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Authors:

Emily H. Emmott

UCL Anthropology, University College London, London UK

emily.emmott@ucl.ac.uk

Abigail E. Page

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

abigail.page@lshtm.ac.uk

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Definition: Caregiving by non-parental caregivers, who provide direct and/or indirect investments to a child

Introduction

Who helped you develop into the person you are today? Most of us may think about a parent or parents, but many of us would also recognise the important role of other people. Perhaps it's a teacher, a grandparent, or a neighbourhood friend. The fact that we are supported by many people in our childhood is, in fact, very unusual: In non-human mammals, support –or investments- for juveniles are typically and solely provided by the biological mother. Only 9-10% of mammals display parental care, where biological fathers are additionally involved in raising offspring, without the support of other helpers (Kleiman & Malcolm, 1981). In humans, we see a notably different system of facultative fathering, where biological fathers may or may not provide investments into their children, combined with a range of additional caregivers beyond the biological parents. These additional caregivers, or alloparents, can include siblings, grandparents and extended kin, as well as non-relatives such as step-parents, friends and neighbours.

Support from alloparents, meaning “other parents,” is arguably an obligate human characteristic. This is because, compared to other primates, humans have an extended childhood and adolescence: while the conceptualisation and timing of adulthood does somewhat vary between cultures, broadly speaking, humans do not become “mature” and self-sustaining until their mid-teens to early 20s. During childhood and adolescence, we experience a prolonged period of physical growth and skills development, making us dependent on sustained support from parents and alloparents to survive, develop and successfully reach adulthood. Non-parental caregivers are therefore necessary for successful reproduction and childrearing in humans- although who supports parents and how varies cross-culturally.

But how did alloparenting evolve? Why do alloparents help in childrearing, and how do they influence parental fitness? This chapter provides an overview of alloparenting in humans, outlining different types of alloparenting, broadly addressing the evolution of alloparenting, and providing a brief review of key alloparents in humans across cultures.

Main Text

1. Defining alloparenting

In its essence, alloparenting is a transfer of time, energy, and/or resources to non-offspring, with opportunity costs against any other behaviour. This can be conceptualised as alloparental investments into a non-offspring which, all things being equal, is expected to increase non-offspring biological fitness (with fitness meaning the ability to survive and reproduce). Humans join the 3% of mammalian species where alloparenting is the norm, where successful reproduction and offspring survival is dependent on the help from non-parental caregivers (Lukas & Clutton-Brock, 2012).

To date, research on alloparenting in humans is often referred to as the “cooperative breeding literature.” However, there has been some debate amongst researchers on whether humans should be classified as cooperative breeders at all. Partly, this may be the outcome of some confusion and variation around what cooperative and communal breeding means between disciplines. These terms are often used ambiguously, and sometimes interchangeably, likely exacerbated by the fact that “communal breeding” and “cooperative breeding” is often unaccompanied by clear definitions.

1.1 Is alloparenting the same as cooperative breeding?

In the non-human animal literature, cooperative breeding is defined as a system where a dominant female monopolises breeding, aided by subordinate and non-breeding alloparents who forgo their own reproduction. In contrast, communal breeding refers to a system where multiple females reproduce, often pooling their resources and young (Lukas & Clutton-Brock, 2012). Confusingly, humans have been argued to be both cooperative and communal breeders. The long pre- and post-reproductive life stages in humans have been interpreted as evolved characteristics of reproductive suppression, which is a defining characteristic of cooperative breeding (Lukas & Clutton-Brock, 2012): Older, reproductively mature children may temporarily “forgo reproduction” and help care for their younger siblings, while grandmothers have been argued to have a long post-reproductive lifespan to help care for their grandchildren. At the same time, mothers rarely, if ever, monopolise reproduction in human groups. As a species, we typically live in groups of multiple parents with children, where parents and alloparents share resource and care. This pattern seems to be similar in feature to communal breeders.

Clearly, humans do not fit neatly into either category of communal or cooperative breeding as strictly defined. Instead, humans cooperate broadly and flexibly around reproduction and childrearing, with alloparenting being a norm. With this context, in this chapter we purposely avoid labelling humans as cooperative breeders. Instead, we stick to the terms alloparenting and introduce the term cooperative childrearing. The word “cooperative” is maintained, as there is no denying that alloparenting is a cooperative act (reviewed in more detail below). However, by directing attention to “childrearing,” which is uniquely attributable to humans and children, it clarifies that the human system varies from cooperative breeders in the strictest sense. In humans, alloparenting does not necessarily mean individuals forgo reproduction, while recognising that some alloparents do.

1.2 How is alloparenting conceptualised?

Alloparenting is an inherent part of cooperative childrearing. However, like cooperative and communal breeding, alloparenting as a term has been defined, conceptualised and categorised in different ways within and between disciplines. This is perhaps reflective of the fact that alloparents can invest in different ways, with different pathways of investment transfer. To fully capture the diversity in alloparental investments, alloparenting in humans can be conceptualised in three distinct ways: 1) provisioning vs caregiving, addressing the types of alloparental investments, 2) direct vs indirect, addressing the pathways of alloparental investments, and 3) additive vs substitutive, addressing alloparenting systems.

1.2.1 Types of alloparental investments: Provisioning vs Caregiving

Alloparental investment behaviours can be broadly categorised into provisioning, which is a transfer of resources to parents and/or children, and caregiving, which is a transfer of time and energy to care for the child. Alloparental investments via provisioning can involve any form of resource, including food, wealth, and other materials, and the generation of resources (i.e., production) is often an important aspect of provisioning. For example, hunting behaviour by men in forager populations are often conceptualised as provisioning activities. Similarly, in developed populations, grandparents providing financial transfers to parents and grandchildren can be conceptualised as provisioning. Alloparental investments via caregiving includes physical care and feeding children, as well as teaching

and play. For example, across societies, older children or adults often carry infants and young children, which is a type of caregiving activity.

It is important to note that production activities are often incompatible with caregiving. This means alloparents, like parents, are generally unable to do both things at the same time (Emmott, 2015). In the Hadza hunter-gatherers of Tanzania, for example, mothers are reportedly not able to carry toddlers while they go out and forage for food, and so must leave these relatively young children in camp (Blurton Jones, Hawkes, & O'Connell, 2005). Similarly, in developed populations, the conflict between employment and providing childcare is widely recognised (e.g., see Allen, 2003), as unsurprisingly not many workplaces allow people to bring children on a regular basis. Because of these difficulties in combining provisioning and childcare, alloparents may specialise in providing a particular type of investment.

1. 2.2 Pathways of alloparental investments: Direct vs Indirect

Because alloparenting in humans exists within a social network, alloparenting behaviours can be described in terms of the pathway it takes for the time/energy/resources to be transferred to the child- or how alloparental investments into children “arrive.” Broadly, there are two types of alloparental investment pathways: direct investments and indirect investments.

Direct investments are defined as any form of alloparental time/energy/resource which is transferred directly to the child (Figure 1). For example, in the Gussi of Western Kenya, mothers reportedly assign “sibling alloparents” to their toddlers who become partly responsible for carrying, feeding and generally looking after the younger sibling (LeVine, et al., 1996). In the UK, stepfathers have been found to provide care to their unrelated young children, including playing with children, reading to them, and feeding them (Emmott & Mace, 2014). In Japan, a traditional custom called ‘otoshidama’ exists where kin and non-kin adults gift money directly to children over the New Year period. Under this custom, children generally have the autonomy in how they spend their otoshidama money, and parents are not involved in the “financial transfer” apart from perhaps providing some advice to their children on the ways to spend the money (personal observation by author, EHE). In all

these examples, alloparents invest in children directly without going through other caregivers and parents.

Note, direct investments do not necessarily require direct contact between the alloparent and child. In the Agta foragers from the Philippines, for example, the majority of observed childcare could be defined as passive, proximity-based care without direct engagement. Here, children stay in camp and play together while adults forage, but one or two older adolescents or older adults would stay behind to “keep an eye” on the children (personal observation by author, AEP). Some may question whether such a minimal investment activity is, in fact, meaningful direct alloparenting. However, regardless of the level of effort involved in passive childcare, alloparents are still likely to be experiencing opportunity costs as they could be doing other activities. While passive childcare is often viewed as an “inferior” type of direct investments in Western cultures, passive childcare can be crucial because, regardless what the caregiver is doing for the majority of the time, alloparents are able to react and help the child when required (Meehan, Quinlan, & Malcom, 2013).

Indirect investments are defined as any form of alloparental time/energy/resource transfer made to an individual, who then converts the gained time/energy/resource into direct investments to the child (Figure 1). To put it differently, the transfer from an alloparent to the child is fully mediated by an ‘intermediate’ person. Indirect investments can, for example, be directed towards the parents who then uses this extra support to provide care to the child. In rural Ethiopia, maternal grandmothers were found to frequently contribute to heavy domestic tasks, while paternal grandmothers contributed to agricultural labour, which were both associated with greater child survival (Gibson & Mace, 2005). Here, while grandmothers were not directly engaging with the children, their indirect contributions to household production and labour were likely “transferred” into child quality. Such activities by alloparents can be classified as indirect investments, as the alloparent raises resources or frees some time for the parent, who is then able to direct investments towards the focal child.

[Insert Figure 1 here]

1.2.3 Alloparenting systems: Substitutive vs Additive

Within the cooperative childrearing system, direct and indirect alloparental investments do not happen in isolation, but exist within a dynamic network of caregivers around the child and parents. All things being equal, alloparental investments are expected to have a beneficial effect on child quality. However, whether or not alloparenting has a “net benefit” for child quality depends on if and how other caregivers react to that alloparenting. Broadly, alloparenting can be additive, where it does not influence the level of maternal or paternal investments, or it can be substitutive, where mothers and/or fathers reduce their investments which is “topped-up” by alloparents. While alloparenting under both systems are expected to benefit parental fitness, substitutive alloparenting is not expected to lead to higher child quality. Depending on the quality of alloparental investments, substitutive alloparenting may even have a detrimental effect on child fitness.

Additive alloparental investments are transfers of time/energy/resources into the child, which does not influence the investment behaviour of mothers and/or fathers (Figure 2). This has sometimes been discussed as “constant breeder input,” where parental investments are insensitive to the behaviour of alloparents (Kushnick, 2012). Whether alloparenting is additive – as in, whether parental investments are insensitive to the help from others - may depend on whether the parental investment behaviours are replaceable. For example, breastfeeding is (usually) dependent on the mother, and alloparents may have less scope to influence breastfeeding compared to other types of parental investment behaviours (Kushnick, 2012), particularly in contexts where formula milk is not readily available.

In an additive alloparenting system, children always experience a “net gain.” Additive investments are therefore expected to lead to higher child quality, and it may be more likely to be found in contexts where parents optimise child quality over quantity (and therefore parents do not “reduce” investments when others provide help). For example, in a UK sample, contact with maternal and paternal grandparents were not associated with differential levels of maternal or paternal caregiving (Emmott, 2015), suggesting grandparental direct investments in this population may be additive. In contemporary China, living near maternal grandparents and availability of them as alloparents was not associated with differential levels of maternal caregiving (Chen, Short, & Entwistle, 2000).

Substitutive alloparental investments are transfers of time/energy/resources into the child, which then ‘releases’ parents from having to make those investments (Figure 2). Parents then redirect their energy into other activities, helping them achieve higher fitness. This is sometimes referred to as “load lightening,” where the more help parents receive from alloparents, the less investments they provide to their children (Kushnick, 2012). For example, in the Maya and Pume, for every 10% increase in direct alloparental care was associated with a 25% decrease in the probability of maternal caregiving, estimated to be a potential saving of 165?kcal per day (Kramer & Veile, 2018). This suggests that alloparents in these populations were allowing mothers to withdraw from childcare, giving them extra time and energy to carry out other activities. Similarly, in the Aka foragers of the Central African Republic, grandmother caregiving was associated with a reduction in maternal childcare and an increase in maternal foraging activities (Meehan, Quinlan, & Malcom, 2013), suggesting grandmothers were substituting maternal caregiving which allowed mothers to divert her time and energy into production.

[Insert Figure 2 here]

With substitutive investments, alloparenting does not necessarily lead to a “net gain” for children due to the reduced investments from mothers and/or fathers. For example, in the Maya and Pume example previously mentioned, direct alloparental care was not associated with increased physical child quality, measured by child weight (Kramer & Veile, 2018). In fact, if the alloparenting quality is inferior, receiving substitutive investments from alloparents could lead to reduced child fitness. For instance, in the UK, availability of grandmothers as alloparents has been associated with lower levels of breastfeeding (Emmott & Mace, 2015), presumably as grandmothers are able to “substitute” infant feeding via formula, thereby increasing the incentives for mothers to stop breastfeeding. Given the benefits of breastmilk for infant development, such substitutive alloparenting may not be beneficial for children. Similarly, in the Agta foragers, maternal and paternal grandmothers have been observed to become the main caregiver of an infant while the mother temporarily left camp to look for work. However, because this led to breastfeeding cessation, and grandmothers did not have access to formula and/or clean water, it was not uncommon for these infants to become very malnourished, parasitised, suffer from severe gastrointestinal disease, and sometimes die as a result (personal

observation by author, AEP). In such cases, alloparenting, despite all the best intentions, does not lead to benefits for the child.

While substitutive investments do not necessarily lead to higher child quality, they may nonetheless increase parental fitness via increased fertility. Such substitutive investment systems may be more prevalent in populations where it's adaptive for parents to optimise child quantity over quality. For instance, in contemporary Thailand, residence with paternal kin after marriage was associated with higher fertility for parents, but it did not influence child outcomes (Snopkowski & Sear, 2013). The consequence of increased fertility may also be increased sibling competition, with potentially negative consequences for child outcomes (Lawson, Alvergne, & Gibson, 2012).

Whether alloparenting is substitutive or additive may vary between maternal and paternal kin: From an evolutionary perspective, there is an unequal cost to reproduction between the sexes, where males can reproduce "cheaply" by providing relatively unlimited sperm, while females pay a higher cost due to their larger, limited eggs. In mammals, this is followed by a long gestation and lactation period for females, which is energetically expensive. Because of this asymmetry in the costs in reproduction, we hypothesise a sexual conflict between the sexes where the optimal number of offspring is expected to be higher for males than females. Given this mis-match, there may be greater incentives for paternal kin (i.e., father's family) to help parents achieve higher fertility by providing substitutive alloparental investments, while maternal kin (i.e., mother's family) may be better inclined to help parents achieve higher child quality. For instance, in the China example mentioned above, living near or with paternal grandparents was associated with reduced maternal caregiving (Chen, Short, & Entwistle, 2000), which could be because paternal grandparents "released" mothers from providing childcare so she could reinvest this energy into activities which lead to higher fertility. Similarly, in the Karo Batak subsistence agriculturalists of Indonesia, receiving help from paternal kin was associated with mothers increasing farmwork, while receiving help from maternal kin was associated with mothers spending more time carrying children (Kushnick, 2012). This could be because paternal kin facilitated higher levels of maternal production which can be transferred into higher fertility (because female reproduction is limited by resources). In contrast, maternal kin may have facilitated higher levels of investments into existing children, thereby increasing child quality.

2. The evolution of alloparenting in humans

When considering the evolution of alloparenting in humans, it is important to note that alloparenting behaviour in itself has been observed across many species. In non-human primates, allomothering (which includes alloparenting and fathering) is common, having been described in 74% of the 154 species where data is available (Tecot & Baden, 2015). However, in most species this behaviour is not a defining feature of their breeding system, and may even be “misfired” alloparenting whereby caregiving behaviours are misdirected to non-offspring.

In contrast, alloparenting in humans is arguably a defining feature of human childrearing, and is observed across human populations: In the Aka foragers, infants have been found to have, on average, 21 different caregivers which include kin and non-kin (Meehan, Quinlan, & Malcom, 2013). In the Hausa of Nigeria (sub-Saharan agriculturalists), children had 4.8 different caregivers on average (LeVine, et al., 1996). In contemporary developed populations, parents rely on relatives such as grandparents, aunts and uncles for childcare, as well as more formal arrangements such as day-care centres and crèches (Allen, 2003; Langer & Ribarich, 2007).

How did alloparenting evolve to become a diverse yet obligate human characteristic? Researchers have argued that alloparenting is both a cause and consequence of our unusual life-history, which involves a “premature” birth of infants, essentially helpless for a substantial postnatal period, followed by an extended childhood and adolescence. The combination of prematurity and slow growth means that human offspring are particularly dependent on alloparental investments for survival and optimal development into adulthood. It has been hypothesised that the level of alloparenting required is so high in humans, that mothers were unable to successfully raise children without alloparents in our evolutionary history (Hrdy, 2009). It has also been hypothesised that alloparenting co-evolved with other species-typical characteristics such as short interbirth intervals leading to multiple dependent children, and a long, post-reproductive lifespan (Hrdy, 2009).

Underpinning the species-level evolution of alloparenting and cooperative childrearing are individual-level selection pressures. For the recipient, the fitness benefits of alloparental support seems intuitive, where children and parents who receive time, energy and/or resources have improved

survival and reproduction (Sear & Coall, 2011). But why do alloparents help, given that it is associated with some form of cost? As with any form of cooperation, the evolution of such helping behaviours is puzzling due to a “free rider” problem: Those who receive help but do not help in return gain the largest fitness benefit, meaning the “free rider” phenotype would rapidly spread through the population, resulting in the population no longer being cooperative. Therefore, assuming selection pressures act on individual traits, alloparenting would only evolve if there are some kind of fitness benefits from helping. Outlined below are the hypothesised individual fitness benefits for alloparenting which may explain the evolution of cooperative childrearing, focusing on indirect fitness benefits (what alloparents gain via improving the survival/reproduction of their relatives) and direct fitness benefits (what fitness benefits alloparents gain by improving their own survival/reproduction).

2.1 Indirect fitness benefits

An individual's inclusive fitness is the sum of their own fitness (i.e. direct fitness) and the fitness of kin (i.e. indirect fitness). Therefore, alloparents may gain indirect benefits by improving the fitness of their relatives. This means alloparenting can evolve via kin selection, where a costly behaviour can be selected for if the fitness benefits gained by the receiver (B), weighted by the coefficient of relatedness between the helper and the receiver (r), is larger than the fitness costs incurred by the helper ($rB > C$). In case of additive alloparental investments, investing in related children is expected to increase the alloparent's inclusive fitness if this resulted in increased survival and future reproductive success of that child. In case of substitutive alloparental investments, alloparenting may increase inclusive fitness by facilitating parents who are relatives to decrease parental investments into a specific child, allowing them to invest more in fertility (i.e., having more children) and/or increasing investments in other children.

If kin selection is an important aspect of alloparenting, we would expect alloparents to preferentially help relatives. Evidence strongly supports the role of relatedness as drivers of alloparenting in humans: For example, across traditional societies, maternal grandmother presence has been found to be more likely to be associated with higher child survival compared to paternal grandmother presence, supposedly due to higher relatedness certainty amongst maternal kin (Sear &

Mace, 2008). Similarly, in contemporary societies, maternal grandparents have been found to invest more in their grandchildren than paternal grandparents (Pollet, Nelissen, & Nettle, 2009).

However, regardless of relatedness, when benefits of cooperation are low, the motivation to allomother can diminish and alloparenting may consequently be withheld. In humans and other animals, evidence suggests that alloparenting is sensitive by broader “pay-offs,” which can be influenced by factors such as reproductive value, resources/wealth and local competition (Sear & Mace, 2008). While kin selection and indirect fitness benefits are a pervasive explanation for cooperative behaviour, it is important to note that it is not the sole explanation for alloparenting. In humans, parents and children frequently live amongst and cooperate with friends and other non-relatives. Even if parents, children and alloparents are related, alloparents may help for different reasons - gaining both direct and indirect fitness benefits. Just because two individuals are related does not mean their cooperation is only motivated by indirect fitness benefits. To fully understand why alloparents provide help, it is essential to consider what individuals gain beyond indirect fitness benefits.

2.2 Direct fitness benefits

Kin selection is unlikely to explain all cases of alloparenting, as cross-cultural evidence suggests humans frequently help raise unrelated children. Instead, alloparents may be motivated to help raise children because they gain a ‘direct benefit’ leading to higher fitness. For instance, individuals may gain valuable parenting experience which improves their parenting skill, leading to higher reproductive success in the future. Alloparenting may also serve as a costly signal which helps alloparents access reproductive opportunities, or it can be part of a reciprocal relationship in the broader cooperative social system. All these pathways may increase the individual's fitness, promoting the maintenance of cooperative childrearing.

2.2.1 learning-to-mother / parenting experience

The learning-to-mother hypothesis, first proposed by Jane Lancaster, posits that young, non-reproductively active females may alloparent to learn and develop their mothering skills, since more

experienced mothers tend to have better infant outcomes. This has been broadened to parenting more generally, where male and female helpers could gain direct benefits via caregiving skills development (Kramer & Veile, 2018). Such “parenting practice” could be adaptive for alloparents if offspring are highly vulnerable and dependent on high quality care for survival.

To date, this hypothesis has been mainly discussed in the context of female alloparenting found amongst non-human primates. For example, in female vervet monkeys, alloparenting experience before their first birth was associated with higher survival of their firstborn infants (Fairbanks, 1990). However, for this hypothesis to be convincing, there are some questions which need to be addressed: First, if infants are so vulnerable, why would mothers allow inexperienced, unskilled individuals to provide childcare? This is likely to cost mothers and infants rather than help, and in fact this has been proposed as one of the reasons why alloparenting is not more widely observed among primates (Hrdy, 2009). Second, does alloparenting actually lead to parenting skills development and higher reproductive success in adulthood? The evidence is currently sparse. For example, an analysis of Mayan data found that girls who spent more time in allocare did not have more surviving children as adults (Kramer & Veile, 2018). Importantly, the parenting experience hypothesis only applies to direct alloparental investments, involving direct care, and does not explain any form of indirect investments commonly observed among humans. Nonetheless, future studies could investigate the parenting experience hypothesis in humans, for example by explicitly testing whether caregiving by pre-reproductive individuals lead to higher parenting skills in later life.

2.2.2 Costly signalling & mating effort

The Bateman’s principle states that male reproductive success is limited by access to females, while female reproductive success is limited by access to resources. This means females across species are generally the choosier sex in terms of reproduction, and males need to compete and advertise their quality. Men may therefore opt to incur the cost of alloparenting as a way to signal his quality, known as “costly signalling.” Costly signalling via provisioning for mothers and children may be a particularly important factor for male alloparenting in humans: While non-human primates males rarely share food with others, hunting followed by extensive food-sharing is observed widely across forager populations. Some have argued that hunting and food-sharing by men function as a costly signal, where men “show off” their health and skill, becoming more attractive to potential reproductive

partners. For example, in the Mermain islanders of Australia, men cooperatively hunt turtles which is shared with the group, meaning turtle-hunters provision parents (indirect alloparental investments) as well as children (direct alloparental investments). In this population, turtle hunting has been argued to be a form of costly signalling as hunting turtles successfully require high levels of skill, which is socially recognised (Smith, Bird, & Bird, 2003). Compared to other men, turtle-hunters have more reproductive partners (Smith, Bird & Bird, 2003), suggesting this provisioning activity in this particular population may be directly benefiting male reproductive success.

Given female reproduction is limited by resources, men could also provide allocare in exchange for mating opportunities, similar in concept to a reciprocal exchange (see Reciprocity section below). Alloparenting by stepfathers is one such example, where it has been hypothesised that stepfathers provide care to stepchildren in order to form and maintain a reproductive pair with mothers (Anderson, 2000). In the US, stepfathers were on average less educated and had lower levels of income than fathers (Anderson, 2000). Partnering with mothers (rather than women with no children) and helping raise their children may be a way to overcome their “lower provisioning potential,” allowing them to successfully partner with a woman and eventually have their own children (Anderson, 2000).

Of course, alloparenting as costly signalling and mating effort is primarily applicable to men, or at least for individuals seeking reproductive opportunities – and does not explain alloparenting by other individuals such as women, children and post-reproductive adults. It is also important to note that whether male provisioning and caregiving functions as a costly signal may depend on population context: In the Tsimane forager-horticulturalists from Boliva, for example, patterns of caregiving by men suggested that men were unlikely to be providing alloparental childcare as a costly signal. This is because men tended to provide care when a child’s mother was absent rather than when the child’s mother was present (Winking, Gurven, Kaplan, & Stieglitz, 2009). This suggests that men provided childcare based on the need of alloparenting, rather than the opportunity to “show-off” their potential parenting skills to women. Overall, the costly signalling hypothesis is limited by its ability to alloparenting more generally, and is likely to be only applicable to a small proportion of male alloparents.

3.2.3 Reciprocity

Alloparenting may exist as part of a reciprocal cooperative interaction, understood as “I’ll scratch your back if you scratch mine.” Such cooperation can evolve if the cost of helping someone in the present is outweighed by the benefits the helper receives in return at some point in the future, lessened by the probability that this benefit may or may not occur. In humans, the probability of not receiving the later benefit (i.e., not getting your back scratched) may often be small as we have repeated interactions with the same individuals across large sections of their life. Individuals can also be picky about who they interact with, and may preferentially assort with individuals who cooperated with them previously (an in turn, excluding those who do not cooperate).

Researchers have found significant support for reciprocity driving cooperation across different domains of human behaviour, although few have explicitly explored the role of reciprocity in childrearing. An exception is work by Jaeggi et al (2016) who demonstrate the importance of reciprocity in explaining alloparental caregiving in the Tsimane forager-horticulturalists from Bolivia. In developed populations, reciprocal interactions around alloparenting often involve financial payment, such as professional nannies and childminders (e.g., see Allen 2003), but studies have also described alloparenting between neighbours and friends as part of a reciprocal arrangement. Interestingly, work in other species suggests that the fitness payoffs of cooperating are higher when the environment is marginal and unpredictable (Jaeggi, Hooper, Beheim, Kaplan, & Gurven, 2016), and living in larger groups, cooperating and pooling resources can be an adaptive strategy to buffer against environmental fluctuations. In humans, cooperative childrearing may therefore have evolved to mitigate risks that come with less secure, more variable environments. In this system of reciprocal helping, individuals ultimately end up benefitting as they provide help when they can afford to do so, in exchange for help later on when they are in need.

To summarise, alloparenting can be conceptualised as a cooperative behaviour involving a cost to the helper and a benefit to the recipient. Ultimately, alloparenting is hypothesised to only evolve if there is some form of fitness benefit to the helper. In humans, alloparents likely gain benefits in different ways depending on the context, where alloparenting for close kin brings indirect and direct fitness benefits, while alloparenting for non-relatives, friends and strangers is expected to be associated with direct fitness benefits. This multifaceted cooperation likely facilitated and co-evolved with the unique human life history, ultimately leading to cooperative childrearing from such a broad range of alloparents becoming an obligate human characteristic.

4. Key alloparents across cultures

Who helps with childrearing and how they help varies across societies. This is not surprising given the many different selection pressures which encourages (or discourages) alloparenting, meaning the costs and benefits for alloparenting is likely to be context dependent. Nonetheless, there are particular alloparents in humans who have been frequently identified as important for parents and children.

3.1 Grandparents

The 'Grandmothering hypothesis' states that the unusual postmenopausal lifespan in humans evolved due to the importance of grandmother support for successful reproduction and childrearing (Hrdy, 2009). It posits that reproductive cessation through menopause facilitates allomothing, in that grandmothers can care and provide for their grandchildren without experiencing reproductive conflict with the mother. Studies have shown that grandmothers are more willing to provide alloparental investments (Gibson & Mace, 2005). Alloparental investments from grandmothers may be particularly important during the "costly" period of infancy and young childhood, when children are particularly dependent on others for support.

Grandparents, particularly maternal grandmothers, may be important alloparents in humans. Assuming paternity certainty, grandmothers are 25% related to their grand-offspring, and therefore gain significant indirect fitness benefits due to this cooperation. A review of kin presence and its associations with child survivorship found that maternal grandmother presence was positively correlated with child survival in 69% of studies on traditional, natural fertility populations (n = 46, Sear & Mace, 2008). Paternal grandmothers were positively associated with child survival in 53% of studies (n = 17, Sear & Mace, 2008). Literature on grandmothering in developed populations also highlight they are important providers of childcare and financial support, and may be particularly important for children's psychological and socio-emotional development (Sear & Coall, 2011).

However, the importance of grandmothers as alloparents may be context dependent. In developed populations, grandparents may be particularly important caregivers when families are under stress and/or in need of support (Sear & Coall, 2011), meaning if families are “doing well,” grandmothers may not be particularly important for children and parents. In the Aka foragers, grandmother absence (thereby lack of grandmother alloparenting) was only associated with a negative effect on child developmental outcomes in patrilocal camps, where mothers lived with the father’s relatives (Meehan, Helfrecht, & Quinlan, 2014). The authors suggest the association between grandmother absence and poorer child outcomes was not observed in matrilocal camps, because the availability of other maternal kin as alloparents in these camps buffered the “loss” of a grandmother. This highlights that, while grandmothers are important alloparents in a range of cross-cultural populations, wider alloparental networks can also be important for parents and children. Whether or not grandmothers are key alloparents may therefore depend on who else is around to help beyond grandmothers.

3.2 Siblings & other children

In higher-fertility populations, children often have multiple siblings who can be important caregivers, who frequently provide a lot of the direct alloparenting a child receives (Kramer & Veile, 2018). Importantly, in the Pume and Maya, childcare from siblings was not associated with significant decreases in economic activities or education, suggesting children were not suffering from opportunity costs due to their helping (Kramer & Veile, 2018). This suggests that children, and siblings in particular, may be very willing alloparents as they do not suffer enduring fitness costs from being alloparents. Indeed, studies have shown the “benefits” siblings may bring to children: in the Gambia, older sisters were associated with increased survival of younger siblings (Sear & Mace, 2008).

However, children can also be competitors for parental investments and household resources. As such, having a large number of siblings, and high levels of sibling competition, may lead to poorer fitness outcomes for children (Lawson, Alvergne, & Gibson, 2012). While studies to date investigating the number of siblings and child outcomes in different populations have returned mixed results (Lawson, Alvergne, & Gibson, 2012), a large-scale study using data from 27 countries across sub-Saharan Africa found that higher fertility (and therefore more siblings) was associated with higher child mortality, highlighting the possible detrimental effect sibling competition (Lawson, Alvergne, & Gibson, 2012). Again, this highlights the importance of local context. In situations where resources or

investments are plentiful, siblings may serve as very helpful alloparents. However, in situations where siblings need to compete with each other for resources or investments, siblings may hinder rather than help.

Beyond siblings, other unrelated children can certainly be alloparents. This may be particularly important in societies where children spend time together as a group, such as in the Hadza foragers where children and young adolescents stay in camp and play while adults hunt and forage (Blurton Jones, Hawkes, & O'Connell, 2005), as well as in developed and developing populations where children spend an extended period of time with each other at school. Among the Aka foragers, where a range of alloparents care for children, unrelated children are described as an important part of the wider caregiving network (Meehan, Quinlan, & Malcom, 2013). While children caring for children is not a well-recognised form of caregiving in Western contexts, and in fact sometimes conceptualised as harmful, it is a widely observed behaviour which is likely to impact child quality – and studies show children make meaningful contributions as alloparents (Meehan, Quinlan, & Malcom, 2013).

3.3 Peers of parents and other households

In communal breeding species, other mothers and parents –who may or may not be related- are important sources of support as they pool resources to raise offspring. In humans, parents may form a collaborative network with other households because they live nearby, where parents and alloparents collaborate to raise children. Often, other households in the collaborative network are relatives: For instance, among the Pimbwe, the number of maternal aunts and uncles who were likely of reproductive age (i.e., mother's adult siblings) was associated with higher child weight, particularly for families with low socioeconomic status where parents and children "in need" benefitted by receiving help from aunts and uncles (Hadley, 2004). The benefits of aunts and uncles have also been reported in developed populations, where they are often important caregivers and sources of support for children (Langer & Ribarich, 2007). It is important to note, however, that aunts and uncles are not necessarily expected to be beneficial alloparents, and it is likely to be dependent on local context. In situations where parents experience local resource competition with their adult siblings, the presence of aunts and uncles may even be detrimental.

Given that humans live in complex groups and display high levels of cooperation with unrelated individuals, there is potential that non-kin peers and households are also important alloparents. However, at present, the literature on alloparenting by unrelated peers is generally limited, while there is work on the importance of diverse and unrelated social networks. In the Agta (Philippines) and BaYaka (Republic of Congo) foragers, non-relatives were essential components of mothers' social networks. In these populations, mothers who were directly connected (in terms of proximity) to many individuals in their social network, be them kin or non-kin, had higher fertility. This suggests that having access to a large number of different types of helpers may be important for parents to successfully reproduce (Page, et al., 2017). Having a diverse and flexible social network may be more adapted to tackle variable and unpredictable environments experienced by many hunter-gatherers. In contrast, relying on a limited number of co-resident relatives, who have their own childcare and subsistence demands, may not be an optimal strategy to ensuring childcare demands are met. Overall, this suggests that both individuals beyond your household and your relatives are likely to be important alloparents – at least in forager populations - but this requires further exploration. We can also hypothesise that such unrelated peers and households may be of particular importance in low-fertility populations with neolocal norms, as family members may simply be unavailable for alloparental support.

3.4 Institutional alloparents

In many developed settings, the demographic transition and smaller family sizes have meant parents have fewer relatives to rely on as alloparents. This has also coincided with strong nuclear family norms where parents are perceived as primary caregivers of children (Emmott, 2015). Arguably, the cooperative childrearing system in developed populations now rely less on informal social networks, but more so on institutional alloparenting where the state and other institutions provide or organise support to help raise children. This includes professional workers whose role is to support families and children, such as social workers and teachers, as well as financial provisioning and subsidies via welfare payments and tax breaks. In Nordic countries, for example, childcare is perceived to be a joint responsibility between the parents and the state, and consequently the state guarantees subsidised or free formal childcare for parents (Emmott, 2015). Studies show institutional alloparenting across developed populations may be beneficial for children, with formal childcare associated with better child development (Melhuish, 2004). However, the quality of caregiving by institutional

alloparents are known to vary, and poor-quality care may have detrimental effects on children's outcomes (Melhuish, 2004).

Conclusion

Alloparenting is a diverse yet cross-culturally observed behaviour which exists as part of the cooperative childrearing system in humans, hypothesised to have co-evolved with our unusual life history. Important alloparents include grandparents, children and siblings, and other households - and in developed populations, institutional alloparenting is provided where the state provides financial transfers for families and/or organises "professional alloparents." However, who provides alloparenting and how they help varies within and between populations.

The motivation for alloparents to help raise children depends on the indirect and direct fitness benefits they gain from cooperating. Therefore, in trying to understand the ultimate reasons behind alloparenting (or why alloparenting exists), it is important to consider a multitude of factors such as what individuals gain from helping kin, if they learn new skills, if they achieve social standing, or whether helping now ensures that they receive help in the future. Nonetheless, in particularly harsh environments, co-operators may become competitors for resources. In this sense, an evolutionary approach to alloparenting predicts variations in the structure and nature of cooperative childrearing systems depending on the local population context. In some populations, particular types of kin may be important – such as grandparents and siblings. In other populations, it may be fellow parents and other households who mainly contribute and support childrearing. Whatever the form of cooperative childrearing systems, however, what is clear is that humans require additional support from alloparents for successful childrearing and reproduction.

Cross-References

Cooperation, Kin Selection, Childcare, Grand-Parenting, Helping, Human Reciprocal Altruism

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