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The Goals of Direct Paternal Care Among a South Amerindian Population

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ABSTRACT Human males are remarkable among mammals in the level of investment they provide to their wives and children. However, there has been debate as to the degree to which men actually invest and through which fitness pathways the benefits of familial investment are realized. Much of the previous research exploring these issues has focused on men's roles as providers, but few have explored correlates of men's direct parental care. Although this is reasonable given men's parental emphasis on provisioning, the providing of direct care is more straightforward with a clear provider and recipient and little ambiguity as to the care-giver's intent. Here, we explore contextual correlates of men's direct care among the Tsimane of Bolivia to determine the extent to which such care is patterned to enhance its effectiveness in increasing child wellbeing and the efficient functioning of the family. We also explore whether Tsimane fathers provide care in ways that enhance the positive effect it has on the wife's perception of the care provider. Overall, we find that Tsimane men appear responsive to the needs of children and the family, but show that there is little evidence that men respond to factors expected to increase the impact that men's care has on their reputations with their wives. Am J Phys Anthropol 139:295–304, 2009.

Men marry into long-term reproductive relationships around the world (Murdock, 1949) and account for the production of the majority of calories in most human populations (Ember and Ember, 1983). Fathers also tend to provide some forms of direct care to children, including holding and playing (Hewlett, 1992; Marlowe, 2005). Despite the common life history tradeoff between mating effort and parenting effort, however, these facts do not lead directly to the conclusion that men tradeoff offspring quantity in order to invest in children. The extent of male provisioning and the ultimate motivation behind men's willingness to enter marital unions and provide such investment have been the focus of much recent debate (Anderson et al., 1999; Marlowe, 2003; Hawkes, 2004; Bleige Bird, 2007; Winking et al., 2007; Quinlan and Quinlan, 2008). The fitness pathways through which the benefits of paternal investment are realized define which factors men should respond to by altering their investment levels.

Much of the previous research exploring these issues has focused on men's roles as providers (Anderson et al., 1999; Bleige Bird, 2007), but few have explored correlates of men's direct parental care. Although this is reasonable given men's parental emphasis on provisioning, the providing of direct care is more straightforward, with a clear provider and recipient and little ambiguity as to the purpose of the activity. Here, we present a comprehensive exploration of correlates of men's direct care among the Tsimane of Bolivia in order to shed light on the parameters that define patterns of men's care, and by extension, the ultimate goals of such care.

Evolutionary explanations for the high levels of men's parental involvement have traditionally focused on men's ability to enhance the quality of costly offspring, as well as the productivity of the family unit. Many critics of this model have focused on the spoils of forager men's work effort, pointing out that the foods that men tend to target, and their widespread distribution, serve more to enhance men's social status than benefit their families (Hawkes, 1993; Bleige Bird et al., 2001). Some researchers have forwarded the proposition that the paternal involvement that is evident is a commodity that men offer in order to increase the chances of winning and maintaining a spouse (van Schaik and Paul, 1996; Blurton Jones et al., 2000). The extent to which securing future fertility motivates men's parenting behavior remains an unanswered empirical question.

This article has two main goals. The first is to describe the ways in which children are directly cared for and socialized among the Tsimane, a forager-horticultural group in central Bolivia, and to situate the role that fathers play in this process. The second is to explore the ultimate motivations for the providing of direct paternal care. Rather than focus our attention on the relationship between father's behavior and some outcome measure of fitness, we instead attempt to gauge men's motivations by examining their behavior in reference to factors that

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alter the returns of fitness gains via the proposed pathways. We intend to test the degree to which men pattern the delivery of care to maximize its effectiveness in increasing the wellbeing of the child and/or the efficient functioning of the household. To accomplish this, we test whether men bias the delivery of care 1) when it might prove more efficient in helping the child, such as when the mother or other caretakers are less able to provide care; and 2) toward older children to allow mothers to focus on the care of younger children. Although such patterns are necessary to support the contention that men are investing directly in children's fitness, they might also arise due to men trying to meet wives' expectations. To further explore the degree to which men provide care to *signal* investment to the mother, in order to maintain access to her fertility, we also explore the impacts of factors that affect the strength of such signals and the fertility benefits received. Specifically, we test whether men 3) provide more care when it is more likely to have a greater impact on the mother's impression of the caregiver, such as when she is present to view such behavior; 4) provide more conspicuous forms of care to increase the strength of the signal, particularly in the wife's presence; and 5) provide more care when there is more future fertility to secure by impressing the mother.

MALE PARENTAL CARE IN HUMANS: PATHS TO FITNESS

Human infants are born remarkably helpless, requiring a level of care that significantly reduces the foraging efficiency of the caretaker (Hurtado et al., 1992; Marlowe, 2003). Even after offspring are able to care for themselves, they remain economically dependent until their late teens (Lee and Kramer, 2002; Kaplan and Lancaster, 2003). Despite the high dependency of human offspring, women are able to maintain high fertility rates, resulting in families consisting of multiple children at varying levels of dependence. This compound fertility could never have evolved in the absence of supplemental provisioning of mothers and offspring and/or alloparental caretaking by fathers and other kin (Hrdy, 2005).

Originally, it was argued that men, acting as husbands and fathers, filled the majority of the caloric and labor deficit (referred to here as the provisioning model) (Lovejoy, 1981; Lancaster and Lancaster, 1983; Kaplan et al., 2000). The increased well of offspring need would have led to greater incentive for men to reduce investments in the pursuit of extra fertility and increase those toward enhancing the quality of their existing children. Long-term pair bonds followed as the assured future fertility mediated the opportunity costs of paternal investment (Winking, 2006), greater paternity confidence allowed men to invest in known children, and because they allowed for greater efficiency in the delivery of biparental care and in household production (Murdock, 1949; Brown, 1970, 2003; Lancaster and Lancaster, 1980; Marlowe, 2007).

The streamlining of production led to a division of labor—a strategic assignment of labor tasks based on gender-specific reproductive constraints (Brown, 1970; Gurven and Hill, n.d.; Hurtado et al., 1992). These task assignments increased family efficiency through labor specialization and economies of scale (Kaplan and Lancaster, 2003), and allowed for greater variance in diet (Gurven and Hill, n.d.; Kaplan and Hill, 1992). Implied within the logic of this model is that the primary benefits that men receive from parental investment are in the form of increased offspring quality and that the efficient delivery of biparental investment should be the goal of men's parental behavior.

In the past decade, a number of researchers, following Hawkes (1991), have criticized the provisioning model (Hawkes, 1993; Blurton Jones et al., 2000; Bleige Bird et al., 2001; Hawkes and Bleige Bird, 2002; O'Connell et al., 2002). The main criticisms are that 1) men's foraging strategies in hunter-gatherer populations seem not to be designed to optimize the amount of food going to the nuclear family, but rather to display their mate value and garner social and mating benefits; and 2) the absence of a father does not have a robust and substantial negative effect on offspring survival, and men's marital behavior does not appear linked to the magnitude of this effect (Blurton Jones et al., 2000; Sear et al., in press). The first criticism stems from the observation that men in foraging populations tend to focus on the hunting of large game animals, a strategy often characterized by lower return rates, greater variance in daily success, and widespread distribution of the spoils. Although this may render the strategy an inefficient means of provisioning a family, the successful capture of large game *can* provide an honest signal of overall fitness (Bleige Bird et al., 2001), and the widespread sharing of the meat can provide social and mating benefits as well (Hawkes, 1993). Thus men, in forgoing less ostentatious but predictable foods, are sacrificing child wellbeing in order to garner personal fertility benefits. Men are argued to enter into long-term relationships because the practice provides a solution to male–male competition (Blurton Jones et al., 2000), and/or because of the fertility benefits that the relationships confer (Hawkes et al., 1995). This argument has been referred to as the mating effort model elsewhere (Winking et al., 2007). In response, other researchers have countered that forager men do not exclusively focus on large game (Marlowe, 2003), hunting large game often provides comparable or higher returns than other foraging strategies (Gurven and Hill, n.d.), men often do have some control over the distribution of their production (Gurven, 2004), and that meat is typically more highly valued than other foods (Gurven and Hill, n.d.; Hill, 1988).

Supporting the mating effort model, however, father presence does not seem necessary for the successful rearing of children to adulthood in many populations (Blurton Jones et al., 2000; Sear and Mace, 2008). Reviews of the effects of father presence on mortality, development, and reproductive success show great variation and often weak effects if any (Winking, 2006; Sear and Mace, 2008). To account for the provisioning of mothers and their offspring, necessary to maintain observed fertility rates, researchers pointed to the importance of investments by grandmothers and other kin (Hawkes et al., 1998; Hrdy, 2005).

DIRECT CARE

Here, we define direct care as any behavior aimed at protecting or enhancing child wellbeing that requires physical proximity and direct interaction, such as holding, feeding, playing, and so forth (Kleiman and Malcolm, 1981). Although direct care is relatively rare among Tsimane fathers, we chose to examine this type

of care, because it is a conspicuous and unambiguous form of investment. Unlike economic production, each act of direct care consists of a clear care provider and a care recipient. It is also an activity that would not be performed in the absence of the child, unlike forms of indirect investment (economic production, house construction, community defense, etc.).

Both models predict that women should provide the bulk of direct childcare, something that appears to be true cross-culturally (Konner, 2005). According to the logic of the provisioning model concerning the division of labor, mothers should be the main direct caretakers as they are the sole providers of breast milk, and direct childcare is presumed to be more compatible with (and a superset of) breastfeeding than it is with the more rigorous activities assigned to men. Finally, cultural norms might develop around these efficiency-enhancing strategies, further strengthening the divide by reinforcing the exclusivity of gender roles. Thus, men are expected to play an auxiliary role with respect to direct care, basing the delivery of such care on what the mother is unable to provide and in a way that increases the efficient functioning of the household unit (referred to here as the investment hypothesis).

Proponents of the mating effort model, on the other hand, have proposed that direct care can serve as a commodity that men exchange for access to women's fertility (van Schaik and Paul, 1996; Blurton Jones et al., 2000). Step-parental care has long been viewed as such an exchange (Smuts and Gubernick, 1992; Waynforth and Dunbar, 1995; Anderson, 2000), establishing the fact that both men and women find the benefits of such an interaction as worthwhile. If the choosing of a husband (or short-term partner) is heavily influenced by the promise of parental care, and if the maintenance of a long-term relationship is heavily dependent on the continuation of such care, then it is entirely possible that each unit of investment provided by a man yields greater fitness benefits via greater *access* to fertility than it does via enhanced offspring fitness. An exchange of fertility for investment might be more easily maintained in humans, as reproduction typically takes place in long-term iteroparous relationships. Furthermore, unlike any other ape, new offspring are born long before independence is achieved by previous offspring, allowing for a continuous exchange of the respective commodities. Based on this logic, men are expected to be most concerned with maximizing their *perceived* investments in the eyes of their wives (referred to here as the signaling hypothesis).

Among stepfather/offspring relationships, one study provides evidence that men put on parental performances for their wives. Flinn (1988) found that stepfathers were more likely to be observed in agonistic interactions with stepchildren when their wives were not present to view the interaction. No such finding was found for biological fathers. Similar patterns have been reported in nonhuman primate experiments (Keddy Hector et al., 1989).

Although these studies are suggestive, the question remains, to what extent do the proposed fertility benefits motivate men's parental decisions toward resident *biological* children? Anderson et al. argued that the difference between investments offered to resident biological children and nonresident biological children (e.g., living with an ex-wife) was due to the loss of these associated fertility benefits (Anderson et al., 1999). Although there may be alternative explanations to this disparity (e.g., less ability to invest due to distance), their research clearly showed what has been indicated in numerous studies, that fathers tend to invest more and represent less of a threat to resident biological children than to resident step-children (Daly and Wilson, 1985; Flinn, 1988; Marlowe, 1999). This pattern, and the fact that men do not immediately divorce wives upon menopause, counters the argument that men's familial involvement is solely based on fertility benefits, although it is still possible that such benefits represent the *primary* motivation for paternal care (i.e., the marginal returns via increased access to fertility are greater than those realized through increased offspring fitness).

PREDICTIONS

According to the logic of both models, mothers would tend to be the *de facto* caregivers, as childcare as a whole is more conducive to women's obligatory infant care and nursing than it is to male-oriented tasks. Furthermore, this leads to parenting specialization through greater experience, meaning that mothers are more likely to provide care even when both parents are available. According to the provisioning model, men should act to maximize child wellbeing and household functioning, and should therefore play a secondary role in direct care, basing the delivery of such care on what the mother is unable to provide and in a way that enhances family functioning. However, if wives demand husbands to act in such ways, men may do so in order to maintain a good standing in the relationship. Thus, while such a prediction is directly derived from the provisioning model, and null findings would be very damaging to its claims, a positive finding does not necessarily refute the mating effort model. If men do provide direct care in ways that maximize its effectiveness on enhancing offspring wellbeing and family functioning, we expect that: 1) men should more frequently serve as direct care givers when mothers are unavailable for childcare (i.e., absent), or 2) occupied with other chores. Furthermore, we predict that 3) fathers will more often fulfill this role when there are fewer older daughters, as sisters commonly serve as allo-caretakers. Lastly, because mothers are the only ones capable of nursing and thus are frequently obligated to focus their parenting on infants and toddlers, 4) fathers' care will be directed more toward older children than mothers' care.

To further test the signaling hypothesis, we examine how men respond to factors that alter the impact that the delivery of direct care has on enhancing their reputation with their wives and maintaining access to fertility. We expect that 1) fathers should bias their direct care to when mothers are present to view such care; 2) fathers should focus more on conspicuous forms of care, such as playing and feeding, than do mothers; and 3) conspicuous care should comprise a larger proportion of fathers' direct care in the presence of their wives than in their absence. Men should also take into account the amount of fertility they are securing when determining optimal investment levels. They should therefore try harder to impress a younger wife than impressing a post-menopausal one. There are a number of reasons, however, why the amount of time men spend in direct care might change as they (and their wives) age. As men become older, the number of older daughters they have increases, the amount of time they spend in food production might

TABLE 1. Sample structure of children age ≤ 5 and their parents by marital status of biological parents and household composition

Marital status	Together		Divorced		Mother dead	Father dead	
House comp.	Mono[a]	Poly[b]	Single mom[c]	Mom and stepdad	Single dad	Single mom	Total
Individuals							
Children[d] ≤ 5	190	10	14	2	2	2	220
Moms	103	6	8	2	na	1	120
Dads	103	4	na	na	1[d]	na	108

[a] Monogamous.
[b] Polygynous.
[c] In all cases, families were living with or adjacent to maternal kin.
[d] Children were living with father and maternal grandparents during observation. Father remarried shortly after research ended and children remained with maternal kin.

change as dependency load grows, and so forth. Therefore, we will use the amount of time spent in direct care in the absence of wives as a baseline and predict that 4) men will spend comparatively less time in direct care in the presence of older wives.

METHODS

Population

Data were collected among the Tsimane of central lowland Bolivia. The Tsimane are forager-horticulturalists living mostly along the Maniqui River and its tributaries in the Beni Region, Bolivia. Roughly 8,000 individuals reside in some 80 villages comprised of multiple extended families (Instituto Nacional de Estadística, 2003). They derive the majority of their calories from family-maintained fields consisting mainly of rice, plantains, corn, and yucca. Agricultural food is subsidized with jungle game, fish, foraged fruits, and varying levels of market goods (depending heavily on proximity to local markets).

Marriages are very stable among the Tsimane with roughly 20% of marriages ending in divorce (Winking et al., 2007). Although polygyny is practiced, only 10% of marriages were polygynous in the sample communities. Nuclear families are typically the unit of production, particularly for garden foods. Husbands and wives spend considerable amounts of time clearing, planting, weeding, and harvesting crops that are less widely shared among related households within a cluster. Men are typically the sole providers of game and the main providers of fish, while women are largely responsible for childcare, food processing, and household tasks.

Time allocation data

Observations were made in four communities between June 2002 and June 2003 and an additional two communities throughout 2005. To collect time allocation data, households were first divided into residential clusters (typically consisting of extended families). Each cluster was sampled randomly without replacement from 7:00 AM to 7:00 PM in 3-h time blocks (this was changed to 2-h blocks in 2005 season). During these time blocks, the activity, location, and interactants of each individual were recorded every half-hour. If someone was absent during a scan, others were asked about the individual's whereabouts and activity. Direct care was defined as nursing, holding, tending (swinging baby or in physical contact, but no other activity), grooming/cleaning, playing with, feeding, comforting, scolding, or instructing. Child presence was defined as being in the same specific locale within camp (e.g., house, kitchen, yard). Observer presence was defined as being in the same homestead, so that an observer in a family's yard would be considered in the presence of a man in the family's house. This resulted in 836 individuals being observed for 52,802 person scans (averaging 63.2 scans per person).

Determining ages

The level of accuracy for which Tsimane parents knew the age of their children varied greatly. Ages were estimated for young infants (∼<6 months) by simply asking the parents. For many infants, their births were observed during the research period. For older children and adults, ages were determined by demographic interviews conducted by MG that employed a combination of methods, including using well-known dated events, relative age lists, formal records, and so forth. Methods are described at length in Gurven et al. (2007).

Statistical analysis

For tests utilizing the pooled sample over simple categorical variables, chi-square tests are employed. For multivariate tests, we employed the generalized estimating equations method (GEE). This method accounts for the correlated structure of dependent variables arising from repeated measures, controlling for each individual. Unfortunately, there is no standard absolute goodness-of-fit measure, with the GEE method. All analyses but one (see below) use a binary distribution, exchangeable correlation structure, report parameter estimates as logit estimates, and use a dichotomous behavioral variable "parenting" (yes/no) as the dependent variable. One analysis involving the age of recipients of care, uses a normal distribution, exchangeable correlation structure and identity link. All analyses were performed in SPSS 15.0.

RESULTS

Overview of direct care

Out of the sample of 836 individuals from 6 communities, 220 children aged 5 and under were observed for a total of 13,188 person scans. Table 1 shows the marital status of these children's parents and their residence status. Two hundred children (90.9%) were living with both biological parents, 10 of whom were living in 4 polygynous households. The parents of 16 children (7.2%) had divorced (involving 10 families), the mother of two siblings had died, and the father of two siblings had died. Although remarriage is the norm, only two of twelve divorced or widowed mothers in this sample had remarried (this is undoubtedly due to the limiting of the

sample to those with small children), bringing their children into the next marriage. These figures are testament to the stability of Tsimane marriages and indicate that upon marital dissolution, the parental burden falls largely on the mother and her kin.

Figure 1 shows the percentage of time children were directly cared for and by whom (from the child's perspective). Infants under 6 months of age were directly cared for 57.2% of day light hours while in camp, with the rest of time spent mostly sleeping or swinging in a hammock. Of this care, mothers provided 82.5% of direct care in camp during the first 6 months, and 69.1% during the first 6 years. The next three highest contributors were sisters, who accounted for 9.8% of all care in the first 6 years, fathers, who accounted for 7.3%, and maternal aunts, who accounted for 3.7%. All four grandparents accounted for only 3.3% of direct care, with the maternal grandmother providing 2.1% of direct care alone.

Figure 2 demonstrates the amount of time spent offering direct care to various kin while in camp from the caregiver's point of view. As this figure demonstrates, women spend substantially more time in direct care than men, and this trend is apparent from a very early age. Furthermore, while grandmothers may not be a significant source of direct care for any particular child, the fact that they are minor caregivers to a large number of grandchildren results in their spending a fair amount of time in grandparental care.

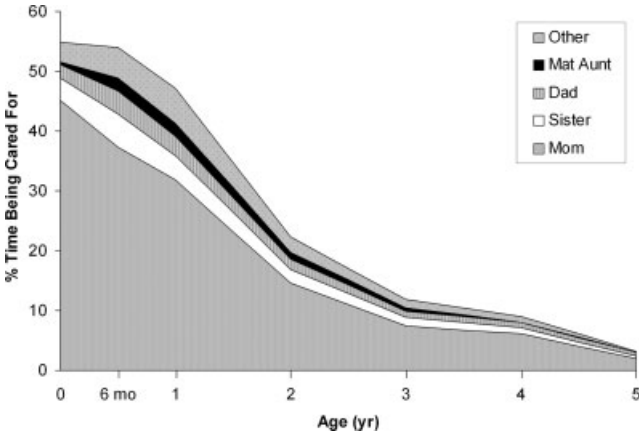

Fig. 1. Percentage of daytime spent being cared for by various caretakers by age (N = 220 children, 8,019 observations while in camp).

Because of the precipitous drop in amounts of direct care offered to children as they age, we limited our sample to parents with at least one child under age 4 for further exploration of parental care. We observed 93 fathers of young children for a total of 6,346 person scans and 102 mothers for 6,794 person scans. While in camp, mothers spent 65.4% of their time in the same immediate location as their small children, and 35.4% of their time in direct parental care. Men spent 51.0% of their time in camp in the same location as their small children and 8.4% of their time in direct care. These figures do not accurately reflect total amounts of time, however, as fathers spent only 31.1% of their time in camp, while mothers spent 61.1% of their time in camp (see Fig. 3). To estimate total amounts of time in these activities, we used in-camp figures as estimates for the amount of time spent in parenting activities while parents were outside of camp (not directly observed) but were recorded as being "with" their children. This calculation results in women spending a projected 58.4% of their total time in the same immediate location of their small children and 31.6% providing direct care. For men, these figures are 27.2% of their total time with their small children and 4.5% of their time in direct care.

Effect of mother's presence on father's care

To explore the effect of the presence of mothers on the probability of men providing any direct care, the sample was limited to cases in which men were directly observed in the presence of a child under 4 who was either being cared for by the man or was *available* for care (i.e., not being cared for by another individual). A total of 83 men were observed during 623 spot observations meeting these criteria. Of these, 535 were recorded while the mother was present, and 88 were recorded while the mother was absent. This means that men

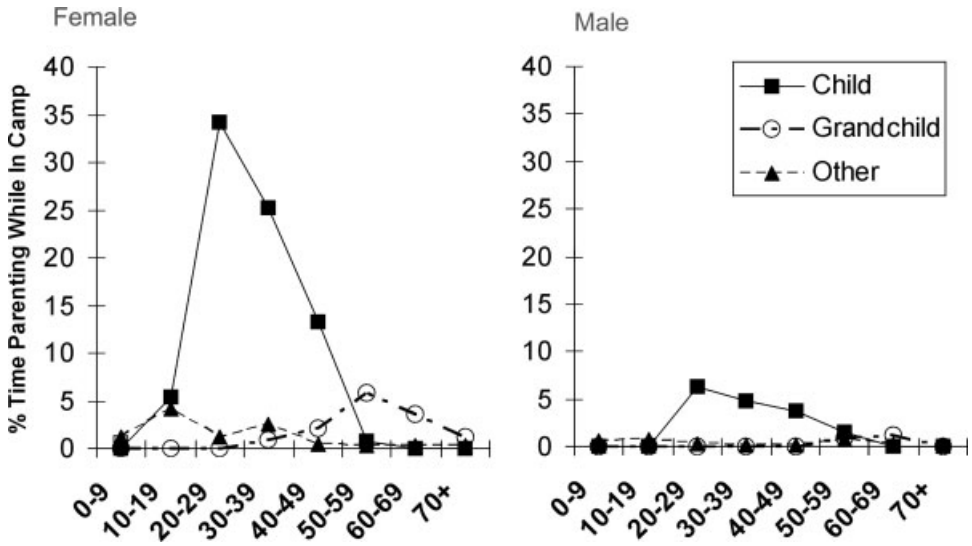

Fig. 2. Percentage of daytime spent providing care by recipient and by age of caregiver.

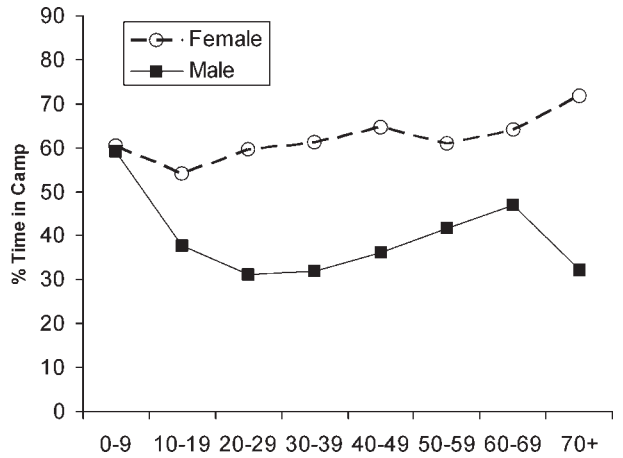

Fig. 3. Percentage of daytime spent in camp.

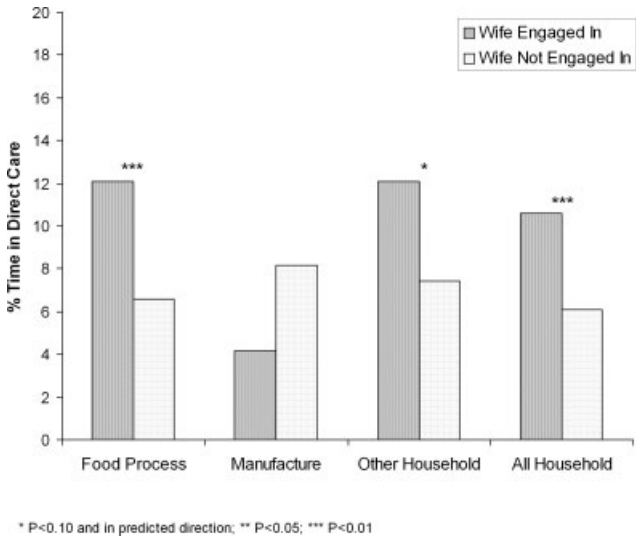

Fig. 4. Projected percent of daytime (controlling for community and age of youngest child) spent in direct care by fathers in camp by whether wives in camp are engaged in various activities.

spent only 1.5% of their total time and 4.8% of the time in camp left alone with a small child in camp. Table 2 shows the results of the GEE analysis concerning the effect of the mother's presence on the probability of men engaging in direct parental care. In support of the investment hypothesis, fathers are significantly *less* likely to provide direct care to an available child when the mother is present. Converting the logit estimates to probabilities (using average values for controls) shows that men were nearly twice as likely to engage in care when the mother was absent (14.7% for wife present, 28.5% for wife absent). Removing cases in which the children were sleeping did not change the significance of the effect of mother's presence (with same controls, $B = -0.919$, $P = 0.002$). In a separate analysis, the effect of the number of adult in-laws present on the probability that men would provide direct care reached one-tailed significance (with same controls, $B = 0.176$, $P = 0.071$). In-laws were present 28% of the time men were with available children, with an average of 1.8 in-laws during these times and resulting in an average 4.6% absolute increase in the probability of men providing care. There was no effect, however, of the number of unrelated adult women present (with same controls, $B = 0.227$, $P = 0.361$).

TABLE 2. GEE analysis of effect of the presence of a child's mother on the probability that the father will engage in direct parental care

Variables in model	*B*	df	Std. error	*P*
Wife present	−0.841	1	0.275	0.002
Number of children < 4 present	−1.025	1	0.602	0.089
Average age of children < 4 present	−0.045	1	0.014	0.001
Community		5		0.005

$N = 85$ men, 641 observations.

Effect of mother's activities on father's care

Table 3 presents the tests of the effect of wife's labor activity on the probability of fathers being observed in direct care. Only cases in which the mother and father were directly observed in the camp were included. This resulted in a sample of 90 men who were observed for a total of 1,719 scans. After controlling for the age of youngest child, age of father, and the community, fathers were more likely to be observed in direct care if the mother was engaged in food processing ($B = 0.656$, $P = 0.002$), general household tasks like cleaning and tending fire ("Other Household") ($B = 0.644$, $P = 0.017$), and when she was engaged in any category of household labor ("All Household") ($B = 0.698$, $P = 0.001$). There was a suggestive, but nonsignificant effect in the opposite direction when mothers were engaged in manufacture ($B = -0.757$, $P = 0.115$). Figure 4 displays the projected time spent in direct care based on the activity of the wife (with control variables set to sample means).

Effect of number of older daughters on father's care

There are a number of factors that could covary with both the number of older daughters and direct care, such as age, length of marriage, time spent in production, and so forth. To isolate the effect of having more *daughters,* we decided to review the effect of the percentage of resident children aged 7 and up that were daughters. Table 4(a) shows the result of a GEE analysis involving men who had at least one child less than 4 years of age and at least one resident child 7-years-old or older. One polygynously married outlier was removed as his 16 children aged 7 and up doubled the next highest number. After controlling for the age of the youngest child, the age of the father, community, and the number of older children in the household, the percentage of these older children that were daughters was significantly associated with fathers providing *less* direct care ($B = 0.008$, $P = 0.035$). Thus, a father with two older children that are both sons spends an estimated 9.6% of his time in camp in direct care (using the means of the control variables), while one with two older daughters only spends 4.3% of his time engaged in direct care. This effect holds even after limiting cases to those in which small children are not being cared for by others [Table 4(b)], suggesting that the effect is not simply due to men with more daughters having less opportunity to provide direct care.

TABLE 3. GEE analysis of effect of mother's labor on probability of men being observed in direct care

Variable	Food processing		Manufacture		Other household		All household	
	B	*P*	*B*	*P*	*B*	*P*	*B*	*P*
Wife engaged in	0.656	0.002	−0.757	0.115	0.644	0.017	0.698	0.001
Age of youngest (yr)	−0.016	0.897	0.037	0.754	0.009	0.943	−0.037	0.770
Age of father	−0.011	0.501	−0.008	0.636	−0.008	0.640	−0.014	0.431
Community		0.635		0.789		0.718		0.544

N = 90 men, 1,719 observations.

TABLE 4. GEE analysis of effect of the percentage of older children that are daughters on the probability that a father of a small child (<4) will engage in direct parental care while in camp

Variables in model	(a) All observations				(b) Observations with available child <4 present			
	B	df	Std. error	*P*	*B*	df	Std. error	*P*
Number of children > 6	0.043	1	0.147	0.772	0.117	1	0.174	0.499
% of children > 6 female	−0.009	1	0.004	0.035	−0.014	1	0.005	0.006
Age of youngest child	0.008	1	0.014	0.541	0.014	1	0.165	0.383
Age of father	0.026	1	0.029	0.374	−0.005	1	0.032	0.870
Community		5		0.353		5		0.001

N = 46 men, 909 observations.

TABLE 5. GEE analysis testing whether fathers tend to provide care to older children

Variables in model	*B*	df	Std. error	*P*
Parent = Father	7.263	1	2.720	0.008
Age of parent	0.434	1	0.139	0.002
Community		5		0.747

The dependent variable is the age of the recipient child in months. N = 61 men (186 observations), 97 women (1,549 observations).

Age of children receiving mother's and father's care

After controlling for community and the age of the parent, the age of the recipient of direct care was significantly higher for fathers' care than those of mothers' care (Table 5) (Parent = Father, B = 7.263, P = 0.008). This included care received by all children aged 18 and under. The estimated marginal means for the average age of the recipient child were 19.0 months for mothers and 26.2 for fathers. Removing instances of nursing increases the average age to 20.0 months for mothers, although the effect remains significant.

Conspicuous care

Figure 5 shows that after excluding nursing, both mothers and fathers spent the greatest amounts of time providing "passive" direct care to children aged 3 and under, including holding and tending. There is no difference between the proportions of direct care that fathers and mothers dedicated to conspicuous care (grooming, feeding, playing, and comforting) (N = 1021 for women, 156 for men, χ^2 = 0.373, P = 0.541), failing to support the prediction of the signaling hypothesis. Reviewing each category separately reveals that women spent significantly more time grooming children than men (12.6% of mother's care, 5.1% of fathers care, χ^2 = 7.414, P = 0.006). However, fathers focused significantly more of their care on playing with children (2.2% of mother's care, 7.7% of father's care, χ^2 = 14.792, P < 0.001), and comforting them (2.5% of mother's care, 6.4% of father's care, χ^2 = 6.819, P = 0.009).

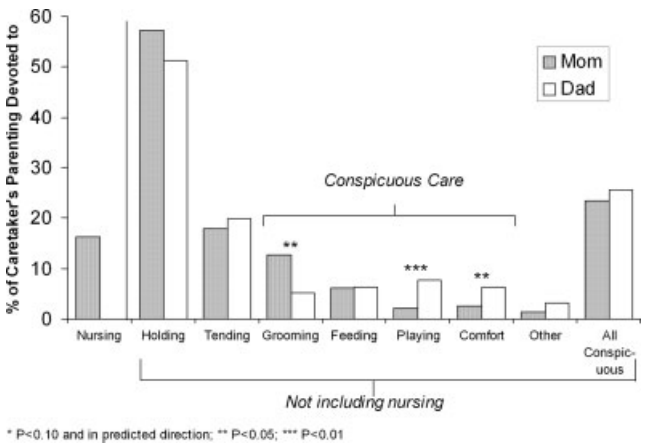

Fig. 5. Percentage of mothers' and fathers' care devoted to different activities.

There are no significant differences in the proportional contributions of the types of care that men provide in the presence or absence of a mother (see Fig. 5 for categories). This is true when evaluating all categories (χ^2 = 5.792, df = 6, P = 0.447, N = 145 observations in presence of mother, 48 in absence), and when reviewing each dyad individually. Conspicuous forms of care accounted for 24.83% of care in the presence of mothers and 20.83% in their absence (χ^2 = 0.317, df = 1, P = 0.573, N = 145 observations in presence of mother, 48 in absence). Because of the limited sample size, however, we cannot assert the null with great confidence.

Effect of mother's age on father's care

The ages of mothers ranged from 14 to 47 with an average of 27.4, over 4 years younger than their husbands' average of 31.8. After controlling for community, average age and number of children aged 3 and under present,

TABLE 6. GEE analyses of effect of mother's age and presence on probability of men being observed in direct care

Variables in model	(a) Without interaction				(b) With interaction			
	B	df	Std. error	*P*	*B*	df	Std. error	*P*
Wife present	−0.862	1	0.286	0.003	0.529	1	0.980	0.590
Number of children < 4 available	−1.002	1	0.594	0.091	−0.960	1	0.591	0.105
Avg age of children < 4 available	−0.042	1	0.014	0.003	−0.042	1	0.014	0.003
Wife age	−0.024	1	0.021	0.255	0.010	1	0.031	0.752
Wife age × wife present	–	–	–	–	−0.051	1	0.034	0.131
Community	–	5	–	0.006	–	5	–	0.006

N = 80 men, 619 observations.

TABLE 7. Predictions and results of the two models

Prediction	Direction	*P* value	Result
Investment hypothesis			
1) Men will provide more care when mother is absent	Predicted	0.002	Supported
2) Men will provide more care when mother is occupied	Predicted	0.001	Supported
3) Men will provide more care when there are fewer older daughters	Predicted	0.035	Supported
4) Men will focus their care toward older children	Predicted	0.002	Supported
Signaling hypothesis			
1) Men will provide more care when mothers are present to view the care	Opposite	0.002	Not Supported[a]
2) Men will focus on conspicuous types of care more than mothers	Predicted	0.541	Equivocal[b]
3) Men will focus on conspicuous types of care more when mothers are present	Predicted	0.573	Not Supported
4) Men will provide more care when younger mothers are present	Predicted	0.131	Not Supported

[a] There was a one-tailed positive effect of the presence of in-laws on the probability of fathers being observed in direct care.
[b] Results were significant and in the predicted direction for two types of conspicuous care, but there was no overall effect.

there was no significant overall effect of mother's age on the probability of men being observed in direct care in the presence of an available child [Table 6(a)]. There was no significant negative interaction effect between the mother's age and her presence [Table 6(b)] (effect of mother's age × mother's presence, $B = -0.051$, $P = 0.131$). This indicates that, relative to the amount of time men spend in direct care in the mother's absence, they do not spend comparatively *more* time in the presence of *younger* mothers.

DISCUSSION

Although fathers provide much less direct care than do mothers, their direct investments are by no means insignificant. If we remove the advantage of numbers that sisters have (there is only one father) and focus on only the sister who provides the most care for each child, sisters account for 7.6% of children's direct care within camp in the first 6 years. This proportion is not significantly different from the amount fathers contribute (fathers = 7.3%, $\chi^2 = 0.182$, df = 1, $P = 0.670$). Therefore, from a child's point of view, fathers are essentially tied as the second highest contributor of direct care. In other natural-fertility populations, resident biological fathers have been found to the second highest contributor as well (Hewlett, 1992; Marlowe, 2005).

Although no formal tests have yet been conducted concerning the reproductive consequences to Tsimane mothers of having alloparental assistance available (for studies involving other populations, see Turke, 1988; Flinn, 1989; Sear et al., 2003), the 30.9% of direct care that nonmothers provide represents a substantial investment of time and energy and must have an impact on women's ability to successfully rear multiple children. The Tsimane (and arguably all humans) therefore satisfy the hallmark criterion of a cooperatively breeding population, in that "allomaternal assistance alters basic quantity-versus-quality life-history tradeoffs underlying maternal decision-making," (Hrdy, 2005, p. 71). And within this cooperative system, it is clear that fathers play an important role, despite the fact that direct care is not their parental specialty. Whether men's direct care contributions are the result of efficiency-enhancing flexibility in the division of labor or men appealing to the expectations of wives is discussed below.

Table 7 summarizes the various predictions and findings. The data provide support for all four of the predictions derived from the investment hypothesis. The average age of the recipients of fathers' care was significantly higher than those of mothers' care, even after removing instances of nursing. Fathers spent more time in direct care while in camp when fewer of their older children were daughters, suggesting that fathers adjust their levels of care relative to the availability of other potential caretakers. Similarly, fathers were more likely to be engaged in direct care when their wives were preoccupied with other tasks. This indicates that fathers substitute for mothers and are more responsive to children when mothers are preoccupied. It also indicates that fathers can liberate mothers to engage in tasks that are not conducive to childcare.

Although fathers were rarely left alone with young children, during this time, they were nearly twice as likely to provide care than when the mother was present to view the care, supporting the investment hypothesis. Furthermore, this pattern contradicts the prediction of the signaling hypothesis—men do not appear to be biasing the delivery of their care to when it can have the most significant impact on their wives' impression. Men *were* significantly more likely to provide direct care in the presence of in-laws (one-tailed), however, suggesting that audience can have an impact on the amount of care that fathers offer.

Contrary to the signaling hypothesis, fathers did not devote more of their direct care to more conspicuous

activities than did mothers, and they both spent similar amounts of time in "passive" forms of care. Men did devote proportionally more time to both playing and comforting, which might represent two of the more conspicuous forms of nonpassive care. Others, however, have argued that rigorous play is designed to complement the style of care provided by mothers (Paquette, 2004), not to impress them. Furthermore, Tsimane fathers did not devote more care to conspicuous forms while in the mothers' presence, although the robustness of this finding was hampered by a small sample size.

Finally, there was no evidence that compared to the time fathers devoted to direct care in the absence of mothers, men did not significantly increase the amount of time they spent in direct care in the presence of *younger* mothers. This is particularly revealing, as younger women not only have more future fertility to offer men, but they also have less to lose from leaving them: they tend to have fewer children that they must take care of, and their possibility of remarriage is most likely greater at these ages (Sweeney, 1997).

Because these tests were observational, alternate explanations must be dealt with. For instance, it might be that mothers are more likely to leave their children alone with fathers who are more attentive, resulting in a spurious result of mother absence being associated with greater direct care. However, the amount of time men spent in direct care in the wife's presence was not associated with the amount of time they were left alone with children (WLS Regression, $N = 80$, $B = 0.047$, $t = 0.615$, $P = 0.540$). Similarly, absent mothers may not be totally unaware. Observers often abound and any gross dereliction is likely to be reported. There is, however, a great range in the degree of interaction during supervision, and it is difficult to imagine that absent mothers would be as well informed as when they could directly observe the care.

It is also important to reiterate that the predictions derived from the two models are not entirely exclusive. As discussed before, those factors that increase the effectiveness of direct paternal care may also be the factors that lead mothers to expect more parental help from fathers. Furthermore, it is possible that women's preferences for providers have led to a sexual selection for men more predisposed to investment, without appropriate time for men to develop strategies to make the most of their investments. Thus while the predictions of the investment hypothesis are more directly derived from the logic of the provisioning model, their confirmation does not necessarily refute the signaling hypothesis.

Similarly, even if we assume that both parents are equally concerned with the wellbeing of their children, it can be argued that men still might have reason for exaggerating their investments. Children represent a public good, and rearing them thus involves a cooperative endeavor (Anderson et al., 1999). Each parent must decide how much to invest in personal versus family interests, and there is undoubtedly some negotiation that takes place between the parents. Note that here, the ultimate benefit of exaggerating investment is not only an increased probability of spousal retention, but also the manipulating of the wife to contribute more labor. Thus men may be motivated to impress wives, regardless of their age.

Ultimately, with the results reported here, we can say that Tsimane fathers provide direct care in a manner that suggests a concern for child wellbeing and family functioning. Men's care was delivered when it was most needed, undoubtedly enabling wives to perform their other duties more effectively. There was, however, only suggestive evidence that men took into account the ability of their direct care to influence their wives' impressions of them. Although we cannot speak as to whether a desire to impress wives affects the *amount* of care being provided by men, it does not appear to have an impact on the manner in which they provide it.

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LITERATURE CITED

Anderson KG. 2000. The life history of American stepfathers in evolutionary perspective. Hum Nat 11:308–333.

Anderson KG, Kaplan H, Lancaster J. 1999. Paternal care by genetic fathers and stepfathers. I. Reports from Albuquerque men. Evol Hum Behav 20:405–431.

Bleige Bird R. 2007. Fishing and the sexual division of labor among the Meriam. Am Anthropol 109:442–451.

Bleige Bird R, Smith EA, Bird DW. 2001. The hunting handicap: costly signaling in human foraging strategies. Behav Ecol Sociobiol 50:9–19.

Blurton Jones NG, Marlowe F, Hawkes K, O'Connel JF. 2000. Paternal investment and hunter-gatherer divorce rates. In: Chagnon N, Cronk L, Irons W, editors. Adaptation and human behavior: an anthropological perspective. New York: Aldine. p 69–90.

Brown JK. 1970. A note on the division of labor by sex. Am Anthropol 72:1073–1078.

Brown JC, Alberts SC, Silk JB, Altman J. 2003. True paternal care in a multi-male primate society. Nature 425:179–181.

Daly M, Wilson M. 1985. Child abuse and other risks of not living with both parents. Ethol Sociobiol 6:155–176.

Ember M, Ember CR. 1983. Marriage, family and kinship. USA: HRAF Press.

Flinn MV. 1988. Step- and genetic parent/offspring relationships in a Caribbean village. Ethol Sociobiol 9:335–369.

Flinn MV. 1989. Household composition and female reproductive strategies in a Trinidadian village. In: Rasa AE, Vogel C, Voland E, editors. The sociobiology of sexual and reproductive strategies. London: Chapman and Hall. p 206–233.

Gurven M. 2004. To give and to give not: the behavioral ecology of human food transfers. Behav Brain Sci 27:543–583.

Gurven M, Kaplan H, Zelada Supa A. 2007. Mortality experience of Tsimane Amerindians: regional variation and temporal trends. Am J Hum Biol 19:376–398.

Hawkes K. 1991. Showing off: tests of an hypothesis about men's foraging goals. Ethol Sociobiol 12:29–54.

Hawkes K. 1993. Why hunter-gatherers work. Curr Anthropol 34:341–361.

Hawkes K. 2004. Mating, parenting, and the evolution of human pair bonds. In: Chapais B, Berman CM, editors. Kinship and behavior in primates. Oxford: Oxford University Press. p 443–474.

Hawkes K, Bleige Bird R. 2002. Showing off, handicap signaling, and the evolution of men's work. Evol Anthropol 11:58–67.

Hawkes K, O'Connel JF, Blurton Jones NG, Alvarez H, Charnov EL. 1998. Grandmothering, menopoause, and the evolution of human life histories. Proc Natl Acad Sci USA 95:1336–1339.

Hawkes K, Rogers AR, Charnov EL. 1995. The male's dilemma: increased offspring production is more paternity to steal. Evol Ecol 9:662–677.

Hewlett BS. 1992. Intimate fathers: the nature and context of Aka Pygmy paternal infant care. Ann Arbor: The University of Michigan Press.
Hill K. 1988. Macronutrient modifications of optimal foraging theory: an approach using indifference curves applied to some modern foragers. Hum Ecol 16:157–197.
Hrdy SB. 2005. Humans as cooperative breeders: an evolutionary and comparative perspective. In: Hewlet BS, Lamb ME, editors. Hunter-gatherer childhoods: evolutionary, developmental, and cultural perspectives. New Brunswick, NJ: Aldine Transaction. p 65–91.
Hurtado AM, Hill K, Kaplan H, Hurtado I. 1992. Trade-offs between female food acquisition and child care among Hiwi and Ache foragers. Hum Nat 3:185–216.
Instituto Nacional de Estadistica. 2003. Bolivia: Caracteristicas sociodemograficas de la poblacion indigena. La Paz: INE.
Kaplan H, Hill K. 1992. The evolutionary ecology of food acquisition. In: Smith EA, Winterhalder B, editors. Evolutionary ecology and human behavior. New York: Aldine. p 167–201.
Kaplan H, Hill K, Lancaster J, Hurtado AM. 2000. A theory of human life history evolution: diet, intelligence, and longevity. Evol Anthropol 9:156–185.
Kaplan HS, Lancaster JB. 2003. An evolutionary and ecological analysis of human fertility, mating patterns, and parental investment. In: Wachter KW, Bulatao RA, editors. Offspring: human fertility behavior in biodemographic perspective. Washington, DC: National Academies Press. p 170–223.
Keddy Hector AC, Seyfarth RM, Raliegh MJ. 1989. Male parental care, female choice and the effect of an audience in vervet monkeys. Anim Behav 38:262–271.
Kleiman DG, Malcolm JR. 1981. The evolution of male parental investment in mammals. In: Gubernick DJ, Klopfer PH, editors. Parental care in mammals. New York: Plenum Press. p 347–387.
Konner M. 2005. Hunter-gatherer infancy and childhood: the !Kung and others. In: Hewlett BS, Lamb ME, editors. Hunter-gatherer childhoods. New Brunswick, NJ: Aldine. p 19–64.
Lancaster JB, Lancaster CS. 1980. The division of labor and the evolution of human-sexuality. Behav Brain Sci 3:193.
Lancaster JB, Lancaster CS. 1983. Parental investment: the hominid adaptation. In: Ortner DJ, editor. How humans adapt: a biocultural odyssey. Washington, DC: Smithsonian Institution Press. p 33–69.
Lee RD, Kramer KL. 2002. Children's economic roles in the Maya family life cycle: Cain, Caldwell and Chayanov revisited. Popul Dev Rev 28:475–499.
Lovejoy O. 1981. The origin of man. Science 211:341–350.
Marlowe F. 1999. Showoffs or providers? The parenting effort of Hadza men. Evol Hum Behav 20:391–404.
Marlowe F. 2003. A critical period for provisioning by Hadza men: implications for pair bonding. Evol Hum Behav 24:217–229.
Marlowe FW. 2005. Who tends Hadza children? In: Hewlett B, Lamb M, editors. Hunter-gatherer childhoods: evolutionary, developmental and cultural perspectives. New Brunswick: Transaction. p 177–190.
Marlowe FW. 2007. Hunting and gathering: the human sexual division of foraging labor. Cross-Cult Res 41:170–195.
Murdock GP. 1949. Social structure. New York: Macmillan.
O'Connell JF, Hawkes K, Lupo D, Blurton Jones NG. 2002. Male strategies and Plio-Pleistocene archaeology. J Hum Evol 43:831–872.
Paquette D. 2004. Theorizing the father-child relationship: mechanisms and developmental outcomes. Hum Dev 47:193–219.
Quinlan RJ, Quinlan MB. 2008. Human lactation, pair-bonds, and alloparents. Hum Nat 19:87–102.
Sear R, Allal N, Mace R. Family matters: kin, demography and child health in a rural Gambian population. In: Bentley GR, Mace R, editors. Substitute parents: biological and social perspectives on alloparenting in human societies. Berghan Books (in press).
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.
Sear R, Mace R, McGregor IA. 2003. The effects of kin on female fertility in rural Gambia. Evol Hum Behav 24:99–112.
Smuts BB, Gubernick DJ. 1992. Male-infant relationships in nonhuman primates: paternal investment or mating effort? In: Hewlett BS, editor. Father-child relations: cultural and biosocial contexts. New York: Aldine. p 1–30.
Sweeney MM. 1997. Remarriage of women and men after divorce: the role of socioeconomic prospects. J Fam Issues 18: 479–502.
Turke P. 1988. Helpers at the nest: childcare networks on Ifaluk. In: Betzig L, Borgerhoff Mulder M, Turke P, editors. Human reproductive behavior: a Darwinian perspective. Cambridge: Cambridge University Press. p 173–188.
van Schaik CP, Paul A. 1996. Male care in primates: does it ever reflect paternity? Evol Anthropol 5:152–156.
Waynforth D, Dunbar RIM. 1995. Conditional mate choice strategies in humans: evidence from lonely hearts advertisements. Behavior 132:755–779.
Winking J. 2006. Are men that bad as fathers? The role of men's investments. Soc Biol 53:100–115.
Winking J, Kaplan H, Gurven M, Rucas S. 2007. Why do men marry and why do they stray? Proc R Soc Lond B Biol Sci 274:1643–1649.