skills from their participation [17,39], including parenting skills [38]. Measuring the costs and benefits to children within playgroups is an important next step.

Overall, these results indicate that the role of children as caregivers should not be ignored by researchers. While children caring for children is often conceptualised as harmful in the West [67], our results reiterate the important and positive role children can occupy as caregivers. Indeed, our findings suggest children can be competent caregivers without conflicting with play, challenging the Western notion of the need to "protect" children from caregiving responsibilities [67].

Siblings and fathers: provisioning rather than childcare?

Despite expectations, siblings were not associated with maternal childcare, and therefore did not appear to substitute childcare outside of playgroups. This is surprising since siblings, particularly sisters, provide a significant amount of childcare across a range of small-scale societies [26], and have been associated with improvements in child survivorship and/or health [12,68] as well as maternal fertility [69,70], although not consistently [71,72]. The lack of significant effect in our results may stem from the importance of older siblings conducting domestic tasks [34] as well as food production activities [26,33,73], rather than caregiving, which we are unable to test in the current data. Certainly, siblings are involved in substantial childcare activities; however, the substitutive effect appears limited to playgroups. Similarly, we found that fathers did not substitute maternal childcare. This is not to suggest they were unhelpful, but rather that their major allomaternal contribution is food and resource provisioning, rather than childcare [22]. Since male production has gone unmeasured in this study, we are likely underestimating the role of fathers.

Limitations

Anthropological studies of childcare are often frustrated by small sample sizes. Thus, a concern is that a couple of 'unusual' households or days may exert overt influence. Here, we have attempted to maximise sample sizes in order to mitigate against this possibility as much as possible, observeing the majority of children in our study population. Nonetheless, this remains

a small and time-limited sample. A second limitation of this work, as highlighted in the discussion above, is that a measurement of provisioning and household tasks is unavailable. Assistance in household tasks, or the provisioning of food both equally 'free up' mothers' time just as childcare does. As a result, our results only paint one-third of the picture; further analysis should reconcile these elements.

Conclusions

Our results underline the importance of a wide range of allomothers in supporting Agta mothers. Playgroups were associated with a significant reduction in maternal childcare; something that may be particularly important in high mortality, high fertility environments where grandparents are unlikely to be alive, co-resident *and* able to help. Unrelated children in playgroups are important allomothers, something which has been under-investigated to date. In many populations, children may be a readily available source of childcare, offering important flexibility to mothers. While allomaternal care is certainly a necessity in supporting the unique life-history strategy of humans, we argue that the individuals who provide this care will vary with social structure and demography. Ultimately, a mother's ability to obtain childcare from a wide range of people may be the key to human demographic success.

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Figures legends

Figure 1: The kinship composition of childcare from the children's perspective (0-1.9 years, left blue bar and 2-5.9 years, right grey bar). Actual percentages given at top of each bar and represents a count of interactions between all children and different allomothers, converted into a percentage. MGM = maternal grandmother, PGM = paternal grandmother, MGF = maternal grandfather, PGF = paternal grandfather.

Figure 2: mean proportion of activities spent in either a) low investment, b) playing, c) caring activities and d) holding children for different categories. Error bars represent SEM.

Tables

Table 1: Mixed-effects model results for the relationship between an instance of allomaternal childcare to a child aged 0-1.9 years and two measures of maternal childcare. MGM = maternal grandmother, PGM = paternal grandmother, MGF = maternal grandfather, PGF = paternal grandfather, extended = extended kin at r = 0.25, distant = distant kin at r < 0.25 & r >= 0.03125 and non = non-kin at r < 0.0325.

	Maternal presence (n = 82,323)				**Maternal childcare if present (n = 63,202)**			
	OR	**L95%CI**	**U95%CI**	**p**	**OR**	**L95%CI**	**U95%CI**	**p**
Father	0.721	0.253	2.057	0.541	1.275	0.658	2.470	0.471
Sister	0.572	0.182	1.794	0.338	0.563	0.275	1.151	0.116
Brother	0.613	0.200	1.881	0.393	0.744	0.368	1.506	0.411
MGM	0.930	0.169	5.116	0.933	0.530	0.175	1.607	0.262
PGM	0.011	0.000	0.598	0.027	0.989	0.032	30.250	0.995
MGF	0.802	0.121	5.331	0.819	0.616	0.161	2.353	0.478
PGF	0.590	0.045	7.803	0.689	0.496	0.091	2.707	0.418
Extended Kin	1.181	0.572	2.437	0.653	0.717	0.457	1.125	0.148
Distant Kin	0.969	0.538	1.745	0.917	1.014	0.697	1.475	0.941
Non-kin	1.508	0.878	2.590	0.137	1.616	1.158	2.254	0.005

Table 2: Mixed-effect model results for the relationship between an instance of allomaternal childcare to a child aged 2-5.9 years and two measures of maternal childcare. MGM = maternal grandmother, PGM = paternal grandmother, MGF = maternal grandfather, PGF = paternal grandfather, extended = extended kin at r = 0.25, distant = distant kin at r < 0.25 & r >= 0.03125 and non = non-kin at r < 0.0325.

	Maternal presence (n = 120,029)				**Maternal childcare if present (n = 65,562)**			
	OR	**L95%CI**	**U95%CI**	**p**	**OR**	**L95%CI**	**U95%CI**	**p**
Father	2.066	0.974	4.384	0.059	1.208	0.642	2.274	0.557
Sister	1.078	0.369	3.152	0.890	1.014	0.470	2.186	0.973
Brother	0.956	0.312	2.932	0.937	1.090	0.498	2.384	0.829
MGM	0.105	0.023	0.471	0.003	0.780	0.196	3.098	0.724
PGM	0.541	0.022	13.299	0.707	0.390	0.044	3.480	0.399
MGF	1.685	0.168	16.890	0.657	0.385	0.068	2.178	0.280
PGF	3.951	0.276	56.536	0.311	0.074	0.011	0.520	0.009
Extended kin	2.139	1.014	4.513	0.046	0.932	0.526	1.651	0.810
Distant kin	0.967	0.586	1.594	0.895	0.982	0.590	1.634	0.945
Non-kin	0.773	0.488	1.226	0.274	1.129	0.761	1.676	0.547
Playgroup	0.154	0.145	0.164	0.000	0.339	0.281	0.410	<0.001
	Interaction Models: Playgroup x Allomother							
Playgroup	0.168	0.156	0.180	<0.001	0.301	0.243	0.373	<0.001
Sister* Playgroup	0.747	0.654	0.854	<0.001	1.765	1.132	2.752	0.012
Playgroup	0.162	0.152	1.164	<0.001	0.428	0.349	0.526	<0.001
Brother*Playgroup	0.737	0.628	1.875	<0.001	0.276	0.157	0.487	<0.001
Playgroup	0.151	0.142	1.153	<0.001	0.366	0.301	0.445	<0.001
Extended kin* Playgroup	1.306	1.036	2.817	0.024	0.308	0.119	0.791	0.014
Playgroup	0.134	0.125	1.134	<0.001	0.299	0.240	0.374	<0.001
Distant kin* Playgroup	1.967	1.699	5.470	<0.001	1.642	1.071	2.518	0.023
Playgroup	0.159	0.148	1.160	<0.001	0.305	0.244	0.382	<0.001
Non-kin* Playgroup	0.885	0.767	2.153	0.096	1.497	0.977	2.294	0.064