RESEARCH CONCLUSIONS[1]

[The Editor welcomes short statements—normally from 300 to 1,000 words—of research results and conclusions. Such statements should not include detailed supporting data, but should make clear reference to the location of such data (published and unpublished) so that interested readers may refer to the material. Sentences should be specific rather than vague. Abstracts of theses may be included, provided they present conclusions rather than only describe what was done. The date of submission will be included, as well as the address of the contributor, so that colleagues may correspond.—EDITOR.]

Hunting Ability and Reproductive Success among Male Ache Foragers: Preliminary Results[2]

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Hunting figures prominently in many theories of hominid evolution (e.g., Darwin 1871), Dart 1953, Hill 1982, Washburn and Lancaster 1968). Although there is considerable debate concerning both the timing of its emergence and its relative importance as a source of nutrition for evolving hominids (Isaac 1981, Binford 1981, Zihlman 1981), it is generally recognized that hunting is the principal foraging activity of modern male hunter-gatherers and probably has been for the last 100,000 years, if not longer (e.g., Isaac 1977; Klein 1977, 1978). This suggests that natural selection should have acted upon and should continue (among extant foragers) to act upon male hunting ability.[3] There are, however, no published data on the relationship between hunting ability and reproductive success for any modern foraging society. In fact, there are very few studies of human groups that directly measure differential reproductive success and the factors that predict it (for some exceptions, see Chagnon 1979, Irons 1979, Blurton-Jones and Howell 1984).

Over the past five years, our research group has studied food acquisition, time allocation to activities, and food redistribution among Ache hunter-gatherers in eastern Paraguay (Hawkes and O'Connell 1984; Hawkes, Hill, and O'Connell 1982; Hill 1983; Hill and Hawkes 1983; Hill et al. 1984*a*, *b*; Hurtado et al. 1984; Kaplan 1983; Kaplan and Hill 1985; Kaplan et al. 1984). Our data clearly show that hunting is the most important male subsistence activity. Ache men hunt daily, spending an average of 6.8 hours per day searching for or in pursuit of game and only .1 hours per day in the acquisition of vegetable resources (Hill 1983, Hill et al. 1984*b*). Men provide 82% of the total calories consumed by the group (Hurtado et al. 1984). Although there are large differences between men in hunting success, all meat acquired by Ache men is shared throughout the group (Kaplan 1983, Kaplan and Hill 1985, Kaplan et al. 1984). Moreover, there is no relationship between how much meat men acquire and how much food they and their families consume (Kaplan and Hill 1985).

This raises an interesting problem. If the children of high-producing males do not eat more than those of low-producing males, how could hunting efficiency be favored by natural selection? Interbirth intervals should be the same for low and high producers. The fact that more efficient hunters (i.e., those who produce more food per unit time spent hunting) actually hunt *more* hours daily than less efficient ones (Hill 1983) suggests that there is some payoff for producing more food. We hypothesized that better hunters receive indirect fitness benefits for the extra food they provide (Hill 1983, Kaplan 1983, Kaplan and Hill 1985). Since food is shared throughout the band, an exceptionally skilled hunter would be a welcome addition to any band. Interband mobility being extremely high among the Ache, we expected that other band members would accord high producers special treatment so that they would remain in the band. We further hypothesized that one possible benefit good hunters might receive is better treatment of their children. If, for example, a child of a good hunter becomes ill, band members might be more willing to remain in one location (campsites are generally occupied for only one night) until the child recovers. Other band members might treat children of good hunters better by grooming them, playing with them, carrying them, etc. Another possible benefit to good hunters might be increased access to mates. Legitimate polygyny is relatively rare among the Ache (accounting for less than 5% of all marriages). Thus, if high producers do have increased access to mates, it will be primarily through extramarital affairs. By having affairs with high producers, females might "persuade" males to remain in the band, thus providing food for all their children. Low-producing males might also be more tolerant of such affairs because the extra food provided by high producers compensates for some loss in confidence of paternity.

This hypothesized trade of food for other fitness benefits leads to a series of predictions: (1) survivorship of children should be higher for high producers than for low producers; (2) high producers should have more extramarital affairs; and (3) high producers should have more illegitimate[4] children. In this report we test these predictions.

The research was conducted with the Northern Ache, whose traditional foraging range encompassed an area of approximately 15,000 km^2 between 24 and 25° south latitude and 54.5 and 56° west longitude. Peaceful contact with the larger Paraguayan society occurred between 1972 and 1978, depending upon the band. The majority of the Northern Ache are currently based at a Catholic mission, Chupa Pou. Although they now practice a mixed economy of jungle foraging and subsistence agriculture, the Ache still forage in mixed-sex bands for considerable periods of time (up to several months) during which no foods other than those acquired in the jungle are consumed (see Hill 1983 and Kaplan 1983).

Data on food acquisition were collected during two separate field sessions, the first from April 1980 to July 1980, the second from October 1981 to May 1982. Data were collected on foraging trips out of the Chupa Pou mission. Only trips which lasted more than five days were sampled. On those trips, foraged foods accounted for more than 95% of the food consumed (agricultural foods were consumed during the first day or two of foraging). On each day of each foraging trip, time spent foraging was measured for every adult male present. This was done by recording the time each man left camp and the time he returned. In addition, a focal individual was sampled on each day; the activities of each focal man were recorded from dawn

[1] Permission to reprint items in this section may be obtained only from their authors.

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[3] We are not suggesting here that there are specific genes which determine hunting ability. We fully expect that the abilities used in hunting are pleiotropically determined and that phenotypic variability in hunting efficiency is determined by both genetic and environmental variability. We simply suggest that, to the extent that some phenotypic variability in hunting success is a function of underlying genetic variability, natural selection should act upon it.

[4] The term "illegitimate" is used here in the technical sense of children born out of wedlock; no value judgment is implied. Whether "illegitimate" children are treated differently is a subject for future research.

until dark. On the basis of 75 days of focal-individual sampling, we found that 87% of time out of camp was spent foraging and that the correlation between time spent out of camp and time spent foraging was quite high (Pearson's $r = .90$ [Hill 1983]). We therefore concluded that time spent out of camp was a reliable measure of time spent foraging.

Foraging productivity was measured by weighing all resources acquired by every adult in the foraging band and determining their caloric values (see Hill et al. 1984*a* for details). Hourly return rates were calculated by dividing the total number of calories acquired on each day by the number of hours spent hunting.[5] Although there is a great deal of temporal variability in foraging success (due to encounter luck with large game), return rates proved fairly consistent over relatively long periods of time. There is a significant positive correlation between individual return rates obtained from the 1980 sample and those obtained from the same individuals during the 1981–82 field session (Pearson's $r = .54$, $p = .02$). Only individuals for whom we have at least 16 days of foraging data ($N = 29$) were chosen for this study so that biases due to encounter luck would not vitiate the tests.

Reproductive histories for the men in our study population were obtained through interviews. For 12 of the 29, the data were obtained through firsthand interviews with the man himself. With one exception, the remainder of the interviews were conducted with a sibling of the man in question. Both the number of live offspring born and the number of offspring which have survived to the present[6] were recorded for each man. Offspring were divided into two categories: sure (ones reported to be definitely the offspring of the man in question) and possible (children who could have been the offspring of the man but might also have been the offspring of another man who also had sexual relations with the mother immediately before her pregnancy). This latter class included mostly children whose mothers were not married to the man in question (illegitimate) and a few children who might have been the products of extramarital affairs with the man's wife. Although we have less confidence in the data on "possible" children for the men whose reproductive histories were obtained from their siblings, cross-checking of information from several sources showed high agreement across respondents.

One additional indirect measure of fitness was obtained. A sample of ten women were interviewed concerning their extramarital affairs, and the number of times each man in our sample was reported as a lover was coded.

Since age significantly predicted number of offspring produced (Pearson's $r = .46$, $p = .006$), men were matched by five-year age-classes for all analyses. If there were more than two men in an age-class, men whose foraging return rates were above the median for that class were randomly matched with those whose rates fell below the median. For the one age-class that included an odd number of men, the man with the median return rate was excluded from the data set. This procedure generated 14 pairs of men matched by age.

All analyses were performed using the Wilcoxon signed rank test for matched pairs. Figure 1 compares the numbers of surviving children born to poor and good hunters, respectively. Good hunters had more children (sure and possible) surviving to the present than did poor hunters, although the differences in the number of sure surviving children were not significant (all p-values are one-tailed probabilities).

A more detailed breakdown of the data is presented in table 1, where the two components of fitness, number of children born and percentage surviving, can be compared. For sure children there was no significant difference between high and low producers in number born ($p = .6$), but a significantly higher percentage of those born to good hunters survived ($p = .05$).[7] Analysis of possible children shows that good hunters had more illegitimate children than poor hunters ($p = .05$). Percentage surviving was not compared for possible children because in only 3 of the 14 pairs did both men produce illegitimate children. When all children (both sure and possible) were considered, there was no significant difference between good and poor hunters in the number of live children born ($p = .4$), but there were significant differences in percentage surviving ($p = .05$).

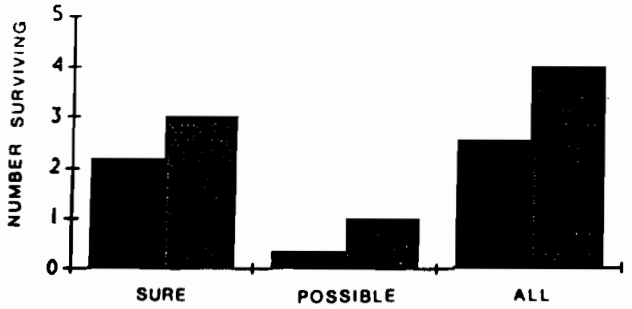

FIG. 1. Mean number of children surviving to the present for poor (*dark bars*) and good (*shaded bars*) hunters. For sure children, $p = .15$; for possible children and all children, $p = .05$.

Finally, a chi-square test was performed on the ten-woman sample reporting on extramarital affairs. Since the sample was small and since many men were not mentioned by these women (possibly because they traveled in different circles), we scored the number of times men in the poor-hunter group were mentioned (12) and the number of times good hunters were mentioned (25). This difference was also significant ($\chi^2 = 4.0$, $p < .05$). Good hunters were reported to have more extramarital affairs.

All the data suggest that good hunters have higher reproductive success than poor hunters. This increase in fitness is due to both increased survivorship of offspring and increased access to extramarital affairs through which illegitimate offspring are produced. It should be kept in mind, however, that the sample is small and our data on illegitimate children are somewhat incomplete (although they are equally so for the two groups). Future research will allow us to expand our sample and to cross-check multiple informant reports so that more reliable reproductive histories will be obtained. Nevertheless, it is impressive that significant differences in reproductive success were found between the two groups even with this small sample.

These data do not necessarily imply a causal relationship between hunting ability and reproductive success. It is possible, for example, that good hunters are more physically robust than poor hunters and that it is this inherited robusticity that is responsible for the higher survivorship of the children of good hunters. Future behavioral and demographic research will focus on specifying the factors responsible for this fitness differential to test for a direct causal connection between hunting-return rates and reproductive success. This may be one case in which a culturally variable and learned behavior specifically affects Darwinian fitness.

Another interesting problem is why women in bands that share meat equally should prefer good hunters as partners in

[5] Only meat calories were included in the calculation of return rates so that the effect of hunting ability on fitness could be tested directly.

[6] Since many of the children in our study population are still quite young and since most child mortality occurs in the first year or two of life, we felt that the measure "survivorship to the present" was preferable to the usual "survivorship to adulthood." The former measure allows us to test survivorship on a much larger population of children.

[7] For tests on percentage surviving, only pairs in which both men had at least one child were included.

TABLE 1

REPRODUCTIVE SUCCESS OF POOR AND GOOD HUNTERS MATCHED BY AGE

AGE-CLASS	SURE CHILDREN						POSSIBLE CHILDREN						ALL CHILDREN					
	Born		% Surviving		No. Surviving		Born		% Survivng		No. Surviving		Born		% Surviving		No. Surviving	
	poor/good		poor/good		poor/good		poor/good		poor/good		poor/good		poor/good		poor/good		poor/good	
20–24 ...	0	1	...	100	0	1	3	0	67	...	2	0	3	1	67	100	2	1
25–29 ...	1	3	0	67	0	2	1	3	100	100	1	3	2	6	50	83	1	5
	2	3	50	100	1	3	0	0	...	...	0	0	2	3	50	100	1	3
30–34 ...	3	3	67	67	2	2	0	1	...	100	0	1	3	4	67	75	2	3
35–39 ...	6	6	67	67	4	4	0	0	...	...	0	0	6	6	67	67	4	4
	7	3	71	67	5	2	0	0	...	...	0	0	7	3	71	67	5	2
	3	1	100	100	3	1	0	1	...	100	0	1	3	2	100	100	3	2
	0	7	...	57	4	0	0	0	...	...	0	0	0	7	...	57	0	4
	2	7	50	43	1	3	0	5	...	60	0	3	2	12	50	50	1	6
40–44 ...	9	7	11	43	1	3	1	1	100	100	1	1	10	8	20	50	2	4
	8	6	50	50	4	3	1	4	100	50	1	2	9	10	56	50	5	5
45–49 ...	2	0	100	...	2	0	0	2	...	50	0	1	2	2	100	50	2	1
50–54 ...	5	4	80	100	4	4	0	0	...	...	0	0	5	4	80	100	4	4
54+	10	10	40	100	4	10	0	3	...	67	0	2	10	13	40	92	4	12
$\bar{X}$ All .	4.14	4.36	57	74	2.21	3.0	.43	1.43	...	...	.36	1.0	4.57	5.79	63	74	2.57	4.0

extramarital affairs.[8] The issue raises the question of what factors contribute to differential reproductive success among women. If the value of the paternal investment children receive is at least partially determined by the hunting skill of the father (or potential fathers) and his confidence of paternity, such factors should affect both marital and extramarital mate choice for women. Women may also attempt to pass on any genetic component of hunting skill to their own sons by choosing good hunters as mates. We are currently examining factors which predict female reproductive success in order to test some of these possibilities.

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[8] Interestingly, the only two men in our sample who had two wives each simultaneously were both very good hunters (Numbers 1 and 5 out of 29).