*Original Research Article*

# Helper Effects on Breeder Allocations to Direct Care

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**Introduction:** Mothers receive childcare and productive assistance from allomaternal helpers in many societies. Although much effort has been aimed toward showing helper effects on maternal reproductive success, less has been directed toward highlighting the full range of potential effects on breeder behavior. I present a model of optimal maternal care with helpers, and tests of derived hypotheses with data collected among the Karo Batak—a group of Indonesian agriculturalists.

**Methods:** To test the model's predictions I compared the effect of women receiving help from patrilateral versus matrilateral kin because those kin may provide help with different maternal responsibilities. The model predicts a decrease in maternal allocation to care that is substitutable with the helper contribution and the helper assists with that type of care; it predicts an increase in care that is nonsubstitutable with the helper contribution or substitutable care when the helper assists with other responsibilities. With the exception of one other, most models have failed to account for an increase.

**Results/Conclusions:** Analyses of time spent carrying children supported the model. With matrilateral helpers, women increased carrying; with patrilateral helpers, they decreased it. Time spent farmworking showed the opposite pattern, suggesting that matrilateral helpers effectively decrease costs, nudging optimal maternal care upward. Patterns of breastfeeding provided little support for the model. The results do, however, suggest potential proximate mechanisms by which helpers influence maternal reproductive success in cooperative breeding societies. Am. J. Hum. Biol. 24:545–550, 2012. 

## INTRODUCTION

Helping behavior, whereby kin provide childcare and productive assistance to mothers, has been documented in a wide range of human societies. This has prompted scholars to categorize humans—along with some birds, carnivores, rodents, and callitrichids—as a cooperative breeding species (e.g., Hrdy, 2005; Turke, 1988). Although most studies of human helpers have focused on their effects on maternal reproductive success (e.g., Kramer, 2005; Mace and Sear, 2005), a number of authors have addressed the effects of helpers on maternal behavior (Bove et al., 2002; Hames, 1988; Kramer, 2009; Marlowe, 2005; Meehan, 2009). Nonetheless, there has been little acknowledgment of the possibility that mothers might increase their allocation to direct care, rather than be relieved of it or keep it steady, when receiving help. Here, I present a simple graphical model of optimal breeder allocations and tests of derived hypotheses with data from an Indonesian farming village. The village is a useful testing grounds because matrilateral and patrilateral kin may provide help with different maternal responsibilities and the model predicts different responses by breeders receiving different types of help.

There are a number of potential effects helpers might have on breeder direct care, where direct care is defined as behavior that increases the fitness of one's offspring through "direct physical contact" such as breastfeeding, carrying, or feeding (Hames, 1988: 237). One possibility is "load lightening" (Brown et al., 1978; Heinsohn, 2004). The more help a breeder receives the less it invests in caring for young itself. A second possibility is "constant breeder input" (Moehlman and Hofer, 1997). A breeder's allocation to direct care is insensitive to the presence of helpers, so parental care remains steady with or without helpers. Although helper and breeder care is additive in both scenarios, the total amount differs. With load-lightening, the sum remains the same with or without helpers; with constant breeder input, the total amount is higher with helpers. Most theoretical treatments of this phenomenon have found that the optimal strategy for breeders always falls within the range delimited by these two possibilities.

As illustrated in Table 1, only the model of Carranza et al. (2008) and the model I present here have predicted an increase in breeder direct care with helpers. Their model assumes that the benefits of parental care (or parental plus helper care) to the current offspring saturates at some point. That is, additional inputs provide no additional increases in offspring direct fitness. If help increases the rate at which the saturation point is reached, the model predicts a "load-lightening" response. If help raises the saturation point, on the other hand, the model predicts an increase in breeder direct care. As such, the predicted increase in direct care is spurred on by a restructuring of the *benefits* to offspring fitness of parental and helper care. I have developed a model that predicts an increase due to restructured costs. These models have important ramifications for our understanding of life history evolution in cooperative breeders (e.g., Kramer, 2005). For instance, they can elucidate the conditions under which

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breeders will increase their energy allocation to parental care rather than increased fertility.

### Model

Using the tradeoff logic of parental investment models (Clutton-Brock, 1991, remains the best review of theory), I have modeled (Fig. 1) the effect of helpers on parental care, $m$. The optimal level of parental care, $m'$ or $m''$, is that which maximizes parental inclusive fitness, measured as the tradeoff between benefits (offspring direct fitness) and costs (decreased ability to invest in other components of fitness). The benefits function, $B''$ with helpers and $B'$ without, is modeled as a monotonically increasing curve with diminishing returns to offspring fitness with increasing parental (or parental plus helper) care. The costs, $C''$ with helpers and $C'$ without, are modeled as a linear function to facilitate a graphical solution. The optimal level of parental care is the point at which marginal costs and benefits are equal (i.e., where a line parallel to the cost function is tangent to the benefit function). In reality, the function might also take any of a number of curvilinear forms (Beauchamp and Kacelnik, 1990), though the most likely, motontonically increasing, would yield qualitiatively similar results.

*TABLE 1. Models of the effect of helpers on breeder behavior in cooperatively breeding species*

| Model and predictions | Helper effect on direct care | | |
|---|---|---|---|
| | Load-lightening | Constant breeder input | Increased care |
| Hatchwell (1999) | | | |
| Chick mortality due to starvation | | X | |
| Chick mortality due to predation | X | | |
| Kokko et al. (2002) | | | |
| Helper desertion possible | X | | |
| Helper desertion not possible | | X | |
| Heinsohn (2004) | | | |
| Cost-benefit model: Low estimate | X | | |
| Cost-benefit model: High estimate | | X | |
| Carranza et al. (2008) | | | |
| Help speeds approach to benefits saturation point | X | | |
| Help increases saturation point of benefits | | | X |
| Kushnick (current paper) | | | |
| Substitutable types of care | X | | |
| Nonsubstitutable types of care, or substitutable but helper assists with some other parental chore | | | X |

The model contrasts forms of maternal direct care that are "substitutable" with the activities of helpers and those that are "nonsubstitutable"—a differentiation that is appreciated by scholars of human cooperative breeding (e.g., Bove et al., 2002; Kramer, 2005; Leonetti, unpublished data), but heretofore never formalized in a graphical parental investment model. Bove et al. (2002), for instance, found that the presence of sibling caretakers decreased the amount of time women spent on domestic chores among the Toba of Argentina, but it had no effect on breastfeeding. Although the girls could help with substitutable chores, they could not help with breastfeeding. Substitutability, thus, would appear to be a robust determinant of time allocation in the context of cooperative breeding, just as it is in the context of household economics, labor, and schooling (Bock, 2002; Gurven and Kaplan, 2006). In addition to chores, substitutable activities might include carrying or watching a child; nonsubstitutable activities might include things that the helper is incapable of doing for physical or competency-related reasons, such as nursing an infant or engaging in an activity that the helper has insufficient skill to carry out.

Figure 1a illustrates the case where parental care is substitutable with the helper contribution and the helper assists with that type of care. The model assumes that the helper contribution, when provided, is a fixed amount, such that the benefits to offspring direct fitness from the helper contribution are added to those from parental care. An inclusive-fitness maximizing parent should decrease her allocation to that type of substitutable care in the presence of helpers who assist with that type of care. Figure 1b illustrates the case where parental care is nonsubstitutable for a helper contribution, or where care is substitutable but helpers provide assistance with other responsibilities. In such cases, the helper's assistance

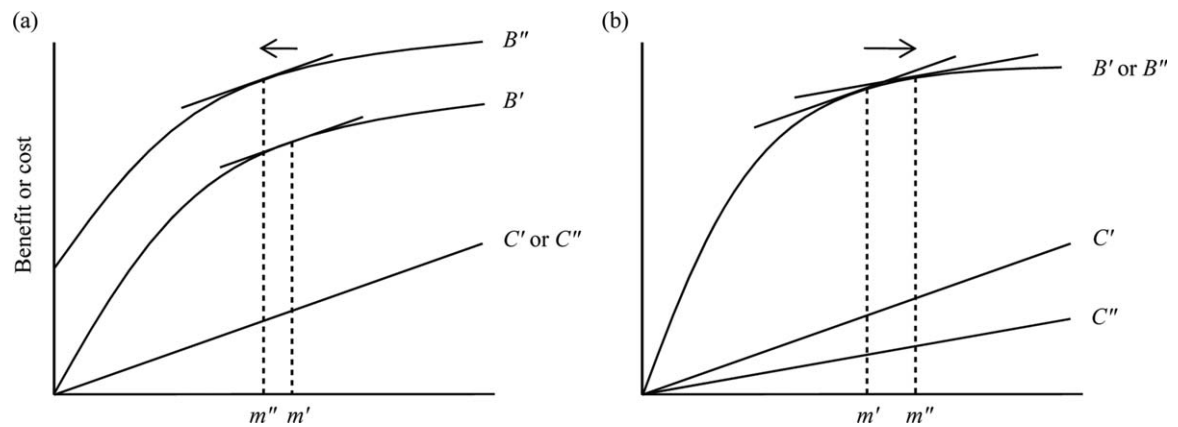


Fig. 1. Optimal allocation of parental care, $m$, with helpers for (a) substitutable and (b) nonsubstitutable care. Line $B''$ and $B'$ designate the benefit to offspring direct fitness for a given level of $m$ with and without help. The cost to parental ability to invest in later offspring is $C'$ without help and $C''$ with help. The optimal level of parental care ($m'$ without helpers and $m''$ with helpers) is reached where marginal costs and benefits are equal (i.e., a line parallel to the cost function is tangent to the benefit function). Arrows show the change in optima when helpers are added.

does nothing to change the benefits of a given level of parental care, but would decrease the costs from $C'$ to $C''$ if it increased the breeder's overall reproductive budget or survival. The inclusive-fitness maximizing strategy in that case should be to increase parental allocation to the nonsubstitutable care in question.

### *Predictions*

(i). Help may lead to an increase in parental care. This follows from the model presented here and the model in Carranza et al. (2008). With the exception of these two models, it is assumed that potential breeder reactions to helper inputs range from decreased to steady allocations to direct care (see Table 1).

(ii). Carrying offspring is a substitutable type of care. A mother with helpers who assist in carrying her offspring should decrease time spent carrying their children, as the marginal fitness benefit is higher when that energy is used toward other activities (Fig. 1a). If helpers provide assistance with other responsibilities, however, mothers with helpers should increase time spent carrying, as it provides a higher marginal fitness benefit than any other activity (Fig. 1b). Among the Karo Batak, matrilateral and patrilateral kin have contrasting ritual obligations to one another, and to a woman and her immediate family, yet little is known about how this might play out on a day-to-day basis. If these obligations carry over to economic and childcare behavior, help from patrilateral or matrilateral kin may have contrasting effects on maternal response to help.

(iii). Nursing an infant is a nonsubstitutable type of care. Mothers with helpers should spend more time nursing their infants, as the marginal fitness benefit for it is higher than for any other potential activity (Fig. 1b).

## METHODS

### *Study population*

The Karo Batak are an Austronesian-speaking group from North Sumatra, Indonesia, who practice subsistence and cash-crop agriculture (Kushnick, 2006; Singarimbun, 1975). Colonial and missionary influences have changed a number of aspects of Karo Batak life and culture. For instance, whereas in the past the Karo Batak lived in elaborate, multiapartment longhouses, today most folks live in modern-style houses built of bamboo, wood, or concrete. Other things have changed much less. For instance, Karo Batak society, today as in the past, centers on five exogamous patrilineal clans. Some key social relations are shaped by marriage, including the obligations of matrilateral (*kalimbubu*) and patrilateral (*anakberu*) kin to each other, as well as to a woman and her immediate family. These roles are well understood in a ritual and emergency context (Needham, 1978; Singarimbun, 1975), but little is known about how they play out on a day-to-day basis. For instance, *anakberu* are responsible for providing feasts at mortuary rituals and to bring an ill villager for medical help, nothing has been documented regarding the obligations of one side or the other to provide daily childcare assistance. It seems likely that help is likely tendered by kin living in close proximity. Among the Karo Batak, there is a tendency toward virilocality, but uxorilocality and other arrangements occur (Kushnick and Fessler, 2011). Mothers are the primary caretakers of children but receive both childcare and productive assistance from husbands, offspring, and adult relatives.

The data presented here were collected in 2004 among the Karo Batak (Kushnick, 2006). The analyses are based on data collected in one of the three "neighborhoods" of Doulu village (3°13′21″N, 98°32′3″E), which is situated in a mountain pass ~1,200 m above sea level, just 2 km from the Medan-Kotacane highway, and 11 km from the "hill station" town of Berastagi. The population of the Doulu neighborhood that I studied was 1,003 people living in 235 households surrounded by vegetable gardens, wet-rice fields, and a few orchards. Most of the people living there are Karo Batak, but a minority (~5%) are Toba Batak or Javanese. Almost everyone in the village is a farmer (93%), but some individuals also engage in entrepreneurialism, or work as teachers, nurses, and civil servants. Only 53% of the families in the neighborhood I studied owned land (Kushnick, 2010). The remainder rented land or worked as hired help on land owned by others. The total fertility rate is 4.38; the age-five mortality rate is 35 deaths per 1,000; the median age at weaning is 24 months (Kushnick, 2006).

### *Data collection and analysis*

Although data on time allocation were collected via direct observation, data on marriage and reproductive histories, and ratings of help from relatives, were collected via interview. All of the procedures used in this study were reviewed and approved by the Human Subjects Review Committee at the University of Washington. All ever-married, primiparous or multiparous, women of reproductive age were asked about the help they receive from various matrilateral and patrilateral kin. Help was defined as productive, childcare, and material assistance provided from the relative to the woman. Matrilateral kin were defined as a woman's mother and father, and all of their sisters and brothers. A woman was rated as a recipient of matrilateral help if she reported that any of these relatives provided help. Patrilateral kin were defined as the mother and father of a woman's husband, and all of their sisters and brothers. A woman was rated as a recipient of patrilateral help if she reported that any of these relatives provided help. Help from patrilateral relatives and help from matrilateral relatives were coded as two binary variables (1 received help, 0 did not receive help).

To collect data on time allocation, instantaneous scan sampling was used to record the activities of 48 women chosen because they coresided with their husbands and their youngest offspring was between birth and 6 years old (Martin and Bateson, 1993). During each observation period, I walked a randomly chosen path through the village and fields for 1 h. At the conclusion of each minute, indicated by a countdown timer, I did a 360° scan and recorded the location and current activity of each woman in the sample. I scheduled observation periods all 7 days of the week spread from sunrise to sunset. The 32 observation periods yielded 864 observations. The 48 women in the sample each provided an unequal number of observations to the sample for two reasons. First, during some observation periods, the women were never spotted. I only

*TABLE 2. Descriptive statistics for (a) carrying, (b) farmworking, and (c) breastfeeding samples*

| | (a) Carrying $N = 48$ | (b) Farmworking $N = 36$ | (c) Breastfeeding $N = 20$ |
|---|---|---|---|
| | Mean ± SE | Mean ± SE | Mean ± SE |
| Mother's Age (yrs.) | 31.33 ± 0.935 | 31.72 ± 1.100 | 30.05 ± 1.431 |
| Child's Age (mo.) | 28.96 ± 2.922 | 29.97 ± 3.454 | 11.00 ± 2.820 |
| Child's Sex (0 boy, 1 girl) | 0.56 ± 0.072 | 0.61 ± 0.082 | 0.50 ± 0.115 |
| Child's Birth Order | 3.08 ± 0.251 | 3.17 ± 0.310 | 3.10 ± 0.429 |
| Matrilateral Help (0 no, 1 yes) | 0.31 ± 0.068 | 0.28 ± 0.076 | 0.40 ± 0.112 |
| Patrilateral Help (0 no, 1 yes) | 0.48 ± 0.073 | 0.50 ± 0.085 | 0.35 ± 0.109 |
| Observations per Woman | 5.67 ± 0.762 | 5.17 ± 0.872 | 6.45 ± 1.321 |
| Carrying (0 no, 1 yes) | 0.15 ± 0.036 | 0.12 ± 0.037 | 0.29 ± 0.071 |
| Working (0 no, 1 yes)G[a] | 0.47 ± 0.051 | 0.49 ± 0.059 | 0.40 ± 0.081 |
| Farmworking (0 no, 1 yes) | 0.30 ± 0.047 | 0.31 ± 0.052 | 0.24 ± 0.062 |

[a]Working includes both household chores and farmwork.

recorded observed behavior and did not supplement this by asking what out-of-view women were doing. Second, women were added to the sample only after I had completed their reproductive history interviews, which were done concurrently with the time allocation study. So the early observation periods had smaller samples of women to be observed than did the later ones (Kushnick, 2006). Scan sampling underestimates the amount of time spent in private (or otherwise out-of-view) activities (Hames, 1992; Martin and Bateson, 1993). Among the Karo Batak, many of a woman's activities are done out in the open or in one's home, but in full view of passersby, including breastfeeding. Nonetheless, there is some variation in house types in Doulu—ranging from single-roomed to multiroomed, bamboo to concrete—so there is some potential for bias.

Logistic regression was used to model the effect of matrilateral and patrilateral helpers on the probability a woman was observed (i) carrying her child, (ii) engaging in farmwork, and (iii) nursing her child. It was necessary to control for two types of nonindependence: to control for within-period nonindependence (Hames, 1992; Martin and Bateson, 1993), the analyses only included the first observation of each women during a given observation period; to control for between-period nonindependence, the robust standard errors were estimated for all parameters in the statistical models (Hosmer and Lemeshow, 2000). This left 272 observations of 48 women in the carrying analyses; 236 observations of 36 women (nonfarmers were excluded) in the farmworking analyses; and, 129 observations of 20 women (those whose youngest child had already been weaned were exluded) in the nursing analyses. All of the models controlled for mother's age (in years), and child's age (in months), sex (0 male, 1 female), and birth order. The carrying and nursing analyses also controlled for whether or not the respondent was observed working, which is farmworking and domestic chores; the farmworking analysis controlled for whether or not the respondent was observed carrying her child. All analyses were done in Stata 10 with $\alpha = 0.05$. Descriptive statistics for the samples are included in Table 2.

## RESULTS

The probability an offspring was observed being carried or nursed by its mother was a montonically decreasing function of age. In the few months after birth, some offspring were observed being carried by their mothers all of the time. By 40 months of age, children were rarely carried by their mothers (though observations were made up to 58 months of age). In the first few months of age some offspring were observed being nursed up to 20–30% of the time by their mothers. By 24 months of age, offspring were rarely observed nursing. Productive, childcare, and material help from adult kin was reported by 31 of 48 women in the sample. Of these, 23 received help from patrilateral kin, 15 from matrilateral kin, and 7 received help from both. With the exception of one woman, all reports of helpful kin came from relatives living in the village.

The logistic regression models used to test the associations between the receipt of matrilateral and patrilateral help on (a) carrying, (b) farmworking, and (c) breastfeeding are presented in Table 3. All of the models controlled for mother's age, and child's age, sex, and birth order. The models used to analyze carrying and breastfeeding also controlled for working. The one used to analyze farmworking also controlled for carrying. Some of the marriages were intravillage and, thus, some of the respondents received help from both matrilateral and patrilateral kin. For this reason, the estimated effect of matrilateral help was adjusted for whether the respondent also received patrilateral help, and vice versa. Odds ratios and their standard errors were calculated using robust estimators. Each of the models proved a good fit to the data—in each, the log pseudolikelihoods were statistically significantly better in the full models than the null ones.

The results in Table 3 can be summarized as follows: (a) Carrying: Matrilateral and patrilateral help had opposite, but statistically significant, effects on the probability a

*TABLE 3. Logistic regression results for (a) carrying, (b) farmworking, and (c) breastfeeding as outcome variables with robust estimation of standard errors*

| | (a) Carrying | (b) Farmworking | (c) Breastfeeding |
|---|---|---|---|
| Odds ratios for predictors[a] | | | |
| Matrilateral Help (0 no, 1 yes)[b,c] | 3.694* | 0.115* | 1.318 n.s. |
| Patrilateral Help (0 no, 1 yes)[b,c] | 0.261* | 4.634*** | 0.088*** |
| Overall model fit | | | |
| *n* (observations) | 272 | 236 | 129 |
| *n* (clusters) | 48 | 36 | 20 |
| Log pseudolikelihood[b,d] | -77.2*** | -103.0*** | -24.5*** |

[a]All estimates adjusted for mother's age, and child's age, sex, and birth order. Models (a) and (c) also adjust for working; Model (b) adjusts for carrying.
[b]Significance: [n.s]. Not significant, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.
[c]Wald test for OR=1.000.
[d]Test that model is better fit than null model.

woman was observed carrying her youngest child. Matrilateral help was associated with an almost four-fold increase in carrying; patrilateral help was associated with an almost four-fold decrease. (b) Farmworking: Matrilateral and patrilateral had opposite, but statistically significant, effects on the probability a women was observed engaged in farmwork. The effects were almost a mirror image of those from the carrying analysis. Respondents who reported help from matrilateral kin were about 12% as likely to be farmworking as those who had not. Respondents who reported help from patrilateral kin were about five times as likely to be farmworking as those who had not. (c) Breastfeeding: Matrilateral and patrilateral help had opposite effects on the probability a woman was observed nursing her infant, but only effect of patrilateral help was statistically significant. Women with matrilateral helpers were about 30% more likely to be observed nursing as those without, but the effect was not statistically significant; women with patrilateral helpers were about 9% as likely to be nursing as those without.

## DISCUSSION

The results support the model's first prediction that help can lead to an increase in maternal allocations to direct care. Karo Batak mothers reporting help from matrilateral kin were more likely to be observed carrying and nursing their children, though only carrying was statistically significant. Valencia et al. (2006) documented an increase in parental allocations to direct care with helpers in azure-winged magpies, *Cyanopicus cyanus*. Only the model presented here and Carranza et al.'s (2008) predict such an increase (see Table 1 for a summary of models and their predictions). In the Carranza et al. (2008) model, which they developed to explain their magpie data, the prediction of an increase stems from restructured benefits to offspring direct fitness with the addition of a helper contribution. In mine, the increase stems from restructured costs. Previous models have predicted a narrower range of possibilities, never an increase, yet have received the lion's share of empirical tests (e.g., Hatchwell, 1999; Luck, 2002). Hatchwell's (1999) graphical model of breeder investment in birds, for instance, predicts a range of strategies from holding parental care constant (referred to as "additive," but identical to constant breeder input) to reductions (referred to as "compensatory," but identical to load lightening) with helpers. Heinsohn's (2004) mathematical model covers a similar range of possibilities. Kokko et al. (2002) present a mathematical model that predicts that breeders should sustain their level of investment when a decrease might lead to helper desertion. It should be noted, however, that this discussion refers specifically to the effects of nonparental helpers. An effect similar to the increase with helpers has been documented when parents synchronize their efforts (e.g., Johnstone and Hinde, 2006). When this is the case, one parent increases the amount of care, and the other parent follows suit.

The results also support the model's second prediction, which can be stated as follows: carrying offspring, since it is a substitutable type of care, should decrease with helpers, but increase when helpers assist with other responsibilities that decrease the cost of parental care. Among the Karo Batak, patrilateral help decreased the amount of time mothers spent carrying offspring and the analyses suggest that the patrilateral helpers were assisting with childcare (since their help increased maternal allocation to farmwork). Further, matrilateral help increased the amount of time mothers spent carrying offspring and the analyses suggest that matrilateral helpers were assisting with nonchildcare labor responsibilities (since their help decreased maternal allocation to farmwork). This highlights a major limitation of this study—i.e., that the precise labor inputs of the two classes of kin is correlational rather than verified with behavioral observations. Nonetheless, the polarity of the effects is striking. A similar opposite effect has been documented in studies of the effect of patrilateral versus matrilateral helpers on components of reproductive success (Leonetti et al., 2005; Sear and Mace, 2008; Voland and Beise, 2002). An important implication of these results is pinpointing a possible mechanism that might explain the ubiquitous observation that help from matrilateral kin—maternal grandmothers, in particular—leads to increased offspring survival (reviewed in Mace and Sear, 2005; Sear and Mace, 2008). The theoretical model and empirical results presented here suggest that an increase in maternal care, rather than the addition of grandmaternal care, might be the proximate cause of higher offspring survivorship. By assisting with work-related responsibilities, rather than direct childcare, matrilateral kin may spur an increase in optimal maternal care (as illustrated in Fig. 1b). At present, insufficient evidence exists to assess the cross-cultural validity of this implication.

The results provided little support for the model's third prediction—because it is a nonsubstitutable type of care, helpers should lead to an increase in breastfeeding. There was a slight increase in breastfeeding with matrilateral help, but the effect was not statistically significant. This may well take root in a lack of statistical power for the following reasons. First, the effect is relatively small which usually requires larger samples to accurately estimate. Second, the sample was, by necessity, pared down to 20 women for the breastfeeding analyses (those whose youngest offspring had already been weaned were excluded). Even so, the effect of patrilateral helpers (a substantive decrease in the amount of breastfeeding) ran markedly counter to prediction. One possible explanation is that the piecemeal approach of the model is overly simplistic. The different types of care, though treated separately here, can be intimately intertwined in reality. Such is the case with breastfeeding and carrying; a mother cannot do the former without also doing the latter. The decrease in breastfeeding with patrilateral help is, thus, probably explained in part by the decreased carrying with patrilateral help. This, however, is an incomplete explanation, as the effect remained in the model even when adjusting for carrying.

From a proximate perspective, the result that patrilateral help leads to less time spent breastfeeding has implications for revealing the mechanism by which patrilateral help, from paternal grandmothers in particular, may lead to an increase in breeder fertility (reviewed in Mace and Sear, 2005). A decrease in the provision of breastfeeding may decrease the duration of postpartum infecundity which, in turn, may lead to shorter birth intervals and, thus, higher fertility (e.g., Valeggia and Ellison, 2001; Wood, 1994). Johnson (1990) documented a similar chain of effects in a different context. This fertility-increasing effect of patrilateral helpers is much less consistently observed cross-culturally than the survival-enhancing

effect of matrilateral helpers (Mace and Sear, 2005), but so is the decrease in breastfeeding with patrilateral helpers. Bove et al. (2002) found that the presence of helpers had no effect on nursing. In her study of two Indian societies, Leonetti (2008) found an increase in breastfeeding among the patrilineal Bengali and a decrease among the matrilateral Khasi.

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## LITERATURE CITED

Beauchamp G, Kacelnik A. 1990. On the fitness function relating parental care to reproductive value. J Theor Biol 146:513–522.

Bock J. 2002. Evolutionary demography and intrahousehold time allocation: schooling and children's labor among the Okavango Delta peoples of Botswana. Am J Hum Biol 14:206–221.

Bove R, Valeggia C, Ellison P. 2002. Girl helpers and time allocation of nursing women among the Toba of Argentina. Hum Nat 13:457–472.

Brown J, Dow D, Brown E, Brown S. 1978. Effects of helpers on feeding of nestlings in the grey-crowned babbler (*Pomatostomus temporalis*). Beh Ecol Sociobiol 4:43–59.

Carranza J, Polo V, Valencia J, Mateos C, de la Cruz C. 2008. How should breeders react when aided by helpers? Anim Behav 75:1535–1542.

Clutton-Brock T. 1991. The evolution of parental care. Princeton, NJ: Princeton University Press. 352 p.

Gurven M, Kaplan H. 2006. Determinants of time allocation across the lifespan: a theoretical model and an application to the Machiguenga and Piro of Peru. Hum Nat 17:1–49.

Hames R. 1992. Time allocation. In: Smith EA, Winterhalder B, editors. Evolutionary ecology and human behavior. Hawthorne, NY: Aldine de Gruyter. p 203–236.

Hames R. 1988. The allocation of parental care among the Ye'kwana. In: Betzig L, Borgerhoff Mulder M, Turke P, editors. Human reproductive behavior: a Darwinian perspective. Cambridge: Cambridge University. p 237–251.

Hatchwell B. 1999. Investment strategies of breeders in cooperative breeding systems. Am Nat 154:205–219.

Hawkes K, O'Connell J, Blurton Jones N, Alvarez H, Charnov E. 1998. Grandmothering, menopause, and the evolution of human life histories. Proc Nat Acad Sci USA 95:1336–1339.

Heinsohn R. 2004. Parental care, load-lightening, and costs. In: Koenig WD, Dickinson JL, editors. Ecology and evolution of cooperative breeding in birds. Cambridge: Cambridge University Press. p 67–80.

Hosmer D, Lemeshow S. 2000. Applied logistic regression. New York: Wiley. 392 p.

Hrdy S. 2005. Evolutionary context of human development: the cooperative breeding model. In: Carter C, Ahnert L, Grossmann K, Hrdy S, Lamb M, Porges S, Sacher N, editors. Attachment and bonding: a new synthesis. Boston: MIT Press. p 9–32.

Johnson P. 1990. Changing household composition, labor patterns, and fertility in a highland New Guinea population. Hum Ecol 18:403–416.

Johnstone RA, Hinde CA. 2006. Negotiation over offspring cared—how should parents respond to each other's efforts? Behav Ecol 17:818–827.

Kokko H, Johnstone R, Wright J. 2002. The evolution of parental and alloparental effort in cooperatively breeding groups: when should helpers pay to stay? Behav Ecol 13:291–300.

Kramer K. 2005. Children's help and the pace of reproduction: cooperative breeding in humans. Evol Anthropol 14:224–237.

Kramer L. 2009. Does it take a family to raise a child? Cooperative breeding and the contribution of Maya siblings, parents and other adults in raising children. In: Bentley G, Mace R, editors. Substitute parents: biological and social perspectives on alloparenting in human societies. NY: Berghahn Books. p 77–99.

Kushnick G. 2006. Parent-offspring conflict among the Karo of North Sumatra, Indonesia. Seattle, WA: University of Washington, Seattle.

Kushnick G. 2010. Resource competition and reproduction in Karo Batak villages. Hum Nat 21:62–81.

Kushnick G, Fessler DMT, 2011. Karo Batak cousin marriage, cosocialization, and the Westermarck hypothesis. Curr Anthropol 52:443–448.

Leonetti D, Nath D, Hemam N, Neill D. 2005. Kinship organization and the impact of grandmothers on reproductive success among the matrilineal Khasi and patrilineal Bengali of Northeast India. In: Voland E, Chasiotis A, Schiefenhoevel W, editors. Grandmotherhood: the evolutionary significance of the second half of female life. New Brunswick, NJ: Rutgers University Press. p 194–214.

Mace R, Sear R. 2005. Are humans communal breeders? In: Voland E, Chasiotis A, Schiefenhoevel W, editors. Grandmotherhood: the evolutionary significance of the second half of female life. Piscataway: Rutgers. p 143–159.

Marlowe F. 2005. Who tends Hadza children? In: Hewlett B, Lamb M, editors. Hunter-gatherer childhoods. Piscataway, NJ: Aldine Transaction. p 177–190.

Martin P, Bateson P. 1993. Measuring behaviour: an introductory guide. NY: Cambridge University.

Meehan C. 2009. Maternal time allocation in two cooperative childrearing societies. Hum Nat 20:375–393.

Moehlman P, Hofer H. 1997. Cooperative breeding, reproductive suppression, and body mass in canids. In: Solomon N, French J, editors. Cooperative breeding in mammals. Cambridge: Cambridge University Press. p 76–128.

Needham R. 1978. Classification and alliance among the Karo: an appreciation. Bijdragen tot de Taal-, Land- en Volkenkunde 134:116–148.

Sear R, Mace R. 2008. Who keeps children alive: a review of the effects of kin on child survival. Evol Hum Behav 29:1–18.

Singarimbun M. 1975. Kinship, descent, and alliance among the Karo Batak. Berkeley: University of California. 246 p.

Valencia J, De la Cruz C, Carranza J, Mateos C. 2006. Parents increase their parental effort when aided by helpers in a cooperatively breeding bird. Anim Behav 71:1021–1028.

Valeggia C, Ellison P. 2001. Lactation, energetics, and postpartum fecundity. In: Ellison P, editor. Reproductive ecology and human evolution. Hawthorne, NY: Aldine de Gruyter. p 85–105.

Voland E, Beise J. 2002. Opposite effects of maternal and paternal grandmothers on infant survival in historical Krummhorn. Behav Ecol Sociobiol 52:435–443.

Wood J. 1994. Dynamics of human reproduction: biology, biometry, demography. Hawthorne, NY: Aldine De Gruyter. 653 p.