Cooperation and Partner Choice Among Agta Hunter-Gatherer Children: An Evolutionary Developmental Perspective

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Abstract

Examining development is essential for a full understanding of behaviour, including how individuals acquire traits and how adaptive evolutionary forces shape these processes. The present study explores cooperative development among the Agta, a Filipino hunter-gatherer population. A simple resource allocation game assessing both levels of cooperation (how much children shared) and patterns of partner choice (who they shared with) was played with 179 children between the ages of 3 and 18. Children were given five resources (candies) and for each was asked whether to keep it for themselves or share with someone else, and if so, who this was. Between-camp variation in children's cooperative behaviour was substantial, and the only strong predictor of children's cooperation was the average level of cooperation among adults in camp; that is, children were more cooperative in camps where adults were more cooperative. Neither age, sex, relatedness or parental levels of cooperation were strongly associated with the amount children shared. Children preferentially shared with close kin (especially siblings), although older children increasingly shared with less-related individuals. Findings are discussed in terms of their implications for understanding cross-cultural patterns of children's cooperation, and broader links with human cooperative childcare and life history evolution.

Keywords: Cooperation; Development; Partner Choice; Hunter-Gatherers; Experimental Games; Agta.

Introduction

Cooperation is key human adaptation, yet relatively little research has investigated how cooperative behaviour develops over childhood, while even less developmental work has occurred in the context of cooperation in small-scale societies, and hunter-gatherers in particular. Developmental research is necessary for a complete understanding of behaviour (Tinbergen 1963), while cross-cultural research, especially in small-scale societies, is required to assess how behaviour develops outside of Western societies, where behaviour may not be representative of current human diversity or our deeper evolutionary history (Henrich *et al.* 2010). This ontogenetic perspective may be especially valuable for understanding human cooperation, as even though children are somewhat dependent on provisioning until adulthood (Kaplan *et al.* 2000), they are not merely burdens to adults, but rather engage in useful cooperative activities such as caring for other children, performing domestic tasks and foraging (Kramer 2010; Crittenden *et al.* 2013; Page *et al.* 2021a).

Although spontaneous helping occurs in children by the age of 12 months (reviewed in (Warneken 2015)), previous research on cooperative development has found that levels of cooperation tend to increase throughout childhood, both in Western (Fehr *et al.* 2008) and small-scale (House *et al.* 2013, 2019; Blake *et al.* 2015; Crittenden & Zes 2015) societies (for an exception, see (House *et al.* 2012)). For instance, across six diverse societies, including hunter-gatherer, horticultural and urban populations, patterns of costly cooperation were similar in all populations until middle childhood (approx. 6-8 years old), after which societies diverged to approximate population-specific adult levels of cooperation ((House *et al.* 2013) see also (House *et al.* 2019)). Thus, in addition to cooperation increasing over childhood, previous research

suggests that children appear to increasingly attune their cooperative behaviour as they develop to correspond to adult patterns of cooperation.

However, the majority of these studies have used experimental methods which either paired children with anonymous others (e.g., (Fehr *et al.* 2008; House *et al.* 2019)) or with unrelated individuals (although partners were known to each other, such as attending the same school or living in the same village; e.g., (House *et al.* 2012, 2013; Blake *et al.* 2015)). These studies may overlook the important role of 'partner choice' in determining cooperative behaviour (Barclay 2013), in that who children are interacting with is likely to impact how much they cooperate. For instance, following kin selection theory (Hamilton 1964), children – all else being equal – may be more likely to cooperate with close kin, rather than non-kin or more distant relatives, because of the indirect fitness benefits accrued by helping close kin grow, survive and reproduce. By only assessing cooperation towards non-kin or strangers, many previous studies may have overlooked how partner choice shapes children's cooperative behaviour. Experimental studies have demonstrated that North American (Olson & Spelke 2008) and Chinese (Lu & Chang 2016) children are more likely to share with kin and friends, relative to strangers (for an exception to this kin-bias among French children, see (Barragan-Jason *et al.* 2021)). In an observational study of food-sharing with Hadza children (Tanzanian hunter-gatherers), resources were preferentially directed towards reciprocal partners and kin (Crittenden & Zes 2015). Other studies in small-scale societies have shown that children preferentially invest in close kin, especially siblings, over more distant kin (Crittenden & Marlowe 2008; Kramer 2010; Page *et al.* 2019). Thus, partner choice likely shapes patterns of cooperation among children, particularly regarding kinship which we focus on in this study.

Partner choice is unlikely to remain static during development. Among two forager populations, the Filipino Agta (the current study population) and the Congolese BaYaka, interactions with non-kin increased throughout childhood (Migliano *et al.* 2017), potentially reflecting the need to establish extensive non-kin networks of cooperation in adulthood (Hill *et al.* 2011; Apicella *et al.* 2012; Dyble *et al.* 2015). Children also need to learn the social and economic skills necessary for independent living, including foraging, mate acquisition and alliance formation (Kaplan *et al.* 2000; Flinn & Ward 2005; Crittenden *et al.* 2013). Learning these skills is likely to require extensive interactions with peers of a similar age, especially in playgroups (Lew-Levy & Boyette 2018; Salali *et al.* 2019; Page *et al.* 2021a), rather than learning solely from siblings (i.e., a greater reliance on distant kin or unrelated individuals, relative to close kin). Collectively, these considerations lead to the broad expectation that cooperation will be directed towards close kin in early childhood, while social and cooperative networks will broaden throughout childhood, including increasing interactions with non-kin. This generalised prediction is predominantly based on our current knowledge of childhood, kinship and cooperation in mobile immediate-return hunter-gatherers, and it is likely that these patterns will vary depending on the local social, ecological and cultural conditions, particularly in non-foraging societies. For instance, children's involvement in subsistence activities varies across populations (Kramer 2005), as does the amount of care provided by siblings (Kramer 2010; Helfrecht *et al.* 2020), while in many Western and industrialised societies children have few siblings and institutions like nurseries and schools bring large numbers of unrelated children together from a young age (David-Barrett 2019). Nonetheless, as a broad prediction we expect that the importance of relationships with non-kin will increase through childhood.

Using a cross-sectional experimental design, we aim to investigate children's cooperative behaviour among the Agta, a population of Filipino hunter-gatherers. Our design allows children to share with multiple partners, permitting an exploration of both how much children share and who they share with. This research asks the following questions: i) Without constraining who children interact with, how do levels of cooperation develop over childhood? and ii) How do patterns of partner choice change throughout ontogeny, with a focus on genetic relatedness? Based on existing research we predict that levels of cooperation will increase with age. We also expect that this developmental trajectory will vary between camps, with cooperation in later childhood matching camp-specific adult-levels of cooperation (previous research has identified substantial variation in cooperation between Agta camps using similar games conducted among adults; (Smith *et al.* 2016)). Regarding the second question (patterns of partner choice), consistent with kin selection theory we predict that much cooperation will be directed towards close kin, especially siblings. Given the necessity of developing alliances and skills for adulthood – which often involves extensive cooperation among non-kin – we also expect that this kin-bias will decrease with age, as children preferentially interact and cooperate with distant kin and non-relatives.

Methods

Ethnographic Background

The Agta are a population of indigenous hunter-gatherers who reside in – and are nominally responsible for co-managing (Major *et al.* 2018) – the Northern Sierra Madre Natural Park in Isabela Province, the Philippines (Minter 2010). Two sub-populations were the focus of this study: the Palanan Agta, who number ~1,000 individuals, and the Maconacon Agta, who number ~250 individuals. These sub-populations are largely separate as they live approximately 50 kilometres apart from one another and share few genealogical links. These Agta populations live predominantly by foraging, especially fishing, but also collecting honey, gathering wild plants, and to a lesser degree hunting. Many foraged resources are traded with the local agricultural non-Agta population for rice and other food or commodities. The Agta are increasingly engaged in agricultural work and wage labour (Dyble *et al.* 2019), often consisting of tending rice fields, harvesting crops, clearing land and housekeeping. Over the total Palanan Agta population, approximately 75% of time engaged in subsistence activities is devoted to foraging, with the remaining 25% spent on agriculture and wage labour. The average camp size is 7 houses (49 individuals), but this varies substantially, from camps consisting of a single dwelling (7 individuals) to large camps of 26 houses (156 individuals). Mobility is high as individuals frequently move camp, although this is variable as some individuals and camps are less mobile than others (Page *et al.* 2016; Smith *et al.* 2016).

Agta children are breastfed on-demand until around two years of age, after which the amount of time and care received from their mother reduces and they increase their participation in mixed-age and sex playgroups where they engage in games, role-play and ‘work-play’ (where foraging is integrated into play; (Page *et al.* 2021a)).

From the age of five or six, children – and particularly girls – become increasingly involved in the household economy, providing childcare to younger siblings (often within the playgroup) and completing domestic tasks (Page *et al.* 2021a, b). As children get older, their time spent foraging increases, especially for boys (Dyble *et al.* 2019). School attendance is also highly variable and largely depends on the distance to the nearest population centre. Initial fieldwork to collect demographic data was conducted between April and June 2013, while additional fieldwork and conducting these experimental games took place between February and October 2014.

Data Collection

Games were conducted with 179 children between the ages of 3 and 18 (mean=8.9; SD=3.2; figure S1), of whom 87 (48.6%) were male. Ages for most children were unknown, so were estimated based on the procedure described in Diekmann *et al.* (2017), which involved combining relative age rankings elicited from the Agta and *a priori* age distributions for each individual using a Bayesian Gibbs sampling approach. Children without ages assigned via this procedure (~25% of children) were given an age estimate based on birth records (if available), reference to children with known ages, and/or the best guess of the researcher. Data were collected from a total of 14 camps (table S1).

To assess cooperation, a simple resource sharing game was developed. In this game, children were told that there were five small individually-wrapped candies, and for each one they had to decide: i) if they wanted to keep the candy for themselves or whether to give it to somebody else; and ii) if they wanted to give the candy away,

to whom. Children were shown each candy sequentially (i.e., one-at-a-time). This design was chosen to be as simple as possible for children to understand, without the need for complex apparatus or detailed explanation. There were no restrictions on age or whether recipients had to be from the same camp, although few children gave to adults (see results) and no-one gave to anyone from a different camp.

Children could also nominate the same recipient repeatedly if they wished. This design permitted an exploration of both levels of cooperation (total amount shared) and patterns of partner choice (who they shared with). As discussed in the introduction, both of these are decisions made repeatedly by children every day – e.g., sharing food, looking after younger children – and are essential for a full understanding of cooperative behaviour.

Games were conducted in private, out of sight and earshot of other children, with just the child, experimenter and translator. Children were told that their decisions were secret, so nobody else would know how much they kept or who they gave to, and that there were no right or wrong answers. The total number of candies earned was given to children after all games were played (this includes both the amount each child kept for themselves and resources given to them by other children). Games were generally played towards the end of our visit to each camp, meaning that gifts were normally given out within a few days of the child participating. The game was played with as many children as possible in each camp (using opportunistic sampling), although some children did not take part because they were too shy, too young to fully understand the game or just did not want to.

Statistical Analysis

Analyses were conducted using *R* version 4.0.4 (R Development Core Team 2021).

Analyses relating to overall levels of cooperation will be described first, with the partner choice analyses described afterwards.

Levels of Cooperation Analyses

The response variable was the total number of resources given to others (between 0 and 5). Predictor variables included: age, sex, average relatedness of the focal child to all other children in camp (derived based on genealogical interviews), and the average amount of resources given to others by adults in camp (using data from similar games conducted with adults; (Smith *et al.* 2016)).

As we were interested in estimating how each predictor variable was associated with the outcome (amount shared), for these effects to be given a potentially causal interpretation the causal relations between variables must be considered. A Directed Acyclic Graph (DAG) representing these assumed casual relationships is displayed in figure S2 (for primers on DAGs and causal inference, see (Pearl & Mackenzie 2019; Hernán & Robins 2020; McElreath 2020)). As nothing can cause age or sex, unadjusted estimates of these effects are likely to be unbiased. We also assume that relatedness between children is also independent of both other predictor variables and potential confounders. Finally, based on previous research with Agta adults we assume that adult levels of cooperation are shaped by factors such as camp stability/repeated interactions, resource availability/need, and storytelling (Smith *et al.* 2016, 2017, 2018). It is possible that these factors directly shape children's levels of cooperation, rather than being mediated through adult levels of cooperation;

however, here we are interested in whether adult levels of cooperation are associated with child levels of cooperation, regardless of whether this is through adult cooperation directly or through factors which shape both adult and child levels of cooperation. Given our hypothesised causal structure, this suggests that each of our predictor variables may be largely independent from one another.

To control for the hierarchical nature of the data (children nested within camps), a multi-level modelling approach was adopted using the package *lme4* (Bates *et al.* 2015). Linear models were initially tested to ensure that a multi-level model was a better fit to the data relative to a single-level model. We planned to use a random-slopes/random-intercepts model to explore whether there were different age trajectories by camp, but due to convergence issues this was not possible, so we proceeded using a random-intercepts only model with 'camp' as the random effect.

As the number of resources given could only vary between 0 and 5, additional robustness checks were performed using poisson models (which are suitable for count data) and ordinal regression models (using 'amount given' as an ordered categorical variable). None of these methods are ideal; linear methods because there are only six possible integer responses, poisson models because of excess '0's in the data (while zero-inflated poisson models may overcome this issue, this approach was not included here due to the output being more difficult to interpret and the complications of applying this method in a mixed-effects setting), and ordinal regressions because the outcomes are integers rather than ordered categories.

However, if all methods provide a similar answer this increases confidence that the results are robust. Analyses were first conducted for each predictor variable in a univariable model, followed by a multivariable model which included all predictor variables. Given the hypothesised DAG (figure S2), which assumes no confounding

between these variables, the univariable and multivariable models ought to provide similar parameter estimates. In addition to the above analyses, we also conducted simple univariable analyses exploring whether mother, father or average-parental levels of cooperation predicted children's levels of cooperation.

To examine the size of children's cooperative networks, additional models were performed assessing the number of unique recipients that the participant shared with (as opposed to total amount shared; for instance, if a child shared four gifts but gave them all to one sibling, then the total number of gifts shared would be '4', while the number of unique recipients would be '1').

Partner Choice Analyses

For the partner choice analyses two sets of models were constructed, depending on the response variable of interest. These models are 'gift-based' so only included individuals who shared resources (i.e., each gift donated is a separate data point). The first analysis assessed whether the relatedness between participant (ego) and recipient was greater than expected by chance, based upon background levels of relatedness between children in camp (with 'relatedness' as the outcome and a binary predictor variable indicating whether relatedness referred to recipients or the camp average). In this analysis, a positive coefficient indicates higher relatedness between ego and nominee compared to ego and the camp average.

The second set of analyses explored whether the age or sex of the participant influenced cooperation towards relatives. Two models were constructed with relatedness between ego and nominee as the response variable: one with ego age and ego sex as predictors, and another with an interaction term between these

covariates (to explore whether these associations differed by age and sex). To further examine patterns of children's cooperation, supplementary analyses were performed to explore how ego's age, sex and relatedness to recipient were associated with: i) recipient's age; ii) the age difference between ego and recipient (calculated by subtracting ego age from recipient age, with negative values meaning recipient was younger than ego); iii) recipient's sex; and iv) whether ego and recipient were of the same sex. For each of these analyses we began with a model including only main effects of ego's age, ego's sex and relatedness, and then explored whether the inclusion of interaction terms improved model fit.

All partner choice analyses were conducted after determining the appropriate random effects structure to adjust for clustering in the data ('ego ID' for multiple nominations by the same individual; 'camp' for camp-level variation; to adjust for potential clustering due to nominations to the same recipient a 'recipient ID' was originally included as a potential random effect, but as inclusion of this parameter resulted in convergence issues and nonsensical results, we used simpler models with just 'ego ID' and 'camp' as random effects). Linear mixed-effects models were used when relatedness and age were the response variables, while logistic mixed-effects models were used when sex was the response variable.

Results

Amount Shared

The mean number of resources shared by children was 1.8 (SD=1.44), with modes at 0 and 3 (table 1). Substantial camp-level variation was observed (figure 1), from a maximum camp average of 3.3 (SD=0.58, $n=3$) to a minimum camp average of 0 (SD=0, $n=9$), meaning that no-one shared with anyone (interestingly, this was also the camp where no adults shared any resources either). A likelihood ratio test confirmed that null multi-level model was a better fit to the data than the null single-level model ($\chi^2(1)=18.53$, $p<0.001$). In this null multi-level model, 24% of the variance in children's cooperation occurred at the camp level.

Table 1: Total number of candies given to others and the number of unique recipients the child shared with ($n=179$). For example, 41 children shared two candies, while 43 children shared with two unique recipients.

Number shared	Count (%) based on total amount given to others	Count (%) based on number of unique recipients shared with
0	53 (29.6%)	53 (29.6%)
1	19 (10.6%)	33 (18.4%)
2	41 (22.9%)	43 (24.0%)
3	48 (26.8%)	37 (20.7%)
4	13 (7.3%)	10 (5.6%)
5	5 (2.8%)	3 (1.7%)

Figure 1: Box-plot displaying the number of resources given, grouped by camp ($n=179$; camps=14). Boxes represent inter-quartile ranges with the black lines within bars indicating the median. Lines extending above and below boxes display upper and lower quartile ranges. Diamonds indicate the mean value for said camp, while the horizontal dashed line indicates the mean for the whole population.

Next, linear multi-level models were performed on each of the four predictor variables (age, sex, relatedness and average adult cooperation in camp) in univariable models, and then together in a multivariable model (table 2). In this multivariable model the assumption of normality is met (figure S3) but equal variances (homoskedasticity) may be slightly violated (figure S4). Consistent with the assumptions encoded in our DAG (figure S2), there was little difference in the coefficients between the univariable and multivariable models, suggesting that these factors are largely independent from one another.

The only factor strongly associated with children's cooperation was the average adult level of cooperation in camp ($b_{\text{full model}}=0.032$, 95% CI=[0.014; 0.48], $p=0.001$), with

children from camps where adults were more cooperative displaying greater cooperation (figure 2). For context, a 70-percentage point increase in adult cooperation (approximately the difference between the most and least cooperative camps) predicted children sharing over two additional resources. There was, at best, a weak positive association between age and children's cooperation ($b_{\text{full model}}=0.050$, 95% CI=[-0.012; 0.112], $p=0.115$; figure S5 and table 2). Results were qualitatively identical when using poisson or ordinal regression methods (table S2).

Table 2: Results of linear multi-level regression models regarding the factors associated with the number of candies given by children ($n=179$, camps=14). Both the univariable (separate) and multivariable (combined) model results are presented here (these results are practical identical, lending support to our hypothesised DAG; figure S2). Positive parameter estimates indicate an increase in the number of resources given to others. 95% confidence intervals are displayed in brackets. Results where $p < 0.05$ are highlighted in bold. SE = standard error.

Variable	Level	Univariable models			Multivariable model		
		Parameter estimate (SE)	95% confidence intervals	p-value	Parameter estimate (SE)	95% confidence intervals	p-value
Age	Individual	0.057 (0.032)	-0.006; 0.120	0.079	0.050 (0.031)	-0.012; 0.112	0.115
Sex	Individual	0.284 (0.196)	-0.103; 0.669	0.149	0.259 (0.193)	-0.126; 0.642	0.181
Related-ness	Individual	-0.830 (2.471)	-5.800; 4.077	0.737	-0.516 (2.263)	-5.070; 3.945	0.820
Adult coop	Camp	0.033 (0.008)	0.016; 0.049	0.001	0.032 (0.008)	0.014; 0.048	0.001

Figure 2: Scatterplot displaying the relationship between child cooperation and average adult levels of cooperation in camp as measured in a giving game ($n=179$; camps=14). Grey circles indicate individual data points (with jitter to avoid overlap). Black diamonds indicate the average levels of cooperation per camp, with the size of the diamond representing the children's sample size in said camp. The regression line is a simple linear regression line of average camp-level adult cooperation on average camp-level children's cooperation (with 95% confidence interval in grey).

Univariable linear multi-level models were also performed to explore whether parental levels of cooperation in similar games predicted children's behaviour. Three separate models were conducted; a mother-only model ($n=155$), a father-only model ($n=145$), and a combined parental model using the average of the parents' scores (if only one parent participated, their data was used; $n=162$). Mother ($b=0.007$, 95% CI=[-0.003; 0.018], $p=0.098$), father ($b=-0.005$, 95% CI=[-0.014; 0.005], $p=0.301$), and joint-parental ($b=0.000$, 95% CI=[-0.012; 0.012], $p=0.984$) cooperation terms were not associated with child levels of cooperation. Comparable results were found using poisson and ordinal regression models (table S3).

While a negligible effect of age on overall levels of children's cooperation was reported, additional models using 'number of unique recipients' did find an effect of age, with older children sharing with a greater number of individuals ($b_{\text{full model}}=0.091$, 95% CI=[0.035; 0.145], $p=0.002$; figure S5 and table S4). Tests of model assumptions are provided in figures S6 and S7 (these results are robust to using poisson or ordinal regression methods; table S4). Given a 10-year increase in age, children were expected to share with approximately one additional person. Together, these models suggest that although children may not have shared more with age, older children did share with more recipients. As with the previous analysis on amount shared, we again found that average adult levels of cooperation were strongly associated with an increased number of recipients, while no associations were reported for sex or relatedness (table S4).

Partner Choice Analyses

The next set of analyses explored the patterns of who children shared resources with. Of the 320 gifts given by children to others, 12 were to adults over the age of 20 (3.8% of all gifts; children who shared with adults tended to be older [mean=12.3; range=6-18], and most of these gifts – 10 of 12 – were to parents or adult siblings). In order to compare interactions between just children, in addition to removing these adult outliers, all recipients over the age of 20 were omitted, resulting in 308 gifts from 125 children.

First, to test whether children selectively gave to close kin, the relatedness coefficient between recipient and ego for each nomination was compared against the average camp relatedness to all children for each child. The average relatedness

between ego and nominees was $r=0.30$ ($SD=0.22$), while the average relatedness to all child camp-mates was $r=0.09$ ($SD=0.05$; figure S8). A linear mixed-effects model was performed with relatedness as the outcome and each individual as a random effect to account for repeated data by the same individual (the addition of 'camp' as a further nested random effect did not improve model fit, so was not included; $\chi^2(1)=0.912$, $p=0.340$). Inclusion of the binary predictor variable (indicating whether relatedness was to recipients or the camp average) found that relatedness between ego and recipient was significantly higher than expected by chance, with recipients possessing a relatedness coefficient with ego 0.21 greater than ego's average relatedness to other children in camp (95% CI=[0.18; 0.24], $p<0.001$). Given the highly-skewed distribution of the data and residuals, both the assumptions of normality and homoskedasticity were violated (figures S9 and S10). However, as the magnitude of the effect is so large, this is unlikely to impact the conclusion that children preferentially shared with close kin.

Next, associations between relatedness and ego age and sex were explored. Ego ID was included as a random effect (the addition of 'camp' as a random effect did not improve model fit, so was omitted; $\chi^2(1)=0.485$, $p=0.486$). Fixed effects were then added to this model. Age was negatively associated with relatedness ($b=-0.015$, 95% CI=[-0.025; -0.005], $p=0.005$), meaning that older participants were more likely to share with less related children; a 10-year increase in age predicted approximately a 0.15 reduction in the coefficient of relatedness between ego and recipient (figure 3). Sex was weakly associated with relatedness, with boys somewhat more likely to share with closer kin ($b=0.06$, 95% CI=[-0.001; 0.131], $p=0.054$). No interaction between age and sex was found ($b=-0.005$, 95% CI=[-0.025; 0.016], $p=0.672$). Tests of normality and homoskedasticity based on the model with age and sex as main

effects indicate that these assumptions are likely to be violated (figures S11 and S12; additional analyses are presented in table S5 which demonstrate that these findings are robust to alternative model specifications).

Additional models are provided in the supplementary information (tables S6 to S9) exploring how ego age, ego sex and relatedness (and their interactions) were associated with: i) recipient age; ii) the age difference between ego and recipient; iii) recipient sex; and iv) whether ego and recipient were of the same sex or not. Briefly, these analyses found that: older children were more likely to share with other older children, donations to younger children were towards closer kin, and there was a same-sex bias in children's nominations.

Figure 3: Proportion of gifts given to either primary kin (light grey; $r=0.5$), distant kin (dark grey; $r<0.5$ but ≥ 0.03125 ; that is, all kin more closely related than second cousins, excluding primary kin) or non-relatives (black; $r<0.03125$) as a function of age group. Numbers in the bars indicate the total number of donations given to each kin category within each age group ($n=308$ gifts from 125 children).

Discussion

These results demonstrate that: i) the only factor strongly associated with levels of children's cooperation among the Agta was the average level of adult cooperation in camp, with higher levels of adult cooperation predicting increased child cooperation; ii) when allowing for partner choice, there is little association between child age and levels of cooperation; iii) older children were more likely to share with a greater number of camp-mates, indicating that older children possess a wider cooperative network; and iv) children preferentially shared with close kin (especially siblings), although this kin-bias decreased with age, as older children shared more with non-kin and less-related children. Together, these results provide an insight into the evolutionary and developmental roots of cooperation among Agta hunter-gatherer children, and have implications for developmental studies of cooperation and the evolution of human childhood and life history more widely.

First, these results highlight the importance of assessing both levels of cooperation and partner choice simultaneously. Many previous studies which did not consider partner choice, and where cooperation was constrained to be between strangers or non-kin, found that cooperation increased with age (e.g., (Fehr *et al.* 2008; House *et al.* 2013, 2019; Blake *et al.* 2015)). However, the present results suggest that this apparent increase in cooperativeness may be an artefact of these previous methodologies; when allowing for partner choice, Agta children between the ages of 3 and 18 were approximately equally cooperative (with perhaps only a marginal increase in cooperativeness with age). Further studies are of course required to explore whether the current findings replicate and how they are modified by the social, ecological and cultural environment, but we tentatively suggest that cooperation with *non-kin* (or more distant relatives) may increase with age, but not

necessarily that cooperation *overall* increases over childhood. Thus, the low levels of cooperation of younger children found in previous studies may be because they could not selectively choose kin as recipients, rather than being less cooperative *per se*.

While little effect of age was found regarding overall levels of cooperation, high levels of between-camp variation were reported. Consistent with previous research (House *et al.* 2013), Agta children were more cooperative in camps where adults were more cooperative. However, the mechanism(s) underlying these patterns is unclear. As adult levels of cooperation were predicted by adaptive factors such as repeated interactions, resource availability and the presence of skilled storytellers (Smith *et al.* 2016, 2017), it is possible that similar adaptive considerations directly shape levels of children's cooperation as well. Alternatively, it may be that adult cooperation is responsive to these adaptive factors, but that children's cooperation is shaped by socially learning from adults in camp, rather than being sensitive to the varying costs and benefits of cooperation under different socioecological conditions. Answering this important question is beyond the scope of the present study; nonetheless, regardless of the mechanism, it does appear that Agta children are behaving in ways broadly consistent with adaptive considerations. One possibility which can appear to be ruled out, however, is simple vertical transmission of cooperative tendencies from parents to children, as there was no evidence that parental levels of cooperation were associated with children's levels of cooperation when controlling for between-camp differences in cooperation. Additionally, while previous research (e.g., (House *et al.* 2013, 2019; Blake *et al.* 2015) only explored variation at the ethnolinguistic level, here we demonstrate that similar variation can be observed within groups, meaning that we cannot assume homogenous

cooperation in children at the cultural group level (Lamba & Mace 2011; Smith *et al.* 2016).

Regarding patterns of partner choice, we find that most sharing is directed towards siblings (52% of all gifts) although in later childhood sharing becomes less nepotistic as children increasingly share with distant-kin and non-relatives. We also find that the size of children's cooperative networks increases with age, as older children share with a greater number of recipients. Thus, although overall levels of cooperation do not vary much with age, who children cooperate with, and the structure of their cooperative networks, changes considerably over childhood.

What are the potential functions of these patterns and what are their implications for human life history? First, these results demonstrate that Agta children willingly share resources with siblings, especially younger siblings, supporting existing literature highlighting the importance of siblings as alloparents (broadly defined here as non-maternal allocare; see (Emmott & Page 2019) for a nuanced discussion). This matches real-world patterns of cooperative childcare, where much allocare is undertaken by older siblings (Kramer 2010; Helfrecht *et al.* 2020; Page *et al.* 2021a), and that this investment may have important fitness consequences (Sear & Mace 2008; Sear & Coall 2011). This suggests that even young children may invest in younger siblings for indirect fitness benefits, perhaps potentially at a cost to their direct fitness. Consistent with this idea, a recent study on a UK cohort found that delayed menarche – a proxy for age at reproduction – was associated with having full siblings, relative to having only half- or step-siblings, suggesting that individuals may delay reproduction (a direct fitness cost) to assist close kin ((Smith 2017); see also (Lenárt *et al.* 2019) for a replication in a Czech cohort). Siblings can of course compete for resources (Lawson & Mace 2009), but overall the current results are

consistent with the idea that aspects of our derived life history, such as our extended childhood period, may in part be due to our system of cooperative childcare where help is preferentially directed towards full siblings (Boomsma 2009).

However, as some cooperation, especially in older children, was increasingly directed towards distant kin and non-relatives, indirect fitness benefits cannot be the sole explanation for why children cooperate, especially in later childhood. As children get older, they become increasingly involved in wider camp and society life, necessitating more extensive interactions and cooperation with less-related individuals (Flinn & Ward 2005; Hill *et al.* 2011; Dyble *et al.* 2015; Salali *et al.* 2019). Speaking very broadly, these results suggest that cooperation in early childhood may function to assist in the alloparenting of siblings for indirect fitness benefits, while in later childhood individuals increasingly cooperate with non-kin peers to forge friendships and learn the necessary skills for navigating adult social life for direct fitness benefits (although even in older children ~40% of all gifts were given to siblings, suggesting that sibling allocare is still an important consideration). It would be extremely enlightening to see whether similar patterns are found in other societies using a comparable methodology.

This study of course possesses limitations. Chief among these is that cooperation is measured via experimental games, meaning that it is not clear how this links to real-world cooperative behaviours (Gurven & Winking 2008). Nonetheless, as behaviour in similar games appeared to reflect real-world food-sharing practices among adult Agta (Smith *et al.* 2016), this provides some support that game behaviour may reflect real-world cooperative behaviour, at least regarding food-sharing. Further bolstering the validity of these findings, the observed patterns of partner choice reflect changes in proximity network patterns over childhood (from close kin when young to more

distant and non-kin in later childhood; (Migliano *et al.* 2017)), demonstrating that behaviour in these games reflects children's real-world interaction networks. The current results also highlight the importance of kinship in shaping patterns of children's allocare, as has been found in many other populations (Crittenden & Marlowe 2008; Kramer 2010), including the Agta (Page *et al.* 2019), indicating that the patterns of results from this simple resource allocation game are congruent with existing empirical work on human alloparenting. These findings are therefore consistent with multiple independent lines of evidence, providing assurance that these results may possess at least some degree of external validity.

Given that low numbers of children participated in certain camps – two camps only had three participants, while eight of the 14 camps included less than 10 children – sample size and statistical power are important potential limitations. When working with small-scale populations these issues are unfortunately frequently unavoidable, but this does mean that the current analyses may be underpowered to detect weak or camp-specific effects. For instance, while the multi-level models regarding overall levels of child cooperation could be fit with random-intercepts at the camp-level, a random-slopes/random-intercepts model (with 'age' as the random slope within camp) was not possible due to convergence issues. Larger sample sizes, or an alternative Bayesian methodological framework (McElreath 2020), may be required to explore these questions in greater detail.

The observed lack of increased cooperation with age, coupled with marked between-camp differences in cooperativeness and highly-structured patterns of partner choice, suggest that childhood may not simply be a time to acquire adult norms. Rather, children's behaviour can be understood as (potentially) adaptive in its own right, either because it benefits them in the present, or is necessary for developing

future social or cultural skills (Lew-Levy & Boyette 2018; Salali *et al.* 2019). That is, when interpreting developmental studies it is important to distinguish between *ultimate* (or *functional*) explanations, in terms of why a behaviour evolved and whether it is (or recently was) adaptive, and *proximate* explanations based on development (how a behaviour is acquired over ontogeny) or mechanism (how a behaviour works; (Tinbergen 1963; Scott-Phillips *et al.* 2011)). Much developmental work on cooperation focuses on the latter *how* questions (*how, from whom, and when* do children learn cooperative behaviour?), especially in terms of cultural transmission (e.g., (House *et al.* 2013; Blake *et al.* 2015; Salali *et al.* 2015)), without necessarily asking *why* these patterns exist and whether said behaviour is adaptive (Bjorklund & Pellegrini 2000; Machluf *et al.* 2014). Of course, children likely acquire some (most?) of their cooperative behaviour through social learning, but this social learning likely reflects fitness-enhancing considerations (Smith 2020; Burton-Chellaw & Amico 2021), while these adaptive behaviours may also be explicable in terms of non-social mechanisms (individual learning, reaction norms, etc.). From the data here it is impossible to assess the relative contributions of these proximate mechanisms (although a simple parent-offspring vertical transmission pathway can be ruled out). Nonetheless, the observed patterns are broadly consistent with a functional interpretation, regardless of the mechanistic pathway; variation in levels of children's cooperation between camps are structured in broadly-adaptive ways (e.g., greater cooperation in more stable camps), while patterns of partner choice are consistent with an adaptive function of helping siblings in early childhood for indirect fitness benefits, followed by increased cooperation and integration with the wider camp in later childhood for direct fitness benefits. While these specific conclusions are tentative and rather speculative, this study has hopefully demonstrated the

potential benefits of taking an evolutionary developmental approach to understanding children's cooperative behaviour.

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Data availability statement

Data and analysis code are openly-available on DM-S's GitHub page:

<https://github.com/djsmith-90/AgtaChildCoop>.

Ethics

Ethical clearance for the project was granted by the University College London ethics review board (UCL Ethics Code 3086/003) and carried out with permission from local government and Agta leaders. Informed consent for all children involved in this study was obtained from all parents/guardians after group and individual consultation, with an explanation of the research in the local language.

Author contributions

ABM and RM conceived the project. DM-S, MD, KM-S and AEP collected the data. DM-S analysed the data. DM-S wrote the manuscript with the input of all authors.

Competing interests

None.

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