An Extended Comment on the Analysis of Risk-Sensitive Foraging Among the Aché of Paraguay and a Brief Reply to Codding et al.

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Introduction

Shortly after the comparative analysis of Codding et al. (2011a) was published online, I prepared a comment on the article that I submitted for publication. In response to feedback from the editors, I eventually revised the manuscript substantially. That revised version has now been published (Koster 2011). In this paper, I share the original submission of the comment, which focuses on important considerations for future studies of risk-sensitive foraging.

Meanwhile, Codding and his colleagues (2011b) have published a response to my comment. They exhibit some confusion about my position, which they describe as "paradoxical." In a reply to their response, I have therefore added some clarifying remarks at the end of this paper.

Original Submission

Although the respective optimal foraging models depend on similar logic, the distinction between patch choice decisions and prey choice decisions is important (Stephens and Krebs 1986). Among the Meriam and the Martu, foragers frequently seem to focus on a single type of resource while exploiting distinct geographic locations and using technologies suited for that resource. The decision between these different kinds of foraging can be modeled as a patch choice problem, much like Sosis's work on Ifaluk (2002). Aché foraging in general can likewise be considered a "patch," but because they search for multiple types of resources simultaneously, the question of which resources to pursue within that patch is best viewed as a prey choice problem. Although their methods might be appropriate for an analysis of risk-sensitive patch choice decision-making, Codding et al. (2011a) have not considered variables that would be needed for a comparable analysis of prey choice. Their apparent misunderstandings of the multifaceted Aché datasets also complicate the interpretability of their analysis.

One misunderstanding is their use of the resource-specific mean values from Table 5 in Kaplan and Hill (1985). Because the analysis in that paper focuses on food sharing, the average package size is calculated from only successfully-harvested resources. Pursuits of game species are sometimes unsuccessful, however, and the average harvests per pursuit are therefore lower than the values used by Codding and his colleagues. Unlike Alvard (1993), Hill and his colleagues do not specify the number of unsuccessful pursuits among the Aché, but because of their importance to prey choice decision-making, the outcomes of unsuccessful pursuits are included in their calculations of profitability (calories/hour) in a separate paper (Table 2 in Hill et al. 1987).

Another misunderstanding by Codding et al. (2011a) is their use of the standard deviations from Table 7 in Kaplan and Hill (1985). Put simply, these standard deviations do not correspond to the averages of package size in Table 5. Instead, they are a measure of harvest asynchrony at the familial level, which is germane to the authors' research on food sharing. To clarify the calculation of that variable, imagine that ten families embarked on a foraging trip that lasted three days. On the

first day, one of the families acquired 9,000 calories of armadillo meat whereas the other families did not harvest armadillos (i.e., family-level standard deviation = 2,846). On the second day, two of the families each harvested 5,000 calories of armadillo meat (i.e., family-level standard deviation = 2,108). On the last day, one family harvested an additional 5,000 calories. (i.e., family-level standard deviation = 1,581). These data would therefore result in a "mean daily standard deviation across families" of 2,178 calories (i.e., the average of the previous three values).

In summary, neither the means nor the standard deviations used by Codding et al. (2011a) accurately reflect the outcomes of pursuits by the Aché, which largely precludes a meaningful analysis of risk-sensitive prey choice decisions.

Regarding a general concern about their approach, Codding and his colleagues seem to assume that the resource-specific mean and variance will be identical for both male and female foragers. Yet, many of the hunted species that are exploited by the Aché are harvested only by men, and there are also resources and patches among the Martu and Meriam that are exploited by only men or women. It is therefore not possible to use observational data to test for sex-related differences between men and women. Although the harvests of some resources may in fact exhibit few sex-related differences, this should not be the default assumption, if only because of the physical differences that distinguish the sexes. Notably, Hill et al. (1987:20) report that Aché men harvest "palm growing shoot" at a greater rate than women. A comparative analysis of risk-sensitive foraging strategies would ideally account for the differing abilities of men and women, likely while controlling for age and experience-related variability in return rates (Walker et al. 2002).

More broadly, it is not clear that estimates of the means and variances of

harvests for different resources provide meaningful information without additional consideration of the length and variability of handling times for those resources. Prey choice models hinge on the opportunity costs associated with handling time. That is, the time spent pursuing an animal is time that cannot be used to seek and pursue alternative prey. To illustrate plainly the importance of handling time, imagine that a successfully harvested tapir consistently provides 228,150 calories. If only 20 percent of the pursuits of tapirs are successful, then the resulting coefficient of variation (CV) would be two, and this prey type would therefore be considered a high-risk resource according to the logic of Codding and his colleagues. Yet, if all pursuits of tapirs last less than one minute, then a hunter risks little by attempting to harvest this profitable, "high-energy" resource. If the pursuit is unsuccessful, that is, then a hunter on a full-day excursion will have considerable time to encounter and pursue other prey, and the minute lost to the tapir's pursuit will have little impact on the daily return rate. By contrast, the energetic benefits of an alternative prey type might exhibit much less variability, as reflected by its CV, but if several hours are invariably needed to track and pursue the animal while precluding opportunities to encounter and pursue other prey (cf. Hill et al. 1987:17), then an unsuccessful pursuit can dramatically reduce the daily return rate. In short, as noted by Winterhalder et al. (1999:306), the riskiness of a decision depends largely on the length of time that a forager must endure the consequences of the decision.

Studies of risk-sensitive foraging among non-human animals are almost exclusively conducted in laboratories, which allows experimental researchers to control the rate and variance of alternative energy gains available to the animals (Ydenberg, Brown, and Stephens 2007:18). A common methodology is to force animals to choose between options

that exhibit the same mean but different variances, often while manipulating the animal's energy budget (Kacelnik and Bateson 1996:404). By contrast, a field-based study of risk-sensitive prey choice poses formidable challenges because the mean and variance differ for each possible combination of pursued resources. Ecologists have devoted relatively little attention to a risk-sensitive extension of the basic prey choice model, but such a model would presumably need to account for the encounter rates and the variability of energetic benefits and handling times of all possible prey types, including those that are not included in the optimal diet set when focusing solely on the maximization of average return rates (David W. Stephens, personal communication, 2 March, 2011). Note that previous attempts to model risk-sensitive prey choice have generally assumed that the energetic benefits and handling times are constant for all items of a particular prey type (e.g., Schmitz and Ritchie 1991), which is unlikely to be true among human foragers. An additional caveat is that not all variation is stochastic variation (Winterhalder et al. 1999), and researchers should consider partitioning the variance associated with variables such as seasonality and the foragers' heterogeneous skills prior to an analysis.

In conclusion, Codding and his colleagues should be commended for their attention to an important problem, and their work underscores the need for models that account for some of the challenging methodological considerations. Increased attention to the temporal fluctuations of intra-familial energetic needs and the resulting state-dependent behavior might also be useful, particularly given that negative energy budgets generally promote increasingly variance-prone decisions among non-human animals (Kacelnik and Bateson 1996). Research on non-human animals also indicates that reproducing individuals may be more variance-prone than non-reproducing individuals if additional energy is needed to reproduce successfully (e.g., Ratikainen et al. 2010). In short, expectations about sex-related sensitivity to risk may be less straightforward than is generally assumed.

Reply to the response by Codding et al. (2011b)

Codding et al. (2011b) are certainly right that much of the apparent daily variation in the family-level harvesting of certain resources likely stems from the failure to either seek the resource or pursue it after an encounter. For instance, many of the resources that are conventionally acquired by Aché women presumably exhibit considerable harvest asynchrony because the women devote much of their time to traveling from one location to another, bypassing opportunities to pursue resources that they encounter along the way (Hurtado et al. 1985:4). Whereas Aché men on foraging treks spend 373 minutes per day seeking and pursuing food (Hill et al. 1985), Aché women devote only 79 minutes per day to the acquisition of food (Hurtado et al. 1985).[1] This variation in time allocated to foraging helps to explain the greater contribution of Aché men to overall food production. Clearly, it would be preferable to compare the mean and variance of return rates by male and female foragers when they are actually foraging, as in the Meriam and Martu datasets (Codding et al. 2011a).

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[1] Whereas the foraging of Aché men entails considerable walking in search of game, Hurtado et al. (1985) distinguish "walking in line" from food-getting activities even though, while walking, Aché women likely encounter resources that they subsequently pursue after they have reached a resting stop or a new campsite. By excluding walking from the amount of time that Aché women devote to acquiring food, I am assuming that they would not ordinarily need to spend much time searching for resources that they could pursue.

Codding and his colleagues suggest that I make a paradoxical argument that foraging by Aché men is both high-risk and reliable. As evidence, they note that I had calculated a CV of 1.1 for the overall, family-level daily harvest and that men's foraging contributes 87 percent of the overall production. Based on figures provided by Kaplan et al. (1990), I had also calculated the family-level CV of harvested game: 1.6. The authors write: "This is equivalent to saying that Aché hunting is simultaneously high-risk and reliable; so reliable that it provides the bulk of acquired food, but so risky that it fails as frequently as Meriam and Martu hunting. This is simply incorrect" (Codding et al. 2011b:3173).

To clarify, I was citing men's contribution to overall production (87 percent) not to suggest that their foraging strategies are reliable, but rather to contextualize the CV that I had calculated. That is, the Aché researchers have not provided the data needed to calculate the respective daily variation of men's and women's foraging. All of the data are aggregated to the level of the family. In other words, the CV of 1.1 reflects the contributions of all members of the family, including both men and women. However, because men contribute most of the production, I was simply observing that this variance probably reflects the daily variation in men's foraging more closely than the variation in women's foraging. In other words, the actual CV of men's foraging is probably not 1.1, but it is presumably closer to that figure than the values that Codding and his colleagues had presented for the resource-specific coefficients of variation (e.g., 0.36 for the harvesting of pacas), which I have noted elsewhere are likely based on a misinterpretation of the Aché data.

Unless I am misreading their argument, Codding et al. (2011b:3174) contend that, when men primarily pursue high-variance resources, then production will be "dominated by the reliable acquisition of low-energy resources,"

which are presumably the resources pursued by women. Yet, the measure of production that I cited (i.e., Aché men contribute 87 percent of the overall calories) is an aggregated statistic, encompassing the production of all men and women over the duration of the study. It does not imply that any particular Aché man reliably contributes most of his family's daily caloric needs. If the high-variance resources are large, then even sporadic harvests can result in a disproportionate contribution to the overall production. For example, imagine that each of 10 Aché women consistently harvests about 3 thousand calories per day over a four-week period while five of the ten men in the group manage to harvest one tapir apiece during that same period. Assuming that a 200 kilogram tapir provides about 200 thousand calories, then men's foraging would provide approximately seventy percent of the *overall* production even if they harvest nothing else during those four weeks. Yet, one could hardly describe men's foraging as "reliable," especially since half of the men in this hypothetical example harvested absolutely nothing. In other words, it can be difficult to infer much about sex-related sensitivity to foraging variance from measures of production that are aggregated across individuals and across time.

Relative to the Martu and the Meriam, do I believe that the foraging returns of Aché men exhibit comparable variance? Based on the available data, I reiterate my impression that the variance of Aché men's foraging is closer to the Martu and Meriam pattern than the analysis of Codding and his colleagues would indicate. That is, whereas their analysis suggests that "Aché resources seem to impose no trade-off between risk and harvest size" (Codding et al. 2011a:2504), I suspect that the differences are not quite as stark. Are they "on par," as Codding and his colleagues (2011b) characterize my position? I am actually agnostic on that point because, to my knowledge, the

data that are needed to make meaningful comparisons are not publicly available.

That is, we would need to know how much the overall harvests of Aché men and women vary when they are actually foraging, which would require consideration of time allocation and a disaggregation of the family-level data provided by Kaplan et al. (1990). If these data were available, then I could envision some interesting comparative analyses, especially if researchers address not only variation in the caloric value of harvested resources but also their macronutrient composition (Hill et al. 1987).

Acknowledgements

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