J.biosoc.Sci, (2009) **41**, 183–193, © 2008 Cambridge University Press
doi:10.1017/S0021932008002988 First published online 23 July 2008

PARENTAL SUPPLY AND OFFSPRING DEMAND AMONGST KARO BATAK MOTHERS AND CHILDREN

GEOFF KUSHNICK

University of Washington-Tacoma, USA

Summary. The resolution of parent–offspring conflict (POC) might sway in favour of the offspring if the parent relies on offspring-supplied information about need. Here, three hypotheses from a resolution model of POC were tested using data on sickness histories and mother–infant interactions from 24 Karo Batak women and their young children from two rural villages in North Sumatra, Indonesia. First, as predicted, offspring with greater need (measured as age and propensity to illness) tended to fuss more often. Second, as expected, observed fussiness predicted the number of suckling occurrences observed during sampling periods. Third, contrary to the prediction, the duration of fussing observed after breast-feeding occurrences was longer than the duration of the breast-feeding occurrences themselves. Parental decisions were made based on offspring-supplied information about need, but offspring failed to garner resources in excess of the parental optimum. This suggests that a POC interpretation is unnecessary to account for these results.

Introduction

The idea that offspring might be equipped to garner more resources than the parentally preferred amount has intuitive appeal for those who have parented or observed others doing so. Trivers's (1974) theory of parent–offspring conflict (POC) has shown that the necessary suite of adaptations for offspring manipulation of parents is evolutionarily tractable. Here, tests of hypotheses derived from this theory are tested with data on illness histories, fussiness and breast-feeding collected from Karo Batak women and their young children in two villages in rural North Sumatra, Indonesia.

The logic of POC theory (Trivers, 1974) can be summarized as follows. Since a parent has an equal chance (0·5) of sharing any randomly selected nuclear gene with each of its offspring, all else being equal, it favours an equal distribution of fitness-enhancing resources amongst them. A given offspring, on the other hand, is more closely related to itself (1·0 chance of sharing a gene) than it is to any of its non-identical-twin siblings and, when all else is equal, should favour an inequitable share of parental resources at the expense of its siblings. Of course, all else is rarely equal and POC is complicated by other factors, including population-level mate infidelity and offspring reproductive value (Clutton Brock, 1991; Mock & Forbes, 1992; Mock & Parker, 1997; Parker *et al*., 2002).

It is useful to differentiate between 'battleground' and 'resolution' models of POC. Battleground models predict parental and offspring optima (and, thus, the magnitude of the conflict in various contexts). They show that POC is mathematically and evolutionarily possible, but are relatively barren in terms of providing testable hypotheses (Mock & Forbes, 1992; Mock & Parker, 1997; Parker *et al*., 2002). In contrast, resolution models concern themselves with finding ESS (Evolutionary Stable Stategy) behaviours for the parent and child, such as optimal begging levels or whether to provide resources in response to offspring demands (Godfray, 1991; Mock & Parker, 1997; Parker *et al*., 2002). Resolution models are based on Trivers's (1974) observation that if parents rely on their offspring to provide information about their current resource 'need' (that is, the benefits gained from the resources are cryptic) offspring might use this to manipulate parental resource allocation (reviewed in Mock & Parker, 1997). Godfray (1991) formalized this idea in terms of honest signalling of need – where need is defined as a measure of the fitness an offspring would gain from a unit of parental investment. The ESS outcome for most resolution models is the *pro rata* compromise, with parental investment somewhere between the parental and offspring optimal levels (Mock & Parker, 1997). Thus, if parents provided resources according to offspring demands, the resolution would be tilted (albeit slightly) in favour of the offspring – an 'offspring wins' resolution.

Parker *et al.* (2002) have argued that POC resolution depends greatly on the continuum of power between parent and offspring (i.e. who physically controls resource distribution) and the interplay of supply and demand. Borrowing from Hussell's (1988) model of food provisioning in tree swallows (*Tachycineta bicolor*), they show that two mechanisms must work in a specific way to net the offspring more than the parental optimal amount of resources (Parker *et al*., 2002; Royle *et al*., 2004). The first is the EDS mechanism, or the effect of demand on supply, which must be positive for an offspring-wins resolution (i.e. parents provide more resources when offspring are more demanding). The second is the ESD mechanism, or the effect of supply on demand. A positive ESD mechanism means that after being provided resources by parents, offspring continue to demand. A negative ESD mechanism means that offspring cease their demands. A neutral ESD mechanism means that offspring demands are unrelated to parental provisioning. Although each possibility has been observed in nature (Royle *et al*., 2004), only with the negative ESD do offspring garner parental resources in excess of the parental optimum. Offspring should cease signalling upon the provision of resources because at that point the net cost of continued solicitation outweighs any additional resources they might procure (Hussell, 1988; Parker *et al*., 2002).

A number of authors have speculated that POC might play a role in shaping parent–child interactions in humans (for one review, see Wells, 2003). Despite this, strong evidence for its influence on actual phenotypes in humans and other animals is scarce (Mock & Forbes, 1992; Royle *et al*., 2004). One possible cause is that parents may allocate investment without informational input from the offspring, thus eliminating one means for being manipulated (Hauser, 1993). Another possibility is 'meshing' – that is, the overlap of parental and offspring fitness interests outweighs the divergence (Bateson, 1994).

In this paper, three hypotheses are examined to test Parker *et al.*'s (2002) model of POC resolution: (1) offspring with greater need should be more demanding of parental resources, where demand is measured as fussiness and need is measured as age and propensity to illness; (2) mothers should supply more resources to more demanding offspring, where resource provisioning is measured as breast-feeding; and, (3) offspring should be less demanding after they have been provided with parental resources.

Ethnographic background

The Karo are one of six Batak *suku* (approximately 'tribe' or 'ethnic group') with traditional homelands in the peri-equatorial highlands of North Sumatra, Indonesia (Singarimbun, 1975; Kipp, 1993). Primarily cash-crop and subsistence agriculturalists, the majority of Karo Batak belong to Protestant and Catholic churches, but to a lesser degree have converted to Islam or retained their animistic beliefs without church affiliation. In the face of pervasive outside influences, many aspects of Karo custom persist (e.g. use of *Bahasa Karo*, kin terminology and strong patrilineality) while others have disappeared or are practised less widely (e.g. only a small number of families live in traditional houses, and cannibalism and intervillage warfare have not been practised for at least 100 years). The majority of Karo Batak live in scattered, ethnically homogeneous villages in the Karo Regency (just north of Lake Toba and west of Medan) and bordering areas of adjoining regencies, such as Aceh Tenggara, Dairi, Deli Serdang, Langkat and Simalungun.

These analyses are based on fieldwork in two Karo Batak villages with contrasting socioeconomic contexts. The first village, Doulu, was chosen because of its closer proximity to trade, health and educational facilities. It is located in a mountainous valley pass approximately 1200 m above sea level (3°13′ N×98°32′ E). Doulu's economy centres on wet-rice (*sawah*) agriculture and a location near the Medan-Berastagi-Aceh Highway. Public transportation between Doulu and the regency capital is frequent and the roads good. Women from Doulu have moderate to high fertility (TFR=4·38), under-5 mortality (37·2 deaths per 1000) is on a par with the national average, and cases of malaria and diarrhoea are infrequent in the sub-district as a whole. The second village, Laubuluh, was chosen because of its relatively farther proximity to trade, health and educational facilities. It is located in the hilly hinterland at approximately 1000 m above sea level that fringes the Karo Regency's highland plateau (3°11′ N×98°16′ E). Laubuluh's economy centres on dry-rice (*ladang*) and citrus agriculture. Public transportation between Laubuluh and the regency capital is infrequent and the roads are variously unimproved or poorly maintained. Women from Laubuluh have moderate to low fertility (TFR=3·28), under-5 mortality (60·4 deaths per 1000) is higher than the national average, and cases of malaria and diarrhoea are relatively frequent in the sub-district as a whole.

Observations in both villages indicate that, although fathers and other relatives help with childcare, mothers are the primary caretakers of their offspring. Dependent infants and toddlers spend considerable time carried by or at the side of their mothers. Breast-feeding occurs just about everywhere, including near homes, in public places around the village and in the fields. The mean age at complete cessation of breast-feeding is slightly lower in Doulu (20·4 months, SD=5·52, n=95) than Laubuluh (21·7 months, SD=4·47, n=113).

Methods

During the period from November 2003 to November 2004, quantitative ethnographic data were collected from amongst a stratified-random sample (n=240) of ever-married Karo Batak women aged 16 to 50 in Doulu and Laubuluh villages. These data included demographic, economic and behavioural data collected via interview, household hazard inspection and systematic observation. Interviews were conducted by trained female research assistants in *Bahasa Indonesia* and *Bahasa Karo*. Data on offspring sickness were collected using the mother's year-by-year recall. Although most of the interviews were conducted privately, other family members were allowed to contribute to the process of recalling sicknesses to maximize data quality. For the analyses presented here, a stratified-random subsample of mother–offspring dyads (n=24) were selected for systematic observation of fussiness and breast-feeding (see Table 1). Female research assistants helped collect data using focal observation methods (Martin & Bateson, 1994) collected at behaviourally determined times. Focal dyads were followed for 90 minutes, starting at various times from morning (08.35h) to late afternoon (16.00h). The sampling periods took place when mothers reported they were likely to breast-feed. Behaviour was recorded for a continuous span of 6 or 9 minutes at a randomly selected time within the 90 minutes of observation. Behaviours of interest were recorded manually, including whether the offspring was fussing, nursing or neither. Occurrences of fussiness were defined as any cry-like vocalization (including whimpers) from the child, regardless of duration and acoustical quality. Cessation of audible vocalization punctuated occurrences (and, as such, rhythmic vocalizations were counted as multiple occurrences). Suckling occurrences were defined as active breast-feeding regardless of duration and voracity. Loss of a 'latch' to the breast punctuated occurrences (and, as such, a single bout of feeding may have been recorded as multiple occurrences).

Statistical analyses included t test and Mann–Whitney comparisons of means (the latter used when comparing latencies, which were not normally distributed) and ordinary least-squares (OLS) regression (Sokal & Rohlf, 1994; Kleinbaum *et al*., 1996). The regression models included bivariate (dependent by predictor) versions, as well as multivariate ones (dependent by predictor with controls). The control variables were chosen because they could have potentially confounded the bivariate relationship. They included: sex of child (0 female, 1 male); age of child in months; and village (0 Doulu, 1 Laubuluh). Diagnostic tests for the regression models were conducted by visual inspection of residual plots. Statistical procedures were used to test the assumptions of Hypotheses 2 and 3 because it was impossible (and unethical) to use experimental methods to establish the temporal precedence of fussing (for the EDS mechanism) or suckling (for the ESD mechanism), as suggested by Kölliker (2003). All statistical tests were conducted in SPSS 13, with significance reported where α=0·05.

Table 1. Detailed summary of mother–infant dyads observed ($n=24$)

				Infant		
Village	Woman identifier	Age	Minutes observed (recorded)	Sex	Age (months)	Birth order
Doulu	Ginting 18	32	90 (9)	b	18	5
	Ginting 30	41	90 (9)	g	10	2
	Karo-karo 10	28	90 (9)	b	3	3
	Karo-karo 24	30	90 (9)	g	6	1
	Karo-karo 3	29	90 (9)	b	3	5
	Karo-karo 9	25	90 (9)	b	24	3
	Sembiring 14	20	90 (9)	b	8	1
	Sembiring 18	28	90 (9)	g	1	3
	Sembiring 19	23	90 (9)	b	14	1
	Sembiring 6	34	90 (9)	g	5	2
	Sembiring 9	25	90 (9)	b	8	1
	Tarigan 1	39	90 (9)	g	26	5
Laubuluh	Ginting 35	32	90 (9)	b	1	4
	Ginting 39	35	90 (9)	b	2	4
	Karo-karo 39	22	90 (9)	g	2	2
	Karo-karo 40	21	90 (9)	b	2	1
	Karo-karo 42	29	90 (6)	b	9	4
	Karo-karo 47	30	90 (6)	b	9	1
	Perangin-angin 12	26	90 (9)	b	9	4
	Perangin-angin 13	36	90 (9)	b	25	1
	Perangin-angin 15	29	90 (9)	b	1	1
	Perangin-angin 20	26	90 (6)	b	21	1
	Perangin-angin 27	26	90 (6)	g	4	2
	Tarigan 15	28	90 (6)	b	11	2

Results

To test Hypothesis 1, the following groups were defined as having the greatest 'need': (a) those offspring who were reported to have suffered more than zero sicknesses per month; (b) those offspring who were reported to have suffered at least 1 sickness in the past year; and (c) those who were less than 6 months old. As predicted and shown in Table 2, each of the groups identified as having greater need had a substantially higher mean number of occurrences of fussiness per minute of observation than their comparison groups, yet only (b) was statistically significantly different, and (a) was only marginally insignificant ($p=0{\cdot}062$).

To further test the hypothesis, two OLS regression models were built (see Table 3 and Fig. 1). Both the bivariate (Model 1A) and multivariate (Model 1B) versions included number of occurrences of fussiness observed per minute (as the dependent variable) and reported sicknesses in the past year (as the predictor of interest). As

Table 2. Comparisons of mean number of occurrences of fussiness per minute by measures of need

Measure	Group	*n*	Mean fussing/ minute	SE	*t*	*p*
a. Sicknesses per month	0	10	0·18	0·058	1·603	0·062
	>0	14	**0·31**	0·056		
b. Sicknesses in past year	0	14	0·18	0·050	2·350	0·014*
	1+	10	**0·36**	0·060		
c. Age of child	Up to 6 months	11	**0·30**	0·054	0·950	0·176
	More than 6 months	13	0·22	0·062		

Note: *t* tests, df=23, one-tailed.
*$p<0{\cdot}05$.

predicted, the estimated coefficients for sicknesses in the past year were positive in both the bivariate and multivariate models, but not statistically significant (though the bivariate model was marginal, $p=0{\cdot}051$). Removing two possible outliers, although there was nothing biologically or behaviourally distinct about them, increased the fit of both models. The estimated coefficient for the predictor in the bivariate model was the same with or without the outliers, but with the outliers removed, the estimate was statistically significant ($\beta=0{\cdot}069$, $p=0{\cdot}039$, $R^2=0{\cdot}196$). The *p* value for the estimated coefficient for the predictor in the multivariate model is improved but was still not statistically significant ($\beta=0{\cdot}061$, $p=0{\cdot}084$, $R^2=0{\cdot}240$).

To test Hypothesis 2, two OLS regression models were built (see Table 3 and Fig. 1). Both the bivariate (Model 2A) and multivariate (Model 2B) versions included number of occurrences of suckling observed per minute (as the dependent variable) and number of occurrences of fussiness observed per minute (as the predictor of interest). As predicted, the estimated coefficients for occurrences of fussiness were positive and statistically significant in both models. Removing three possible outliers, though there was nothing biologically or behaviourally distinctive about them, strengthened the statistical significance of the estimated coefficients, and the fit of both the bivariate ($\beta=0{\cdot}651$, $p<0{\cdot}001$, $R^2=0{\cdot}645$) and multivariate ($\beta=0{\cdot}634$, $p=<0{\cdot}001$, $R^2=0{\cdot}624$) models. Of course, this interpretation rests on the temporal precedence of fussiness, but the regression model only shows association. The mean latency (in seconds) between occurrences of fussiness and the subsequent occurrences of suckling (9·1, SE=5·22) was slightly lower than between the end of suckling and subsequent fussing (10·8, SE=5·31). This difference was not statistically significant when compared using a Mann–Whitney test ($U=98{\cdot}0$, one-tailed, $p=0{\cdot}200$).

To test Hypothesis 3, two OLS regression models were build (see Table 3 and Fig. 1). Both the bivariate (Model 3A) and multivariate (Model 3B) models included mean duration of occurrences of fussiness following occurrences of suckling (as the dependent variable) and mean duration of those occurrences of suckling (as the predictor of interest). Sample sizes were smaller for these models because only sampling periods with at least one observation of suckling were included. Contrary to

Table 3. OLS regression models used to test Hypotheses 1, 2 and 3

		A				B			
		Coeff.	SE	*t*	*p*	Coeff.	SE	*t*	*p*
1.	*Dependent:* Fussiness occurrences/minute	$n=24$; $R^2=0·162$				$n=24$; $R^2=0·209$			
	Predictor: Sicknesses in past year	**0·069**	0·034	2·064	0·051	**0·047**	0·043	1·091	0·289
	Intercept	0·194	—	—	—	0·217	—	—	—
	Sex of child (0 girl, 1 boy)	—	—	—	—	− 0·004	—	—	—
	Age of child (in months)	—	—	—	—	− 0·002	—	—	—
	Village (0 Doulu, 1 Laubuluh)	—	—	—	—	0·071	—	—	—
2.	*Dependent:* Nursing occurrences/minute	$n=24$; $R^2=0·353$				$n=24$; $R^2=0·399$			
	Predictor: Fussiness occurrences/minute	**0·624**	0·180	3·467	0·002**	**0·535**	0·204	2·629	0·017*
	Intercept	0·068	—	—	—	0·121	—	—	—
	Sex of child (0 girl, 1 boy)	—	—	—	—	− 0·047	—	—	—
	Age of child (in months)	—	—	—	—	− 0·003	—	—	—
	Village (0 Doulu, 1 Laubuluh)	—	—	—	—	0·068	—	—	—
3.	*Dependent:* Mean duration of fussiness	$n=16$; $R^2=0·248$				$n=16$; $R^2=0·444$			
	Predictor: Mean duration of nursing	**0·214**	0·100	2·148	0·050*	**0·223**	0·098	2·271	0·044*
	Intercept	7·176	—	—	—	14·733	—	—	—
	Sex of child (0 girl, 1 boy)	—	—	—	—	− 3·891	—	—	—
	Age of child (in months)	—	—	—	—	− 0·495	—	—	—
	Village (0 Doulu, 1 Laubuluh)	—	—	—	—	− 3·417	—	—	—

Note: * $p<0·05$, **$p<0·01$, ***$p<0·001$.

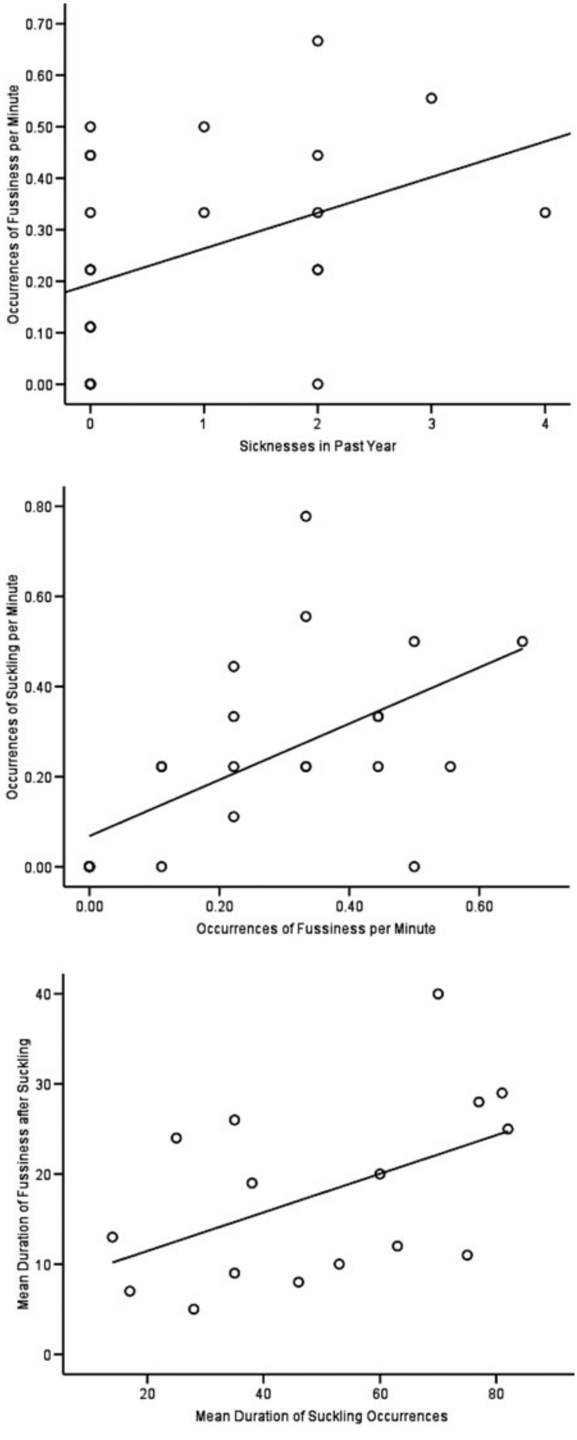

Fig. 1. Plots of bivariate OLS regression models used to test Hypotheses 1, 2 and 3

prediction, the estimated coefficients for mean duration of suckling were positive and statistically significant in both models. Removing one possible outlier, though not biologically or behaviourally distinctive, decreased the fit of the bivariate ($\beta = 0{\cdot}165$, $p = 0{\cdot}084$, $R^2 = 0{\cdot}212$) but increased the fit of the multivariate ($\beta = 0{\cdot}181$, $p = 0{\cdot}056$, $R^2 = 0{\cdot}461$) models. This analysis included variables with a temporal element, so additional tests of the temporal precedence assumption were not done.

Discussion

The results presented here provide support for two of three predictions from Parker *et al.*'s (2002) model of POC resolution. As predicted under Hypothesis 1, offspring fussiness appears to reflect underlying need (measured as age and propensity to illness). As predicted under Hypothesis 2, mothers appear to have provided breast-feeding in response to offspring fussiness. Increased fussiness was strongly associated with increased suckling, and the mean latency from fussing to suckling was shorter than the converse latency (providing support for the presumed causal relationship). Contrary to the prediction of Hypothesis 3, longer periods of suckling were followed by longer periods of fussing. This supports a positive ESD mechanism, rather than the predicted negative one, suggesting that the benefits of the resources provided in response to offspring solicitation were counterbalanced by the costs of additional fussing (Hussell, 1988; Parker *et al.*, 2002; Kölliker, 2003). Taken together, these results suggest that a POC interpretation is unnecessary (Parker *et al.*, 2002). They are, perhaps, more consistent with Bateson's (1994) 'meshing' hypothesis.

From an evolutionary standpoint, we expect indifference to an unrelated individual's signal of 'need' – defined as the marginal fitness benefit of an additional unit of resources (Godfray, 1991). When inclusive-fitness interests overlap, however, such as amongst relatives, there is a lot to gain from the information carried in that signal. For parental investment, need is typically measured as offspring hunger ('short-term need') or some measure of deviation from growth-for-age standards ('long-term need'). In many species, the former is exceedingly difficult to measure (Price *et al.*, 1996; Wright *et al.*, 2002). In this study, short-term need was quasi-controlled through the sampling procedures (arranging for sampling periods when offspring were likely to feed). Three proxy measures of long-term need were used, of which the number of sicknesses in the past year emerged as the strongest. Whether this is an acceptable substitute for standard measures of need is an empirical question that has been answered to some extent here, yet further investigation is needed as the Karo Batak represent only one exceedingly small sample of human diversity. One problem is that sicknesses in the past year is an age-dependent measure (some offspring have experienced less than a full year). When controlling for offspring age, the estimated effect strengthens but loses even the marginal statistical significance of the bivariate version (Models 1A and 1B in Table 3), raising concerns about sample size. Another problem is that if parents already know their offspring's susceptibility to sickness (illness histories were based on recall), they are receiving little or no additional information from their offspring's cries. A number of evolutionary-minded authors are sceptical of fussiness as a signal of need and have pointed to different functions, such as blackmailing and signalling vigour (e.g. Soltis, 2004).

Existing cross-cultural studies of breast-feeding and fussiness are insufficient to judge whether a positive ESD mechanism, like the one observed here, is common in humans. For comparative purposes, it should be noted that positive, neutral and negative ESD mechanisms have been observed in non-human species (Royle *et al.*, 2004), but the negative version may be the most common amongst birds (Kilner & Johnstone, 1997). Nonetheless, the positive mechanism has been observed in budgerigars (*Melopsittacus undulates*; Stamps *et al.*, 1985) and eastern screech owls (*Megascops asio*; Hofstetter & Ritchison, 1998). In humans, offspring may use fussing for purposes other than to convey information about hunger, so we might observe a positive ESD even if the offspring is already sated (e.g. if her complaint has shifted from hunger to post-feeding gas). Further, it should be noted that these observations of the positive ESD mechanism are crude at best, especially when compared with the experimental-coupled-with-regression techniques used by Kölliker (2003) to estimate the true slope of the ESD (and EDS) mechanisms.

An additional prediction that can be derived from Parker *et al.*'s (2002) model was not tested here – that signalling should incur an inclusive fitness cost. Although energetic costs of fussiness have been documented, fitness costs have not been (Wells, 2003). Possible fitness costs include predation and infanticide. The former, though relevant for non-human primates (Hauser, 1993) and perhaps our own evolutionary past, is an unlikely source of fitness costs in modern human infants. The latter is more plausible, as excessive crying appears to be strongly associated with infanticide (Soltis, 2004).

Acknowledgments

The author thanks the people of Doulu and Laubuluh villages. Eric A. Smith, Donna Leonetti, Darryl Holman and an anonymous reviewer provided valuable feeback. Fieldwork was supported by a Dissertation Improvement Grant (#0003951) from the National Science Foundation (USA) and the Andrew W. Mellon Foundation. Research was conducted under the auspices of the Indonesian Academy of Science (LIPI), with sponsorship from the Centre for Population and Manpower Studies (at LIPI) and the University of North Sumatra in Medan.

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