

ANTHROPOLOGY

The life history of human foraging: Cross-cultural and individual variation

Jeremy Koster^{1,2*}, Richard McElreath^{2,3}, Kim Hill⁴, Douglas Yu^{5,6,7}, Glenn Shepard Jr.⁸, Nathalie van Vliet⁹, Michael Gurven¹⁰, Benjamin Trumble^{4,11}, Rebecca Bliege Bird¹², Douglas Bird¹², Brian Coddling¹³, Lauren Coad^{9,14}, Luis Pacheco-Cobos¹⁵, Bruce Winterhalder³, Karen Lupo¹⁶, Dave Schmitt¹⁶, Paul Sillitoe¹⁷, Margaret Franzen¹⁸, Michael Alvard¹⁹, Vivek Venkataraman²⁰, Thomas Kraft¹⁰, Kirk Endicott²¹, Stephen Beckerman¹³, Stuart A. Marks^{22,23}, Thomas Headland²⁴, Margaretha Pangau-Adam^{25,26}, Anders Siren²⁷, Karen Kramer¹³, Russell Greaves¹³, Victoria Reyes-García^{28,29}, Maximilien Guèze²⁹, Romain Duda^{29,30}, Álvaro Fernández-Llamazares³¹, Sandrine Gallois³², Lucentezza Napitupulu²⁹, Roy Ellen³³, John Ziker³⁴, Martin R. Nielsen³⁵, Elspeth Ready^{2,36}, Christopher Healey³⁷, Cody Ross²

Copyright © 2020
The Authors, some
rights reserved;
exclusive licensee
American Association
for the Advancement
of Science. No claim to
original U.S. Government
Works. Distributed
under a Creative
Commons Attribution
NonCommercial
License 4.0 (CC BY-NC).

Human adaptation depends on the integration of slow life history, complex production skills, and extensive sociality. Refining and testing models of the evolution of human life history and cultural learning benefit from increasingly accurate measurement of knowledge, skills, and rates of production with age. We pursue this goal by inferring hunters' increases and declines of skill from approximately 23,000 hunting records generated by more than 1800 individuals at 40 locations. The data reveal an average age of peak productivity between 30 and 35 years of age, although high skill is maintained throughout much of adulthood. In addition, there is substantial variation both among individuals and sites. Within study sites, variation among individuals depends more on heterogeneity in rates of decline than in rates of increase. This analysis sharpens questions about the coevolution of human life history and cultural adaptation.

INTRODUCTION

Among hominoids, humans are distinguished by a suite of life history traits that includes a prolonged juvenile and adolescent period, short interbirth intervals, and an extended postreproductive life span (1). Multiple conceptual models have been advanced to explain the evolution of these traits, focusing on distinctive human behaviors such as pair bonding and alloparental care from grandparents and others (2–4). Any satisfactory model of human life history evolution must simultaneously account for the large brains that characterize our species. Foraging complexity and competitive social challenges have been alternately championed as the evolutionary prime mover of encephalization, while others combine perspectives by citing the advantages of flexible cultural learning among juveniles as a solution to social and ecological challenges (5).

Progress is made in these debates via models that integrate growth, reproduction, cognitive development, skill development, sociality, and cultural evolution. The most advanced attempt that we know is the optimal control model of González-Forero and Gardner (6). Drawing on observed rates of brain and somatic growth, their model estimates the relative importance of different ecological and social challenges to the evolution of intelligence. In comparison to alternatives, the ecological challenge of acquiring food emerges as the strongest predictor of the observed pattern of human growth. In this model, brains develop first followed by the body because this sequence allows a longer period of learning and ultimately higher adult productivity. This finding complements recent comparative work on the prominence of foraging complexity as a predictor of primate brain sizes (7). These findings and predictions direct our attention

¹Department of Anthropology, University of Cincinnati, Cincinnati, OH, USA. ²Department of Human Behavior, Evolution, and Culture, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany. ³Department of Anthropology and Graduate Group in Ecology, University of California, Davis, CA, USA. ⁴School of Human Evolution and Social Change, Arizona State University, Tempe, AZ, USA. ⁵State Key Laboratory of Genetic Resources and Evolution, Kunming Institute of Zoology, Kunming, China. ⁶School of Biological Sciences, University of East Anglia, Norwich, UK. ⁷Center for Excellence in Animal Evolution and Genetics, Chinese Academy of Sciences, Kunming, China. ⁸Division of Human Sciences, Museu Paraense Emílio Goeldi, Belém, Brazil. ⁹Center for International Forestry Research, Bogor, Indonesia. ¹⁰Department of Anthropology, University of California, Santa Barbara, Santa Barbara, CA, USA. ¹¹Center for Evolution and Medicine, Arizona State University, Tempe, AZ, USA. ¹²Department of Anthropology, Pennsylvania State University, University Park, PA, USA. ¹³Department of Anthropology, University of Utah, Salt Lake City, UT, USA. ¹⁴Interdisciplinary Centre for Conservation Science, University of Oxford, Oxford, UK. ¹⁵Facultad de Biología, Universidad Veracruzana, Xalapa, Veracruz, Mexico. ¹⁶Department of Anthropology, Southern Methodist University, Dallas, TX, USA. ¹⁷Anthropology Department, Durham University, Durham, UK. ¹⁸Unaffiliated. ¹⁹Department of Anthropology, Texas A&M University, College Station, TX, USA. ²⁰Institute for Advanced Study in Toulouse, Toulouse, France. ²¹Department of Anthropology, Dartmouth College, Hanover, NH, USA. ²²Department of Biology, University of Richmond, Richmond, VA, USA. ²³Department of Anthropology, University of the Free State, 205 Nelson Mandela Drive, Bloemfontein 9300, South Africa. ²⁴Department of Anthropology, SIL International, Dallas, TX, USA. ²⁵Department of Conservation Biology, University of Göttingen, Göttingen, Germany. ²⁶Biology Department—FMIPA, Cenderawasih University, Papua, Indonesia. ²⁷Department of Geography and Geology, University of Turku, Turku, Finland. ²⁸Institució Catalana de Recerca i Estudis Avançats (ICREA), Barcelona, Spain. ²⁹Institut de Ciència i Tecnologia Ambientals, Universitat Autònoma de Barcelona, Barcelona, Spain. ³⁰Unit Medical Anthropology and Ecology of Disease Emergence, Institut Pasteur, Paris, France. ³¹Helsinki Institute of Sustainability Science (HELSUS), Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland. ³²Faculty of Archaeology, Leiden University, Leiden, Netherlands. ³³School of Anthropology and Conservation, University of Kent, Canterbury, UK. ³⁴Department of Anthropology, Boise State University, Boise, ID, USA. ³⁵Department of Food and Resource Economics, University of Copenhagen, Frederiksberg, Denmark. ³⁶Department of Anthropology, University of Florida, Gainesville, FL, USA. ³⁷School of Culture, History and Language, Australian National University, Canberra, Australian Capital Territory, Australia.

*Corresponding author. Email: jeremy.koster@uc.edu

to age-related variation in foraging skill in human societies. To the extent that foraging complexity underlies the evolution of human life history traits, we anticipate protracted mastery of foraging tasks across the life span.

Here, we focus on age as a predictor of harvests in the largest yet assembled database of hunting returns (Fig. 1). We focus on subsistence hunting for multiple reasons. First, because hunting returns are evident at the conclusion of an excursion; the modeling of hunting inputs and outputs generally requires fewer assumptions than the analogous analysis of agricultural or pastoralist returns. Second, increased hunting is often cited as an adaptive shift that coincides with other distinguishing features of the genus *Homo* (8). However, we note that none of the societies in our sample rely exclusively on hunting (or foraging more generally). Contemporary hunting is not a primitive economy, but rather a recurring one that integrates with other means of production. The data should be evaluated accordingly.

RESULTS

There are many ways to summarize the model inferences. We focus on three foundational issues that motivated the analysis.

- 1) What is the overall pattern of skill development?
- 2) How variable is this pattern within and between societies?
- 3) Which components of the model—increases early in life or declines later in life—describe variation?

At the highest level of pooling, the model provides a statistical answer to the question, “What is a typical human life history of foraging skill?” This is very much an abstraction, one that attempts to factor away all the variation in production functions and associated elasticities to reveal an underlying, dimensionless life history. It cannot say much about absolute levels of production, either within or between societies. However, it can inform comparisons of relative skill at different stages of life.

The statistically average hunter in this sample peaks at 33 years of age (top left plot, Fig. 2). However, this peak is not sharp. At age

18, this fictional average hunter has 89% of maximum skill. In addition, skill declines slowly, such that skill falls below 89% of maximum only after age 56. The blue shading around the posterior mean in this plot shows the entire posterior distribution, fading out to transparent as probability declines. There is correspondingly a lot of information in this sample about the global mean.

While the overall pattern is clear, not every site nor individual forager exhibits the same pattern. The site-level plots in Fig. 2 illustrate this variation. Each site displays the mean skill function for each hunter in the sample. While there is substantial uncertainty about individual skill curves, there is good evidence of individual-level variation at some sites, such as the Matsigenka (9 MTS), the Colombian site (11 CLB), the Aché (16 ACH), and the Martu (35 MRT). Differences among individuals can be quite large. Some individuals have half the adult skill of others in the same community.

For each site, the figure also shows the age of peak skill for a statistically average hunter at that site, as indicated by the vertical dashed lines. While these peak ages cluster around 30 years of age, there is noteworthy variation. On the low end, the Matsigenka (9 MTS) and Wola (40 WOL) peak early, near 24 years of age. Note that the best hunters at these sites tend to peak even earlier, a trend that is also evident among the Bari (7 BAR). On the higher end, the Aché (16 ACH) and Valley Bisa (28 BIS) peak at 37 and 45, respectively, but with relatively slow declines.

These skill functions are inputs into site-specific production functions that also include labor and technology inputs that vary in importance across sites. This means that the relationship between production and age can be different from the relationship between skill and age. In the Supplementary Materials, we therefore present alternative versions of the plot that incorporate the other components of production (figs. S5 to S7). One feature of the production components is that variation can arise from different sources, which, in turn, have different implications for age-related variation in harvests at the individual level. Furthermore, at some sites (e.g., the Dolgan, site 30), the skill functions for individual hunters cluster around a

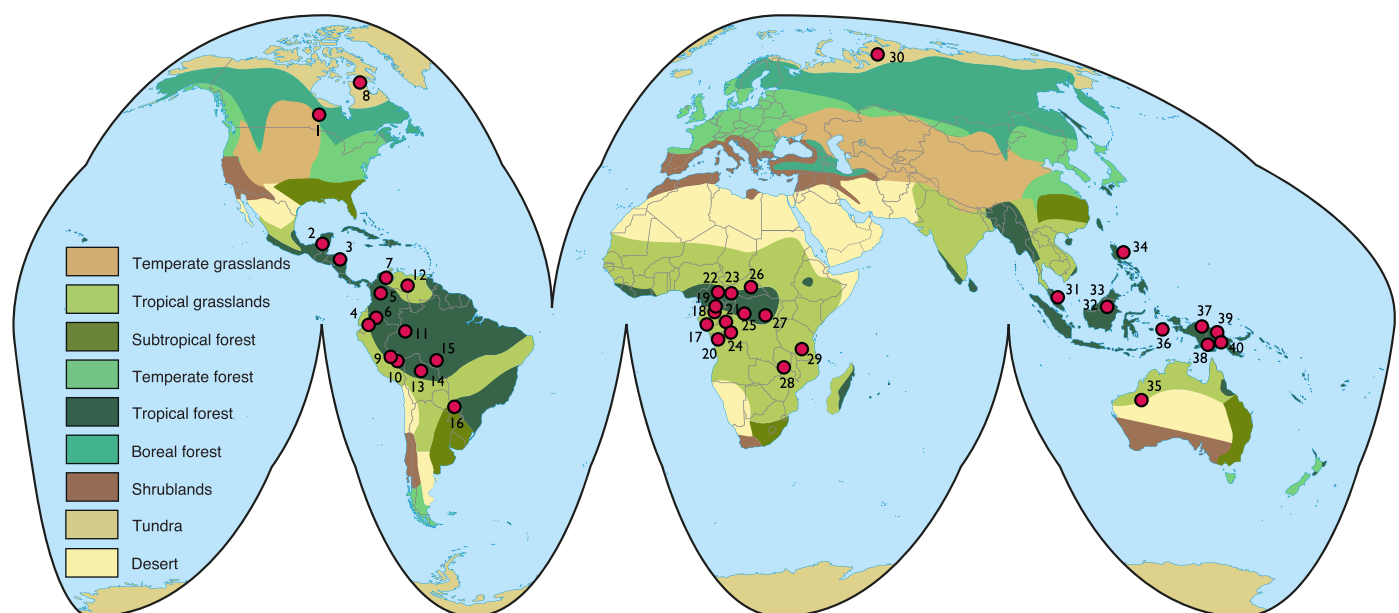


Fig. 1. Distribution of study sites. For the key, see Table 1.

Table 1. Study sites and their numerical and text codes. See the help file of the cchunts package for related citations.

Number	Code	Country	Group	Dataset in cchunts package
1	CRE	Canada	Cree	Winterhalder
2	MYA	Belize	Maya	Pacheco
3	MYN	Nicaragua	Mayangna	Koster
4	QUI	Ecuador	Quichua	Siren
5	ECH	Colombia	Embera Chami	Ross
6	WAO	Ecuador	Waorani	Franzen
7	BAR	Venezuela	Bari	Beckerman
8	INU	Canada	Inuit	Ready
9	MTS	Peru	Matsigenka	Yu_et_al
10	PIR	Peru	Piro	Alvard
11	CLB	Colombia		Van_Vliet_et_al_South_America_sites
12	PME	Venezuela	Pume	Kramer_Greaves
13	TS1	Bolivia	Tsimane	Fernandez_Llamazares
14	TS2	Bolivia	Tsimane	Reyes-Garcia
15	TS3	Bolivia	Tsimane	Trumble_Gurven
16	ACH	Paraguay	Aché	Hill_Kintigh
17	GB1	Gabon		Coad
18	GB2	Gabon		Van_Vliet_et_al_Gabon
19	GB3	Gabon		Van_Vliet_et_al_Ovan
20	CN1	DR Congo		Van_Vliet_et_al_Phlanga
21	GB4	Gabon		Van_Vliet_et_al_Djoutou
22	BK1	Cameroon	Baka	Gallois
23	BK2	Cameroon	Baka	Duda
24	CN2	Congo		Van_Vliet_et_al_Ingolo
25	CN3	Congo		Van_Vliet_et_al_Ngombe
26	BFA	Central African Republic	Bofi and Aka	Lupo_Schmitt
27	CN4	DR Congo		Van_Vliet_et_al_Baego
28	BIS	Zambia	Valley Bisa	Marks
29	HEH	Tanzania		Nielsen
30	DLG	Russia	Dolgan	Ziker
31	BTK	Malaysia	Batek	Venkataraman_et_al
32	PN1	Indonesia	Punan	Gueze
33	PN2	Indonesia	Punan	Napitupulu
34	AGT	Philippines	Agta	Headland
35	MRT	Australia	Martu	Bird_Bird_Codding
36	NUA	Indonesia	Nuaulu	Ellen
37	NIM	Indonesia	Nimboran	Pangau_Adam
38	NEN	Papua New Guinea	Nen	Healey_Nen_PNG
39	MAR	Papua New Guinea	Maring	Healey
40	WOL	Papua New Guinea	Wola	Sillitoe

central mean. However, this does not necessarily support inferences that hunters at these sites have equal skill because there may be insufficient evidence to distinguish them. For an alternative perspective on the anticipated variation among hunters within sites, we simulate variation from the posterior samples of the model (fig. S8).

Last, skill functions vary both within sites and between sites. Which components of skill contribute to this variation? To address this question, we examine the model parameters that measure variation in the components k (rate of increase) and m (rate of decline) of the skill function. Since this is a nonlinear model, we cannot exactly partition total variance. The impact of variation in a component of skill depends on the values of all the other components. We can, however, consider relative sizes of components of variation on the latent scale.

First, we find moderately greater variation in m than k within sites (note the cyan curve in the top left plot of Fig. 3). By contrast, between-site heterogeneity in age-related skill is divided roughly evenly between variation in m and k (see the orange curve in the top left plot in Fig. 3). Some caution is necessary in these comparisons because the relationship between m and k is not additive. However, the implication is that among individuals within a given ecology, skill varies more later in life than earlier in life.

We also find a modest positive correlation between k and m (top right plot), suggesting that hunters who develop skill relatively quickly also show advanced skill later in life. Each cyan density in the top right plot is the posterior correlation between hunters' k and m parameters at a given site. This correlation is particularly pronounced for the Aché and modest otherwise. This may reflect the lack of longitudinal data on individual hunters at most study sites, limiting what can be learned about this correlation. In contrast, the Aché site contains enough longitudinal data on individuals to make stronger inferences about the correlation.

Last, relative variation in m and k can be decomposed within and between sites. We show the posterior distributions of the SDs in both k (bottom left) and m (bottom right) in Fig. 3. The cyan densities are the SDs within sites. This corresponds to the plausible values for variation among individuals. The orange densities are the SDs among sites, corresponding to the plausible values for variation in site-level averages. The dashed curves in both plots show the prior distributions, which were the same for both within and between components. For both k and m , there is relatively less information about variation among sites. As a result, the orange curves remain flatter than the cyan curves. There is substantially more information about variation within sites, and so the cyan curves are rather peaked in both cases. While there is a hint that variation between sites contributes more to variation in k , while variation within sites contributes more to variation in m , strong inferences cannot be drawn until more information is available for inferring the between-site variance.

DISCUSSION

Overall, these results provide an empirical counterpoint to computational models of life history evolution [e.g., (6, 9)]. On the one hand, there is agreement among models about the central tendencies for the ontogeny of skill, which accelerates most rapidly during childhood and adolescence before reaching a plateau during adulthood. In all study sites, skill peaks after physical and reproductive maturity. This result is largely consistent with predictions of embodied capital

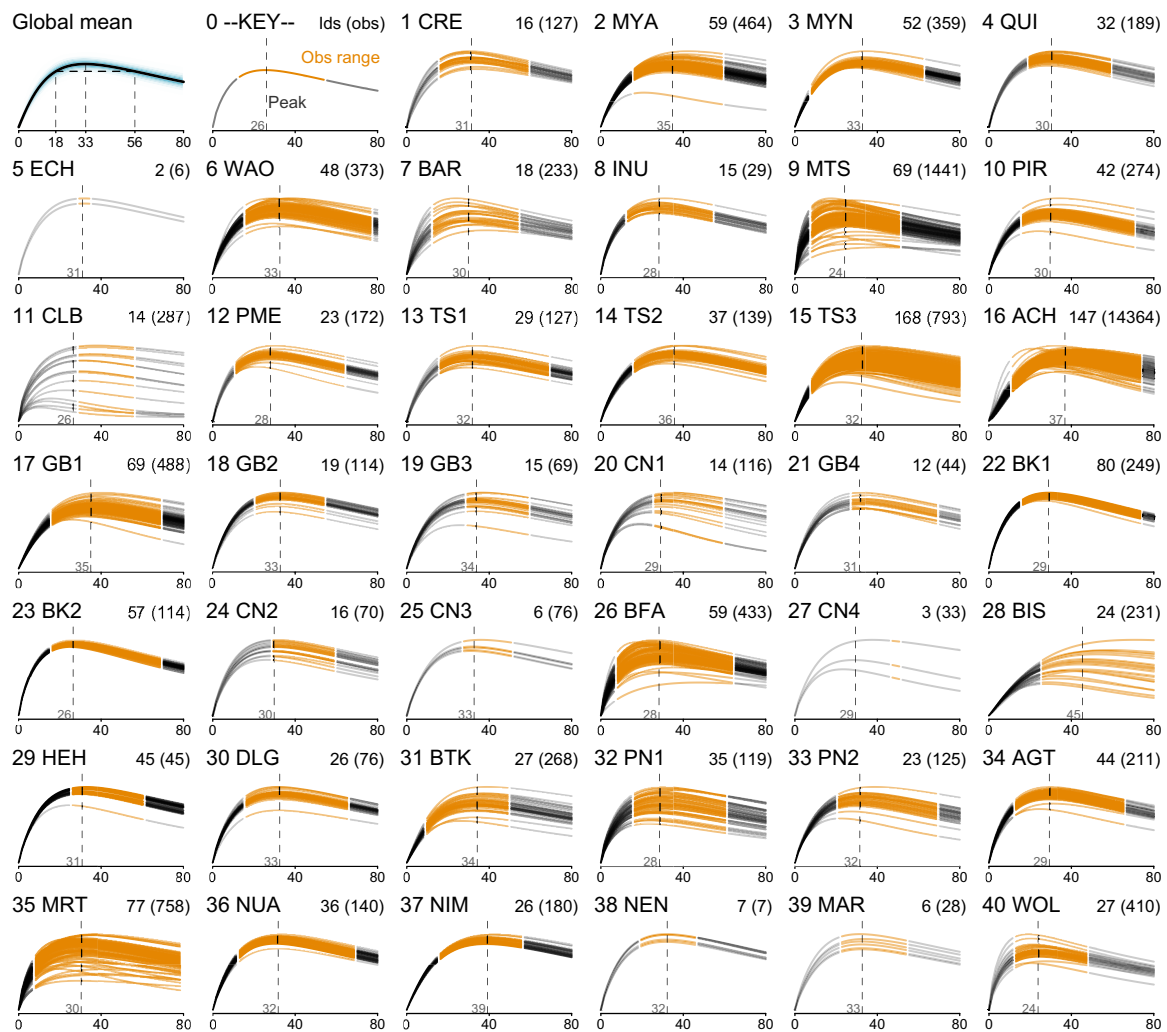


Fig. 2. Skill functions. The figure depicts the global average of skill (top left plot) and skill at the respective study sites. Within study sites, each curve is the posterior mean skill for an individual hunter, standardized to the maximum within each site. In the header of each plot, the site number and three-letter code are shown along with the number of individual hunters in each sample, followed by the number of observed harvests in parentheses. The orange span of ages corresponds to ages observed within each site, while the gray ranges were unobserved and are instead implied by the underlying model. The vertical dashed lines show the average ages at peak within sites.

theory (4), although, on average, the empirical data do not reveal the distinct peaks in skill during middle age that are evident in previous studies of the Aché (10, 11). Instead, the empirical model suggests that skill starts to plateau by early adulthood and that only moderate increases are evident subsequently. Declines are typically slow, such that an 80-year-old may retain two-thirds of maximum skill.

Another noteworthy result is the extent of variability in skill, both among and within sites. Cross-cultural variation is evident in the rate at which hunters develop peak skill. Within sites, the rate at which hunters develop skill is relatively homogeneous compared to the variation that distinguishes young hunters in different study sites. To explain cross-cultural variation in the development of foraging proficiency, it is common and reasonable for anthropologists to emphasize ecological predictors, such as extrinsic mortality risks [e.g., (12)]. However, varying rates of skill development may stem as well from mediating social factors that relate only indirectly to ecological differences. Additional theorizing is needed to generate hypotheses about the cross-cultural ontogeny of foraging skill in re-

sponse to variables such as experience, motivation, opportunities for social learning, and the physical and cognitive demands of hunting in different socioecological environments. As opposed to a canalized human life history strategy, this study suggests potential developmental plasticity in traits associated with hunting skill, which manifest not only in contemporary settings but also potentially in ancestral settings. These results further imply that singular study sites can rarely be viewed as straightforward analogs for evolutionarily relevant environments (13).

Within the respective study sites, the model brings new attention to the variation in skill among individual hunters. What explains this variation? Data and theory suggest that physical strength and stamina, accumulated knowledge, and motivation all plausibly contribute to age-related variation (14, 15). In most empirical datasets, however, only data on the hunters' ages are available as predictors, not other attributes of the individuals. The peak in the average skill function at approximately 33 years old is also near the age when physical strength and ecological knowledge plateau (15–18). From a

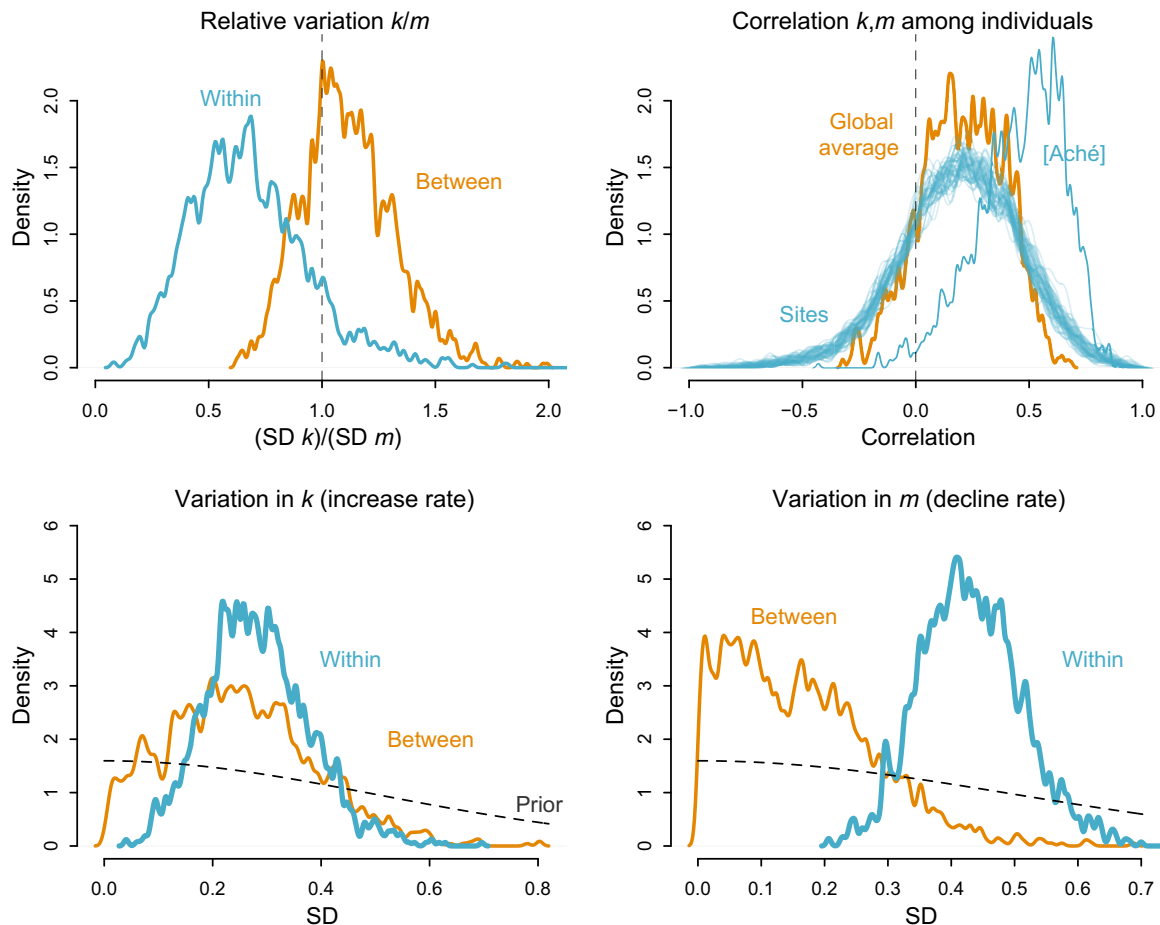


Fig. 3. Variation in components of skill. (Top left) Relative variation in k and m . The horizontal axis is the ratio of the SD of k to the SD of m . The vertical dashed line at 1 indicates equality of variances. The orange density is between-site variation. The cyan density is within-site variation. There is more variation in declines (m) than increases (k) in skill within sites, whereas the ratio is roughly equivalent across sites. **(Top right)** Correlation between k and m among individuals within sites. The orange density is the global average. Each cyan density represents a single site. The Ach e stand out and are labeled separately. **(Bottom left and bottom right)** Variation in k (left) and m (right) comparing variation within and between sites.

theoretical perspective, an optimal life history should develop these components together, with the important caveat that brain growth may need to precede body growth, to enable learning (9). To distinguish the relative importance of phenotypic traits to variation in hunting skill across the life span, data are needed that link measurements of these attributes to individual-level hunting returns, ideally longitudinally. In the interim, the currently available data suggest that individual hunters develop physical and cognitive abilities in concert, resulting in high hunting success by their late 20s and early 30s.

Estimates from empirical studies provide inputs to the parameterization of computational life history models. Our analysis of hunting by age provides refined estimates of the average skill function, a target of inference for recent theoretical work (6, 9). However, the added clarity about average skill is belied by the substantial heterogeneity that is evident among individual hunters. For future theoretical developments about the unique human life history pattern, this variation in skill merits careful attention. Prevailing hypotheses about the adaptive shift to hunting by human ancestors assert that reciprocal food sharing in small bands was necessary to smooth variance in consumption, given that daily harvests by hunters are unpredictable (19–21). In this literature, variability in the skill of individual hunters

has received relatively little consideration (22). Our analysis suggests that this variability typifies communities of human foragers while concomitantly altering the effectiveness of food sharing for buffering risk. That is, when hunters vary substantially in their skill and productivity, there are asymmetric benefits to participation in risk-pooling distribution systems. To the extent that prosociality and other traits in the human lineage stem from the cooperative challenges posed by this asymmetry, the high variation in hunting skill across the life span merits further attention.

MATERIALS AND METHODS

The total sample contains 23,747 observations of 1821 individual foragers across 40 study sites (Fig. 1). There is substantial imbalance in sample size across units. One site contributes only six trips from two individuals. Another contributes more than 14,000 trips from 147 individuals. Some individuals contribute only a single outcome, while others contribute dozens. The majority of the sample comprises male hunters, with too little data on female hunters to infer generalizable sex differences. Most sites contribute primarily cross-sectional data, while a few others exhibit impressive time series.

Because skill cannot be directly observed, what is required is a model with latent age-varying skill, which informs a production function for observable foraging returns. The model is described in detail in the Supplementary Materials. Building on earlier research (10), our modeling framework was developed in a grant proposal and reviewed before seeing the assembled sample. Using a Cobb-Douglas production function common to economic research, we model hunting returns (harvest) on excursions as a standard log-linear function of skill, labor inputs, and auxiliary inputs from technology and cooperation

$$\text{harvest} = S^\eta L^\beta \alpha \quad (1)$$

where S represents the hunter's skill with its elasticity, η , the labor input and its elasticity are represented by L^β , and α is a linear model for covariates such as group size, the number of assistants, the use of dogs, and the use of firearms. These latter variables have been shown to influence hunting returns (23–26). Note that production requires both skill and labor; if either is zero, then there is no harvest. The respective elasticities reflect the proportional effects that skill and labor have on harvests. That is, increasing either skill or labor results in increased harvests, but the scale of the increase is reflected in the elasticities. Our parameterization of the function does not impose constant returns to scale [cf. (27)].

Data on hunting returns pose the particular challenge of including many zeroes (for hunting trips in which nothing was acquired), and the harvests on successful hunting trips exhibit positive skew. We therefore adapt the Cobb-Douglas function in Eq. 1 to a zero-augmented model in which the zeroes and nonzero harvests are modeled via separate functions, as detailed in the Supplementary Materials. As in previous work (10), we use a Bernoulli distribution to model the probability of success versus failure, and the distribution of nonzero harvests is assumed to follow a gamma distribution.

To model latent skill across the life span, we adapt the von Bertalanffy growth model (28). The benefit of the model is that individuals' skill is assumed to be lowest at birth with eventual declines due to senescence. Within these constraints, the functional form of the model potentially exhibits considerable diversity depending on the empirical data. Age-related variation in skill is determined by a rate of growth, k , and a rate of decline, m . The growth component, k , potentially includes ecological knowledge, strength, cognitive function, and other traits that underlie foraging success but that exhibit reduced acceleration with age. For simplicity, the composite of these attributes can be dubbed knowledge. For a hunter of age x , the growth function, K , is represented by

$$K(x) = 1 - \exp(-kx) \quad (2)$$

where k is a parameter greater than zero that reflects the rate of increase.

The declining component, m , reflects the senescence of traits related to hunting skill. For a forager of age x , the decline in productive ability, M , decreases at a constant rate given by

$$M(x) = \exp(-mx)^\# \quad (3)$$

where m is a parameter greater than zero that reflects the rate of decline.

Age-specific skill is then represented by the weighted product of the two preceding functions

$$S(x) = M(x) K(x)^b \quad (4)$$

where b represents the elasticity for knowledge in the skill function. As detailed in the Supplementary Materials, the von Bertalanffy model permits diverse functional forms of skill across the life span, ranging from approximately sigmoidal to roughly quadratic shapes. Although we assume that the growth and senescence components of skill relate to proximate mechanisms, such as age-related variation in ecological knowledge and physical abilities, the available data do not allow us to examine those proximate mechanisms [cf. (15, 18)]. As a result, age-related variation in skill must be inferred from its effects on the observed productivity of hunters of heterogeneous ages.

The statistical model allows the von Bertalanffy parameters to vary across individuals, reflecting different rates of increasing skill or senescence among hunters. The parameters also vary across study sites, allowing for different rates of increase and decline in heterogeneous environments. As noted previously, we model hunting returns using a zero-augmented gamma model, and the respective skill functions of hunters and societies are estimated jointly from the Bernoulli and gamma functions. It would have been possible to estimate separate, correlated individual-level and site-level skill functions for the Bernoulli and gamma functions, respectively. Our modeling approach instead assumes that increases in skill have comparable effects in terms of reducing the probability of unsuccessful excursions and increases in the amount of meat acquired on successful outings. This assumption receives support from an earlier analysis of the Aché dataset, which suggests that there is a positive correlation (and no evident tradeoff) between hunters' probabilities of acquiring something and the amounts that are harvested on successful trips (10).

In addition to the varying effects on the skill parameters, the model also allows the parameters for labor inputs and covariates in the linear model to vary across study sites. Missing data, particularly for hunt duration and technological variables, are common and addressed using Bayesian imputation and averaging methods.

At some study sites, hunters work cooperatively to harvest prey, and the data on these excursions assign the hunting returns to the group, not individual hunters. In those cases, we replace individual hunter skill in the production equation with the weighted average of the skill of the group members. The statistical model follows the principles of a multiple membership model (29, 30). When hunters are observed in different combinations of groups, it is possible to distinguish differences in skill between them.

We cannot rule out selection biases that complicate inferences. For instance, if there were a study site where highly skilled hunters are active regardless of environmental conditions and the relatively unskilled hunters are active only when returns are expected to be particularly favorable, then the estimated variation in hunters' skill would likely be lower than a site where hunting activity occurs independently of skill.

We fit our model using a Hamiltonian Monte Carlo sampling algorithm in the Rstan package, version 2.16.1 (31). We implemented the model both as a forward simulation and as a statistical model. The forward simulation validates that the statistical model can recover parameters from data with known values. The statistical model, estimated from 10 chains of 500 iterations, exhibits efficient mixing and adequate diagnostics. The data and convenience functions are included as part of the cchunts R package, which is available alongside the model posterior, coding scripts, and accompanying information about the Open Science Framework (<https://osf.io/2kzb6/>).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/6/26/eaax9070/DC1>

REFERENCES AND NOTES

- J. H. Jones, Primates and the evolution of long, slow life histories. *Curr. Biol.* **21**, R708–R717 (2011).
- C. O. Lovejoy, The origin of man. *Science* **211**, 341–350 (1981).
- K. Hawkes, J. F. O'Connell, N. B. Jones, H. Alvarez, E. L. Charnov, Grandmothering, menopause, and the evolution of human life histories. *Proc. Natl. Acad. Sci. U.S.A.* **95**, 1336–1339 (1998).
- H. Kaplan, K. Hill, J. Lancaster, A. M. Hurtado, A theory of human life history evolution: Diet, intelligence, and longevity. *Evol. Anthropol.* **9**, 156–185 (2000).
- E. Herrmann, J. Call, M. V. Hernández-Lloreda, B. Hare, M. Tomasello, Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science* **317**, 1360–1366 (2007).
- M. González-Forero, A. Gardner, Inference of ecological and social drivers of human brain-size evolution. *Nature* **557**, 554–557 (2018).
- A. R. DeCasien, S. A. Williams, J. P. Higham, Primate brain size is predicted by diet but not sociality. *Nat. Ecol. Evol.* **1**, 0112 (2017).
- R. A. Foley, The evolutionary consequences of increased carnivory in hominids, in *The Early Human Diet: The Role of Meat; Meat-Eating and Human Evolution*, C. B. Stanford, H. T. Bunn, Eds. (Oxford Univ. Press, 2001), pp. 305–331.
- M. González-Forero, T. Faulwasser, L. Lehmann, A model for brain life history evolution. *PLoS Comput. Biol.* **13**, e1005380 (2017).
- R. McElreath, J. Koster, Using multilevel models to estimate variation in foraging returns. Effects of failure rate, harvest size, age, and individual heterogeneity. *Hum. Nat.* **25**, 100–120 (2014).
- R. Walker, K. Hill, H. Kaplan, G. McMillan, Age-dependency in hunting ability among the Ache of Eastern Paraguay. *J. Hum. Evol.* **42**, 639–657 (2002).
- N. Blurton Jones, K. Hawkes, P. Draper, Foraging returns of !Kung adults and children: Why didn't !Kung children forage? *J. Anthropol. Res.* **50**, 217–248 (1994).
- W. Irons, Adaptively relevant environments versus the environment of evolutionary adaptedness. *Evol. Anthropol.* **6**, 194–204 (1998).
- N. Blurton Jones, F. W. Marlowe, Selection for delayed maturity: Does it take 20 years to learn to hunt and gather? *Hum. Nat.* **13**, 199–238 (2002).
- M. Gurven, H. Kaplan, M. Gutierrez, How long does it take to become a proficient hunter? Implications for the evolution of extended development and long life span. *J. Hum. Evol.* **51**, 454–470 (2006).
- S. Zent, E. López-Zent, Ethnobotanical convergence, divergence, and change among the Hoti of the Venezuelan Guayana. *Adv. Econ. Bot.* **15**, 37–78 (2004).
- K. Demps, F. Zorondo-Rodríguez, C. García, V. Reyes-García, Social learning across the life cycle: Cultural knowledge acquisition for honey collection among the Jenu Kuruba, India. *Evol. Hum. Behav.* **33**, 460–470 (2012).
- J. Koster, O. Bruno, J. L. Burns, Wisdom of the elders? Ethnobiological knowledge across the lifespan. *Curr. Anthropol.* **57**, 113–121 (2016).
- G. Isaac, The food-sharing behavior of protohuman hominids. *Sci. Am.* **238**, 90–108 (1978).
- B. Winterhalder, Diet choice, risk, and food sharing in a stochastic environment. *J. Anthropol. Archaeol.* **5**, 369–392 (1986).
- H. S. Kaplan, E. Schniter, V. L. Smith, B. J. Wilson, Risk and the evolution of human exchange. *Proc. Biol. Sci.* **279**, 2930–2935 (2012).
- R. Boyd, The evolution of reciprocity when conditions vary, in *Coalitions and Alliances in Humans and Other Animals*, A. Harcourt, F. DeWaal, Eds. (Oxford Univ. Press, 1992), pp. 473–489.
- R. B. Hames, A comparison of the efficiencies of the shotgun and the bow in neotropical forest hunting. *Hum. Ecol.* **7**, 219–252 (1979).
- E. A. Smith, Inuit foraging groups: Some simple models incorporating conflicts of interest, relatedness, and central-place sharing. *Ethol. Sociobiol.* **6**, 27–47 (1985).
- M. Alvard, Shotguns and sustainable hunting in the Neotropics. *Oryx* **29**, 58–66 (1995).
- J. M. Koster, Hunting with dogs in Nicaragua: An optimal foraging approach. *Curr. Anthropol.* **49**, 935–944 (2008).
- K. J. Arrow, H. B. Chenery, B. S. Minhas, R. M. Solow, Capital-labor substitution and economic efficiency. *Rev. Econ. Stat.* **43**, 225–250 (1961).
- L. von Bertalanffy, Untersuchungen Über Die Gesetzmäßigkeit Des Wachstums: I. Teil: Allgemeine Grundlagen Der Theorie; Mathematische Und Physiologische Gesetzmäßigkeiten Des Wachstums Bei Wassertieren. *Wilhelm Roux Arch. Entwickl. Mech. Org.* **131**, 613–652 (1934).
- W. J. Browne, H. Goldstein, J. Rasbash, Multiple membership multiple classification (MMMC) models. *Stat. Model.* **1**, 103–124 (2001).
- B. Aven, H. Hillmann, Structural role complementarity in entrepreneurial teams. *Manage. Sci.* **64**, 5688–5704 (2018).
- Stan Development Team, RStan: The R interface to Stan (2016). R package version 2.14.1.

Acknowledgments: Audiences in London, Lausanne, Nijmegen, Aarhus, UCLA, and the University of Utah contributed useful feedback on draft analyses and interpretations, as did the anonymous reviewers. The map was created with the multimedia department at the Max Planck Institute for Evolutionary Anthropology. **Funding:** This study was funded by the NSF (#1534548). **Author contributions:** J.K. and R.M. conceived the study, analyzed the data, and wrote the paper. All other authors contributed hard-earned field data. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Supplementary data and code are available at <https://osf.io/2kzb6/>. Additional data related to this paper may be requested from the authors.

Submitted 3 May 2019
Accepted 17 March 2020
Published 24 June 2020
10.1126/sciadv.aax9070

Citation: J. Koster, R. McElreath, K. Hill, D. Yu, G. Shepard Jr., N. van Vliet, M. Gurven, B. Trumble, R. B. Bird, D. Bird, B. Codding, L. Coad, L. Pacheco-Cobos, B. Winterhalder, K. Lupo, D. Schmitt, P. Sillitoe, M. Franzen, M. Alvard, V. Venkataraman, T. Kraft, K. Endicott, S. Beckerman, S. A. Marks, T. Headland, M. Pangau-Adam, A. Siren, K. Kramer, R. Greaves, V. Reyes-García, M. Guèze, R. Duda, Á. Fernández-Llamazares, S. Gallois, L. Napitupulu, R. Ellen, J. Ziker, M. R. Nielsen, E. Ready, C. Healey, C. Ross, The life history of human foraging: Cross-cultural and individual variation. *Sci. Adv.* **6**, eaax9070 (2020).

The life history of human foraging: Cross-cultural and individual variation

Jeremy Koster, Richard McElreath, Kim Hill, Douglas Yu, Glenn Shepard, Jr., Nathalie van Vliet, Michael Gurven, Benjamin Trumble, Rebecca Bliege Bird, Douglas Bird, Brian Coddling, Lauren Coad, Luis Pacheco-Cobos, Bruce Winterhalder, Karen Lupo, Dave Schmitt, Paul Sillitoe, Margaret Franzen, Michael Alvard, Vivek Venkataraman, Thomas Kraft, Kirk Endicott, Stephen Beckerman, Stuart A. Marks, Thomas Headland, Margaretha Pangau-Adam, Anders Siren, Karen Kramer, Russell Greaves, Victoria Reyes-García, Maximilien Guéze, Romain Duda, Álvaro Fernández-Llamazares, Sandrine Gallois, Lucentezza Napitupulu, Roy Ellen, John Ziker, Martin R. Nielsen, Elspeth Ready, Christopher Healey and Cody Ross

Sci Adv 6 (26), eaax9070.
DOI: 10.1126/sciadv.aax9070

ARTICLE TOOLS

<http://advances.sciencemag.org/content/6/26/eaax9070>

SUPPLEMENTARY MATERIALS

<http://advances.sciencemag.org/content/suppl/2020/06/22/6.26.eaax9070.DC1>

REFERENCES

This article cites 28 articles, 3 of which you can access for free
<http://advances.sciencemag.org/content/6/26/eaax9070#BIBL>

PERMISSIONS

<http://www.sciencemag.org/help/reprints-and-permissions>

Use of this article is subject to the [Terms of Service](#)

Science Advances (ISSN 2375-2548) is published by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. The title *Science Advances* is a registered trademark of AAAS.

Copyright © 2020 The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original U.S. Government Works. Distributed under a Creative Commons Attribution NonCommercial License 4.0 (CC BY-NC).

Supplementary Materials for

The life history of human foraging: Cross-cultural and individual variation

Jeremy Koster*, Richard McElreath, Kim Hill, Douglas Yu, Glenn Shepard Jr., Nathalie van Vliet, Michael Gurven, Benjamin Trumble, Rebecca Bliege Bird, Douglas Bird, Brian Coddington, Lauren Coad, Luis Pacheco-Cobos, Bruce Winterhalder, Karen Lupo, Dave Schmitt, Paul Sillitoe, Margaret Franzen, Michael Alvard, Vivek Venkataraman, Thomas Kraft, Kirk Endicott, Stephen Beckerman, Stuart A. Marks, Thomas Headland, Margaretha Pangau-Adam, Anders Siren, Karen Kramer, Russell Greaves, Victoria Reyes-García, Maximilien Guèze, Romain Duda, Álvaro Fernández-Llamazares, Sandrine Gallois, Lucentezza Napitupulu, Roy Ellen, John Ziker, Martin R. Nielsen, Elspeth Ready, Christopher Healey, Cody Ross

*Corresponding author. Email: jeremy.koster@uc.edu

Published 24 June 2020, *Sci. Adv.* **6**, eaax9070 (2020)
DOI: 10.1126/sciadv.aax9070

This PDF file includes:

- Description of the data
- The life history foraging model
- Formal model definition
- Supplemental Results
- Figs. S1 to S12
- Appendix A

SUPPLEMENTAL MATERIALS

1. DESCRIPTION OF THE DATA

The total sample contains 1,821 individual hunter, 23,747 hunter-level outcomes, and 21,160 trips across 40 study sites. To compile the dataset, the first author searched for relevant studies on subsistence hunting in the anthropological and biological literature, subsequently contacting authors to invite them to contribute data. The contributors submitted data in a standardized format that included variables for the biomass acquired on terrestrial hunting trips, the ages of the hunters at the time of the hunt, the duration of the trip, the hunting weaponry carried by the hunters, and the presence of dogs or assistants (the distinction between hunters and assistants was left to the discretion of contributors, who were counseled to conceptualize "hunters" as those individuals who made active contributions to detecting and pursuing prey). Our data are restricted to hunting, and exclude gathering, because of the paucity of data on gathered plant foods.

There is tremendous imbalance in sample size across units. One site contributes only 6 trips from 2 individuals. Another contributes more than 14,000 trips from 147 individuals. Some individuals contribute only a single outcome, while others contribute dozens. The majority of the sample comprises male hunters, with too little data on female hunters to infer generalizable sex differences. (This does not imply that men's production and skill is more relevant to human evolution, nor that women's foraging skill would necessarily exhibit either the same or a different functional relationship with age.) Most sites contribute primarily cross-sectional data, while a few others exhibit impressive time series. The statistical framework is designed to make use of all these data.

2. THE LIFE HISTORY FORAGING MODEL

Since skill cannot be directly observed, what is required is a model with latent age-varying skill. This unobservable skill feeds into a production function for observable hunting returns. In this section, we define a framework that satisfies this requirement. We explain it one piece at a time, with a focus on the scientific justification.

One advantage of the latent skill approach is that it allows us to use different observations from different contexts—both solo and group hunting, for example—to infer a common underlying dimension of skill. But modeling even the simplest foraging data benefits from this approach, as hunting returns often are highly zero-augmented. Separate production functions for zeros and non-zeros are needed to describe such data. In principle, more than one dimension of latent skill could be modeled. We restrict ourselves to only one in the current analysis. With more detailed data, describing additional dimensions should be possible.

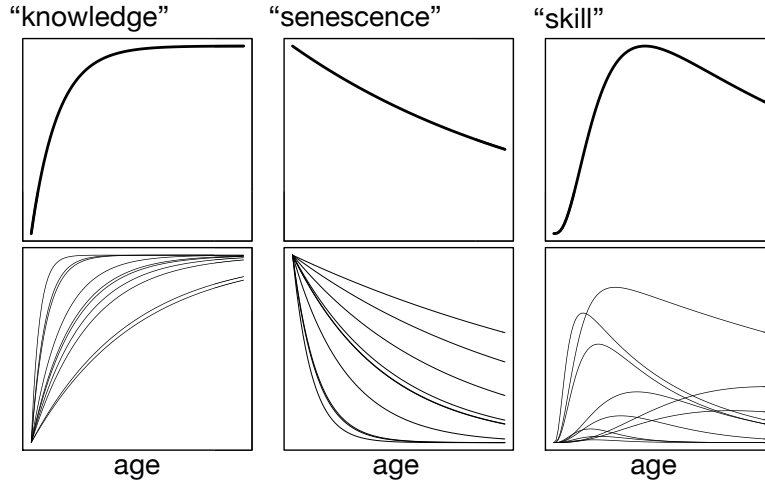


FIGURE S1. The age-specific skill model. Top row: Increasing components, “knowledge,” and decreasing components, “senescence,” multiply to produce relative productive potential at each age, “skill.” Bottom row: Variation in the components combines to produce a diverse array of possible skill functions.

2.1. Latent skill model. One of the simplest life history models is the von Bertalanffy asymptotic growth model. We use this model to represent the increasing components of hunting skill as a function of age. These increasing components include knowledge, strength, cognitive function, and many other aspects that contribute to hunting success and increase but decelerate with age. For convenience, label the composite of these components *knowledge*. Assume that the rate of change in knowledge with respect to age x is given by $dK/dx = k(1 - K(x))$. This means only that knowledge increases at a rate proportional to the remaining distance to the maximum—the more there is left to learn, the more one learns. Solving this differential equation yields the age-specific knowledge of a hunter at age x :

$$K(x) = 1 - \exp(-kx) \quad (1)$$

where $k > 0$ is a parameter that determines the rate of increase. To account for senescence, we assume that production capacity M declines at a constant rate, given by $dM/dx = -mM(x)$. Solving this yields:

$$M(x) = \exp(-mx) \quad (2)$$

where $m > 0$ represents the rate of decline. The total age-specific skill is given by a weighted product of these two functions:

$$S(x) = M(x)K(x)^b \quad (3)$$

where the parameter b controls the relative importance of K . In economic terms, b is the knowledge elasticity of skill. We assume that k and m may vary across individuals—some people learn faster or senesce more slowly—while b is a property of the production context at a given study site.

This model is among the simplest we can construct. Nevertheless, it is capable of describing diverse age-specific skill curves. Figure S1 illustrates the general shapes of each component of the model, as well as how variation in each component may produce variable life histories. Each plot in this figure shows age on the horizontal axes. The top row of the figure illustrates the general shape of each component (left and middle) and one possible resulting lifetime skill curve (right). The bottom row shows 10 different, randomly simulated knowledge and senescence curves, with their implied random skill curves. These demonstrate that even a model as simple as this one, with only three parameters, is nevertheless capable of producing many diverse age-specific curves. This approach brings two more advantages, as compared to the use of polynomial functions of age. First, the parameters have straightforward biological interpretations. Second, these functions do not exhibit instabilities such as Runge’s phenomenon that complicate fitting and prediction.

These functions also have clear weaknesses. Neither the rate of gain k nor the rate of loss m is plausibly constant over large age ranges. The rate of variation in body growth, for example, will produce rate variability in skill growth. And near the end of life, skill loss should accelerate rather than slow down. Although the data analyzed in this paper do not span the age ranges in which this variation would occur, we should be cautious about overgeneralizing from this analysis.

The final component of the core skill model is partial pooling of information. Since these data contain repeat measurements on the same units—individuals and sites—as well as substantial imbalance in sampling of these units, partial pooling via multilevel modeling provides superior estimates. We employ two levels of hierarchical pooling (Figure S2). First, the life history parameters k and m are pooled across individuals within each site (left column, Figure S2). In standard terminology, k_{id} and m_{id} for each individual are random effects drawn from a bivariate distribution. Each site also has its own value for b , reflecting variation in the relative importance of knowledge across sites. Therefore each site has its own distribution of skill functions (middle column). Finally, the site distributions are pooled together to regularize inference at the second level (right column), producing a distribution of site distributions. To an extent, this global distribution is a statistical fiction that is necessary to pool information properly among sites. However, it is also a target of inference, providing a weighted summary of all of the evidence across sites. The weights arise from the structure of the multilevel model and are functions of the sample sizes, the differences in site means, and the variation among those means. For example, a site could have a large sample size but contribute little to the global mean if its own mean were extreme.

2.2. Production model. Skill is not directly observable. Rather, we must infer it by its effects on hunting productivity. This requires introducing a layer of production functions through which skill acts. The production data available to us contain two correlated components: (1) the probability of a successful trip that produces a non-zero harvest and (2) the size of harvests obtained on successful trips. We model each with a standard log-linear function of labor, skill, and technology. Specifically, for successful trips, the mean expected harvest at skill S is given by:

$$h(S) = S^{\eta_b} L^{\beta_b} \exp \alpha_b \quad (4)$$

where η_b is the elasticity of skill, which determines the magnitude of skill differences on harvest, L^{β_b} is the labor allocated with its elasticity β_b , and α_b is a linear model including terms for technology and cooperation variables. (In this equation, the b subscript denotes

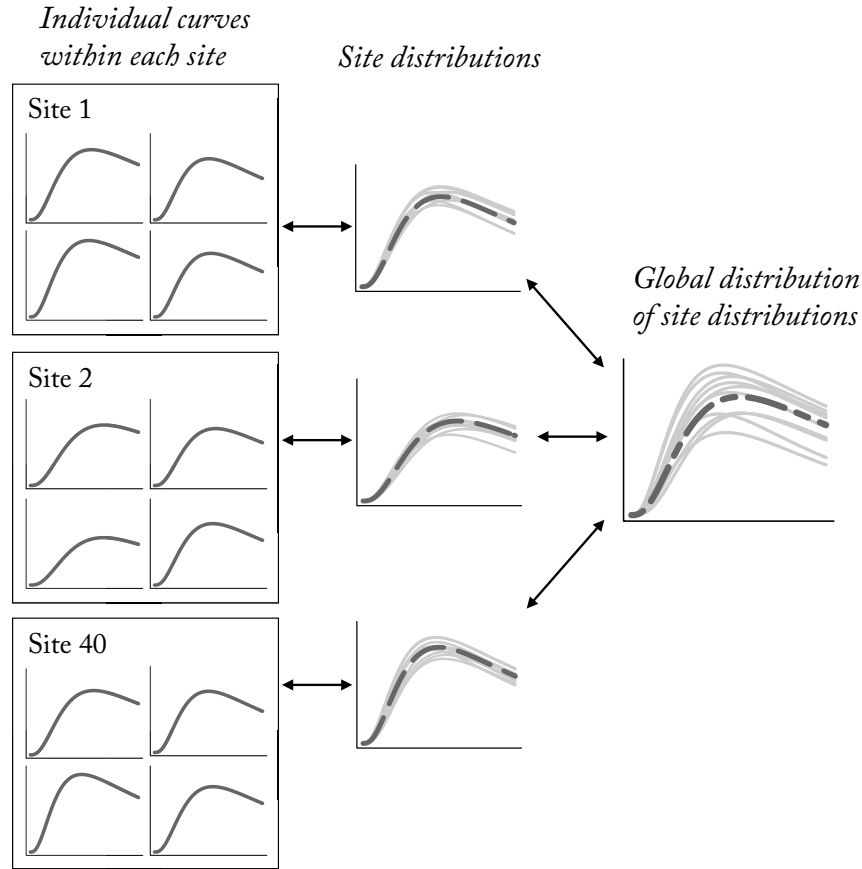


FIGURE S2. Hierarchical structure of skill functions within the inferential model. Within each site (left) a skill curve is inferred for each hunter. Individuals within each site are pooled using a distribution of individual skill curves (middle). Finally, the distributions of parameters within each site are again pooled using a distribution of distributions (right). This formulation allows variation among individuals to vary by site.

that this is the function for the non-zero harvests, as distinguished from the subsequent Bernoulli function for successes and failures in Equation 5, which features the p subscript.) Notice that harvest increases with both skill and labor, but that the elasticity of each determines the impact of any increase. The full distribution of harvests is assumed to follow a gamma distribution, which allows for the highly skewed distributions typical of many hunting data sets. However, a log-normal distribution of harvests would work as well. The important features are to impose a zero lower bound and to allow for positive skew. If we had detailed data on the encounters and pursuits of individual prey types, we could build a mixture distribution to better describe observed harvest sizes. But such data are available in very few cases. For comparability across sites and compatibility with the logit function described next (equation 5), we have proportionally standardized harvests relative to average harvest sizes at the respective study sites. When evaluating sources of variation in the data, it is important to bear in mind this standardization, which limits the inferences that can be made about between-site variation in this analysis.

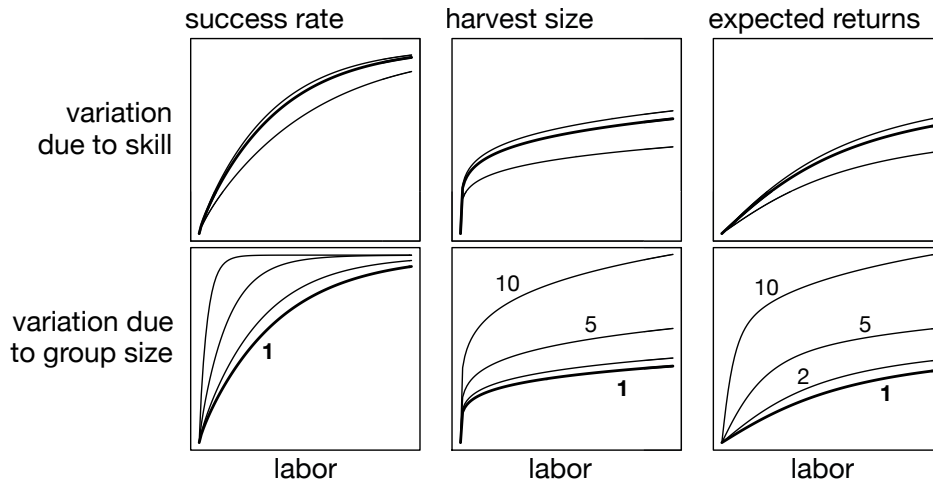


FIGURE S3. Example production functions for observed harvests. Expected harvest (righthand column) is the product of the probability of a non-zero harvest (lefthand column) and the expected size of a non-zero harvest (middle column). The top row shows how each component may vary with skill. The bottom row shows how each may vary with number of hunters.

A similar approach provides a Bernoulli distribution of success/failure. The probability that a trip produces a non-zero harvest is:

$$p(S) = 2(\text{logit}^{-1}(S^{\eta_p} L^{\beta_p} \exp \alpha_p) - \frac{1}{2}) \quad (5)$$

The terms enclosed within the interior parentheses recapitulate the log-linear production function of the above equation (4). The remainder of the function re-scales the log-linear model so that $p(S)$ varies continuously from zero to one and $p(0) = 0$.

This is a descriptive approach. It has the advantage of being able to describe many possible relationships between skill, labor, and technology. Figure S3 illustrates some of the model's features. Each plot in this figure shows labor input—hours allocated to foraging—on the horizontal axis. From left to right, the plots show the probability of a non-zero harvest, the expected harvest size on a successful trip, and the expected returns resulting from the product of the two. Each row illustrates the impact of one type of variation—variation in individual skill in the top row and variation in hunting group size in the bottom row. The first thing to notice is that the function implies monotonic returns to labor. Marginal returns must always either increase or decrease with labor. Second, skill and labor can influence hunting success and harvest size quite differently. There is no assumption that skill or labor is equally important for both components of production. And since technology can influence elasticity of skill and labor, technology can have independent effects as well.

2.3. Cooperative trips and aggregated harvests. Many of the hunting trips in our sample are cooperative, in the sense that multiple hunters of varying skill interact in producing returns. The harvests on these trips may be assignable to individual hunters or alternatively credited to the group as a whole. We handle cooperative trips by treating them as analogous to technology, with group size represented as a coefficient in the production equation.

When returns are aggregated to the level of the group rather than assigned to individual hunter, we replace individual hunter skill in the production equation with a weighted average of the skill of the group members.

2.4. Missing values and measurement error. Our sample embodies common statistical challenges. First, there are many missing values, notably for trip duration and the presence of dogs on trips. Second, there is measurement error, notably for individual ages. The customary solution to these problems is to drop all cases with any missing values and to replace uncertain measurements with their means. Instead of dropping cases with missing values, however, we model the unknown values. This allows Bayesian imputation of missing values, averaging over uncertainty in unobserved durations. We rely upon the same principle to handle measurement error in age. In some cases, co-authors who contributed datasets to our sample assigned a standard error to the recorded ages of hunters. Within the model, each hunter’s date-of-birth is replaced with an unknown parameter with a prior centered on the recorded age and with standard deviation equal to the recorded standard error. In a few cases, no age is recorded for an individual. In those cases, we assign a vague prior that covers the entire range of observed ages.

2.5. Inference. The full model contains just under 28,000 parameters. Many of these correspond to missing durations and age uncertainties, and so contribute little fit to the sample. Many of the remaining parameters arise from the hierarchical structure of the life history model. These parameters do not make it easier to fit the sample, but rather harder. They reduce overfitting, by pooling information among sampling units. For the remaining parameters, we adopt regularizing priors that are more conservative than the implied flat priors of typical non-Bayesian procedures. We present a complete description of the priors in the supplemental code. Having fit alternative parameterizations of the model, we believe the results that we present in the next sections are qualitatively robust to changes in priors and even the hierarchical structure of the model. To facilitate alternative estimates of model parameters, though, we provide our annotated modeling code in this supplemental material (Appendix A), and we provide the full code and auxiliary scripts in the online supplements (<https://osf.io/2kzb6/>).

3. FORMAL MODEL DEFINITION

As a complement to the above qualitative description of the modeling approach, we turn to a formal description of the model. Let y be an indicator variable for hunting success (produced a non-zero harvest) and h any observed non-zero harvest. Let i index observed outcomes (harvests). Then:

$$y_i \sim \text{Bernoulli}(p_i)$$

$$h_i \sim \text{Gamma}(\mu_{i2}, \nu_{\text{site}[i]})$$

The expressions for p and μ specify the production functions, indexed by j for the outcome type (for successes or harvest size, respectively):

$$p_i = 2(\text{logit}^{-1}(\mu_{i1}) - \frac{1}{2})$$

$$\log(\mu_{ij}) = \eta_{\text{site}[i]j} S_{\text{trip}[i]} + \beta_{\text{site}[i]1j} \log L_i + \alpha_{ij}$$

The labor input is L_i , the duration of the trip, standardized so that the average trip at each site has $L = 1$.

The skill input S into the above is given by the average skill among the individuals contributing labor to a particular observed harvest:

$$S_{\text{trip}[i]} = n_{\text{trip}[i]}^{-1} \sum_{f=1}^{n_{\text{trip}[i]}} \exp(-m_{\text{id}[f]} \ell_{\text{id}[f], \text{trip}[i]}) (1 - \exp(-k_{\text{id}[f]} \ell_{\text{id}[f], \text{trip}[i]}))^{b_{\text{site}[\text{trip}[i]]}}$$

where n is the number of productive foragers for trip $[i]$ (excluding individuals categorized as assistants, such as porters) and $\text{id}[f]$ is the forager ID of the f -th forager on each trip. This means that for aggregated harvests, in which individual contributions cannot be identified, the model uses average skill. The age $\ell_{f, \text{trip}[i]}$ is the estimated age for forager f at the time of trip $[i]$. We describe the age model further down. Note that all ages within the model are standardized by dividing calendar age by the reference age of 80, making $\ell = 1$ equivalent to 80 years old.

The intercept component of each production function, α_{ij} , is composed from:

- A site-specific intercept $a_{\text{site}[i]j}$
- A site-specific and outcome-type specific set of coefficients (elasticities) for the impact of group size, number of assistants, firearms, and dogs. The latter two variables are binary variables indicating whether the hunter had use of a gun (as opposed to other weaponry) or at least one dog.

On the log scale, these combine additively:

$$\alpha_{ij} = a_{\text{site}[i]j} + \text{groupsize} + \text{assistants} + \text{firearms} + \text{dogs}$$

All of these effects are allowed to vary by site as random effects. These assumptions are visible in precise detail in the statistical code.

Random effects on skill. The life history parameters k , m , and b make use of partial pooling both within and between sites. We use a two-level pooling structure that allows each site to have its own covariance between k and m . Specifically, let ID be the unique ID number of each forager. Then each k_{ID} and m_{ID} are defined by:

$$\begin{aligned} k_{\text{ID}} &= \exp(W_1 + V_{\text{site}[\text{ID}],1} + v_{\text{ID},1}) \\ m_{\text{ID}} &= \exp(W_2 + V_{\text{site}[\text{ID}],2} + v_{\text{ID},2}) \end{aligned}$$

The parameters W_1 and W_2 are overall means, across all sites, and the parameters $V_{s,1}$ and $V_{s,2}$ are the offsets of these means for site s . This leaves $v_{\text{ID},1}$ and $v_{\text{ID},2}$ as the offsets for individual ID .

Starting at the lowest level, each pair of parameters $v_{\text{ID}} = \{v_{\text{ID},1}, v_{\text{ID},2}\}$ are allocated probability from a bivariate normal:

$$\begin{aligned} v_{\text{ID}} &\sim \text{MVNormal}((0, 0), \Sigma_{\text{site}[\text{ID}]}) \\ \Sigma_S &= \begin{pmatrix} \sigma_{S,1}^2 & \sigma_{S,1}\sigma_{S,2}\rho_S \\ \sigma_{S,1}\sigma_{S,2}\rho_S & \sigma_{S,2}^2 \end{pmatrix} \end{aligned}$$

Each site is characterized by 6 parameters: site-level offsets for k , m , and b , as well as standard deviations for hunter-level k and m and their correlation ρ . These 6 parameters are themselves pooled across sites. This produces the distinction between variance among sites and the variance of the individual hunters, as described in the text.

Age error model. We accommodate uncertainty in observed ages by defining:

$$\begin{aligned} \ell_{\text{ID},i} &= (\text{age}_i - v_{\text{ID}})/80 \\ v_{\text{ID}} &\sim \text{Normal}(l_{\text{ID}}, e_{\text{ID}}) \end{aligned}$$

where l_{ID} is the observed year of birth and e_{ID} is the assigned standard error. In the limit where $e_{\text{ID}} \rightarrow 0$, the age is purportedly known with certainty. Some sites reported ages using uniform intervals. We converted those to Gaussian representations with equivalent variances, so that the imputed ages were unconstrained. In most cases, when a researcher records a uniform age interval, they imply that the true age is closer to the middle of the interval and do not imply that it is impossible for the true age to be outside the interval. To allow this information into the model, we had to use something other than a uniform probability distribution. Gaussian is the most conservative choice, in that case. The irony of the effort put into dealing with age uncertainty is that it has no detectable impact on inference. Fixing all of the ages at their central value produces the same inferences that we reported in the main text. On the one hand, this is disappointing, because it really was not trivial to model the uncertainty, and it did not seem to matter much. On the other hand, it is important to do the right thing, even if it turns out not to matter.

4. SUPPLEMENTAL RESULTS

4.1. Production functions. The skill functions presented in Figure 2 of the main text are inputs into site-specific production functions. These functions have their own elasticities and therefore characteristic shapes. Here we present alternatives to Figure 2 that illustrate these production functions. There are three different perspectives on the production function. The first component is the probability of success at each age. The second component is the distribution of harvest sizes at each age. These two components multiply to produce the distribution of expected harvests at each age.

To make these components easier to understand, consider all four implied components of the production function for only the Aché sample (Figure S4). The orange functions in the upper-left are the same latent skill functions as in the main text. The red functions in the upper-right are the probabilities of success for each hunter, with the horizontal dashed line showing 50% success rate. The points are the raw data—the proportion of successes at each observed age, aggregated across individuals who were observed at those ages. The lower-left blue functions are the expected harvest sizes, conditional on a non-zero harvest. Again the points are raw data—the average harvest observed at each age. The violet functions in the lower-right are just the product of the red and blue functions, showing the expected production at each age.

Each component may be of interest in itself. In some sites, such as the Aché (16 ACH), the success of each hunt contributes more to variation than does the harvest size. The red curves in Figure S4 vary more both across age and across individuals than do the blue curves. As a result, more of the variation in the resulting expected production curves, seen in violet, arises from success rates rather than variation in harvest sizes. As seen in the subsequent plots (Figure S5, Figure S6, Figure S7) the Matsigenka sample (9 MTS) shows the same pattern—more variation in success rates than harvest sizes. This is possibly a result of the prey types available at the respective sites. Regardless of the explanation, decomposing the expected production in this way shows how skill can influence some aspects more than others.

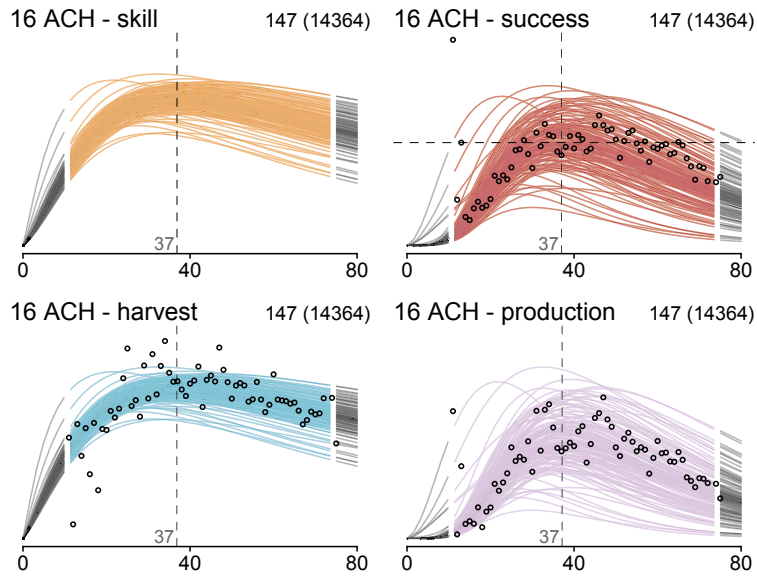


FIGURE S4. Components of the forager production functions for the Aché sample. See text for description.

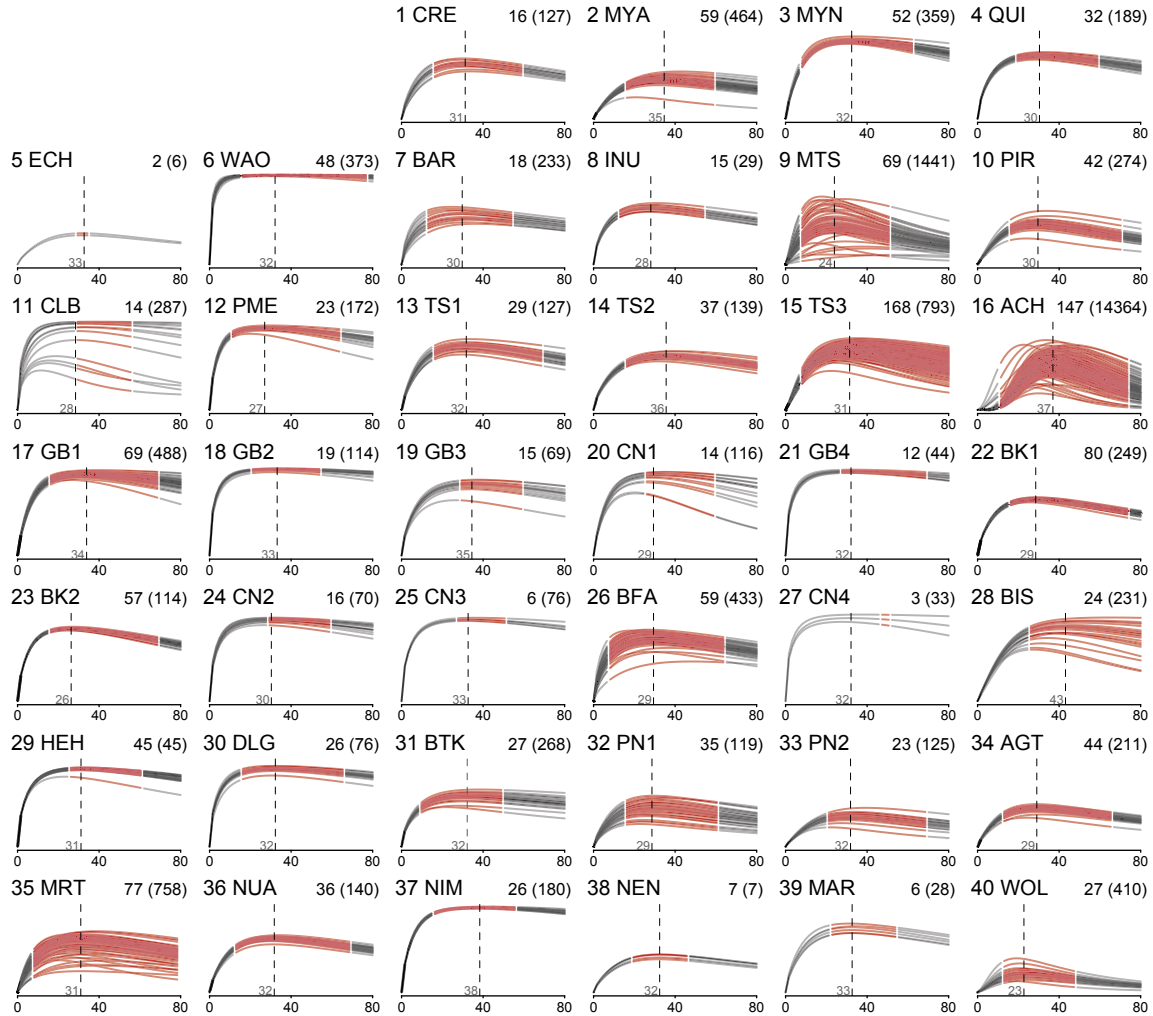


FIGURE S5. Posterior mean probabilities of hunting success across age. The axis ranges from 0 to 1, and is the probability of hunting success (a non-zero harvest). Model predictions are for a solitary excursion by a lone hunter without companions or assistants, and the predictions assume average hunt duration and the absence of dogs and firearms. Several sites, such as GB4 (21) and DLG (30), show essentially no variation in hunting success, since virtually all documented trips result in a non-zero harvest. Other sites, such as MRT (35) and WOL (40), show substantial failure rates and variation arising from it. nb: Variation in methods for documenting unsuccessful hunts imposes limitations on comparisons across sites – see the help files in the *cchunts* package for details.

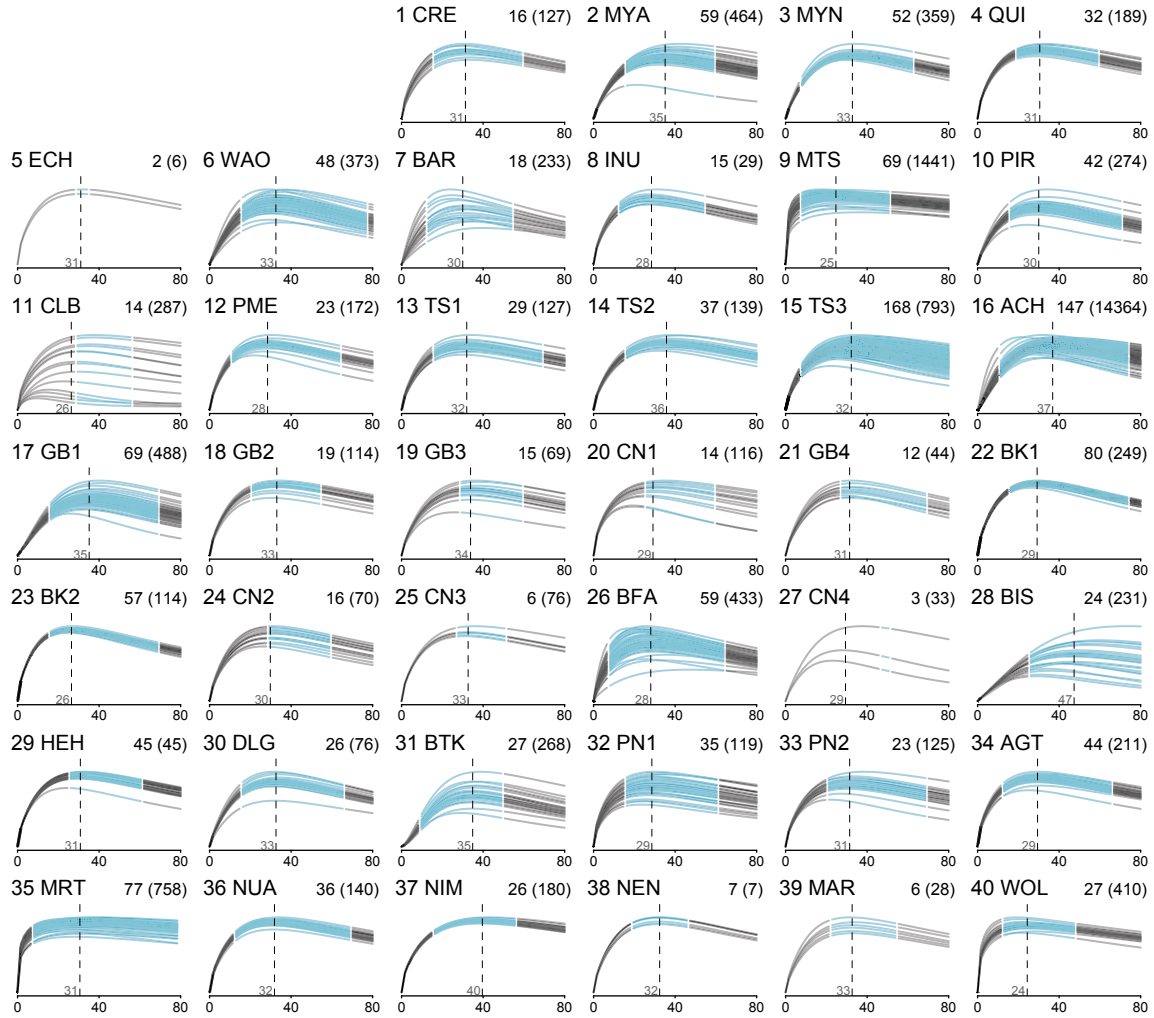


FIGURE S6. Posterior mean non-zero harvest size across age. Model predictions are for a solitary excursion by a lone hunter without companions or assistants, and the predictions assume average hunt duration and the absence of dogs and firearms. The vertical axis is proportion of maximum harvest at each site. While the units are not comparable across sites, therefore, hunter-level variation within sites is informative.

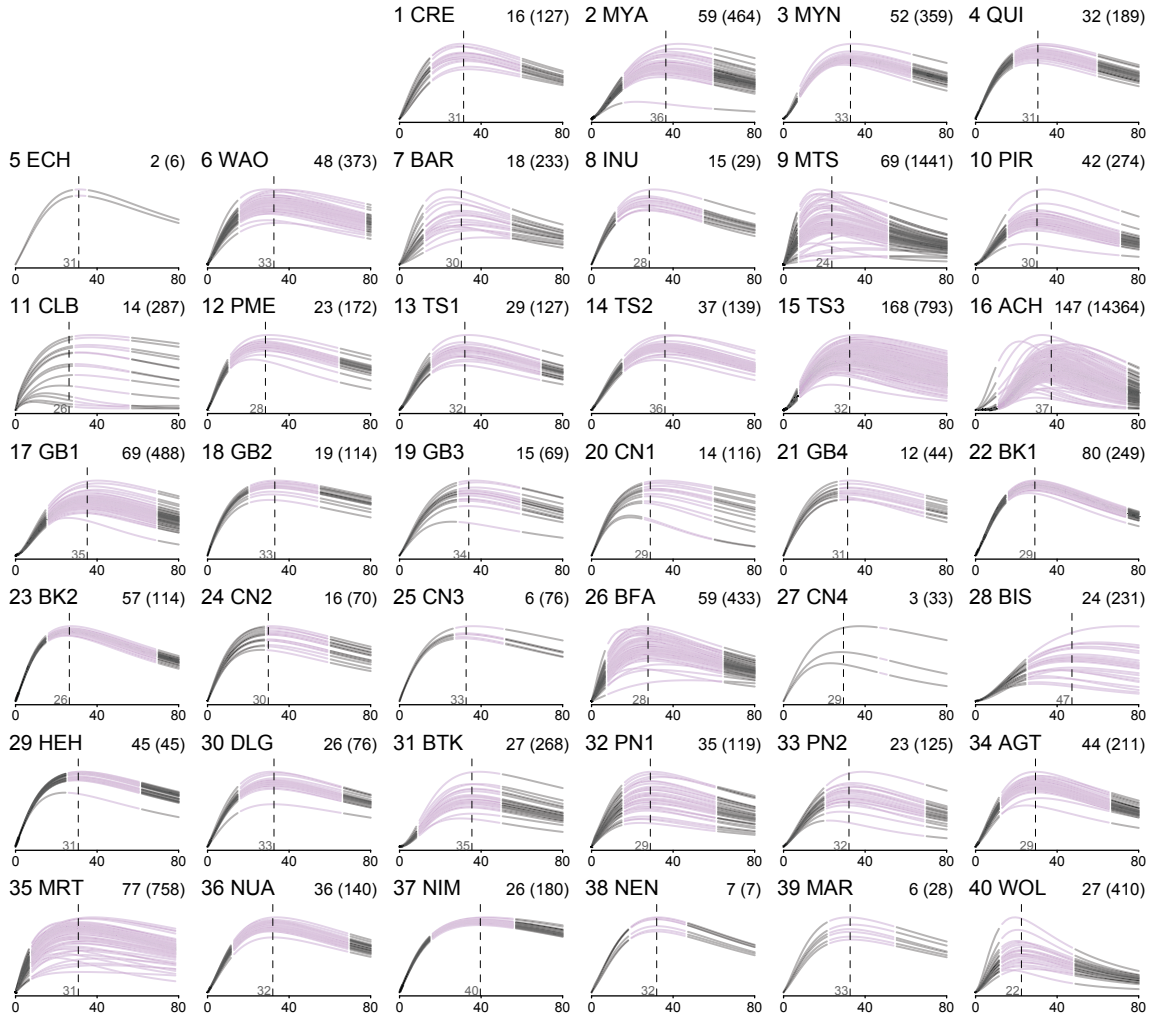


FIGURE S7. Expected production across age. These functions are the product of the success function and the expected harvest function. In considering relative expected energy contributions of individuals at different ages, these curves are perhaps the most relevant representations of the data.

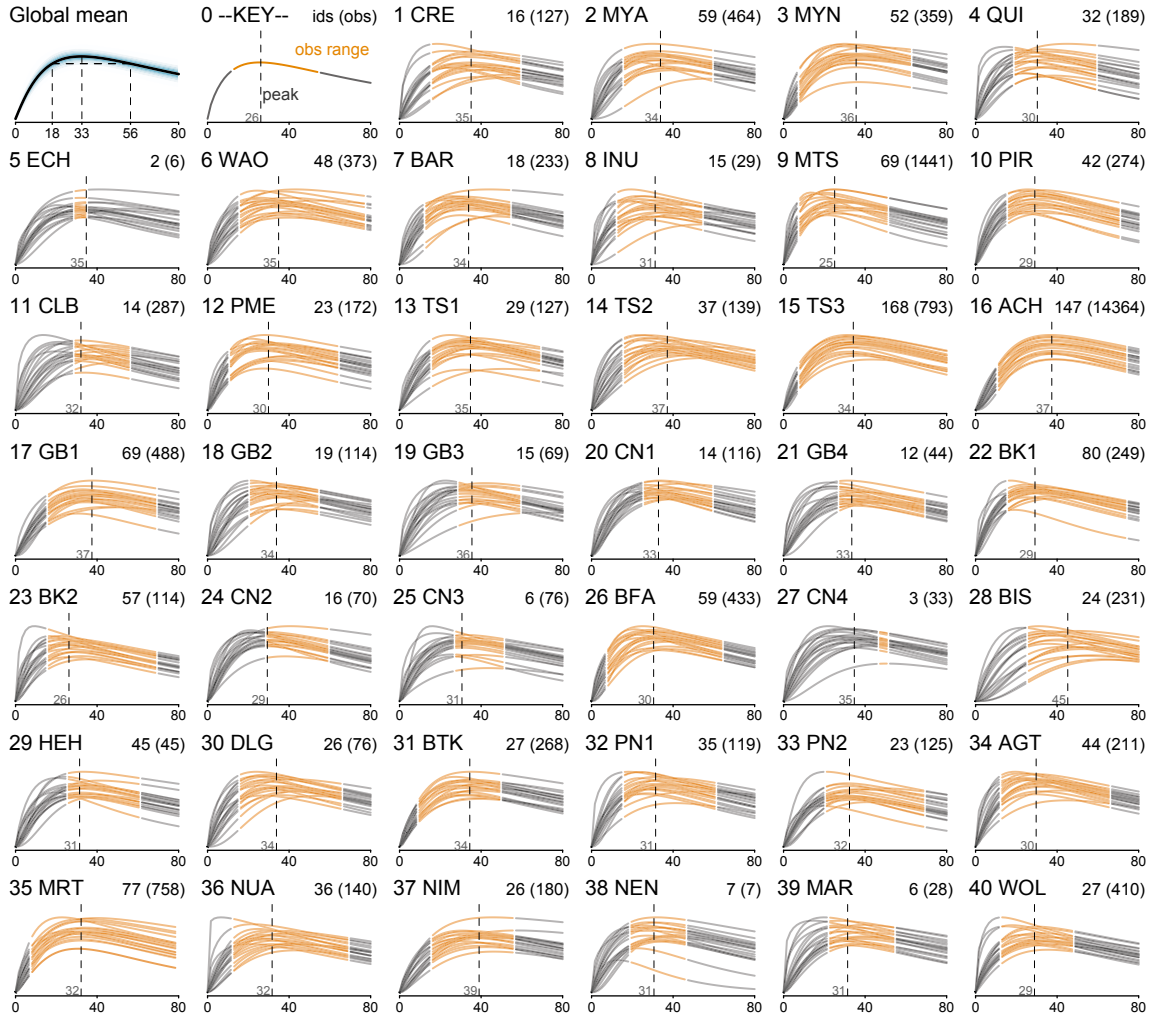


FIGURE S8. Simulated samples from the posterior distributions of skill functions in each site. This figure is similar to the skill grid in the main text, but it shows simulated hunters, not the posterior means for the observed hunters. This representation of the skill functions shows that, at many study sites, the model expects more empirical variation than can be seen in the previous skill figure (Figure 2).

Marginal posterior distributions. Many of the parameters in the production functions are interesting in themselves. For example, the marginal effects of group size and technology potentially inform debates about human subsistence strategies. In the figures that follow, we present marginal posterior distributions for all of these parameters, labeled informatively. In general, many of the parameters exhibit cross-cultural variation. For instance, in a small number of sites, the use of firearms or dogs increases the respective probabilities of a successful hunt or the amounts of biomass acquired. In most sites, however, the posterior distributions of these parameters are largely indistinguishable from the priors. (In some cases, this potentially reflects the lack of variation in the use of firearms or dogs within sites.) The elasticities of labor and skill inputs exhibit analogous cross-site variation.

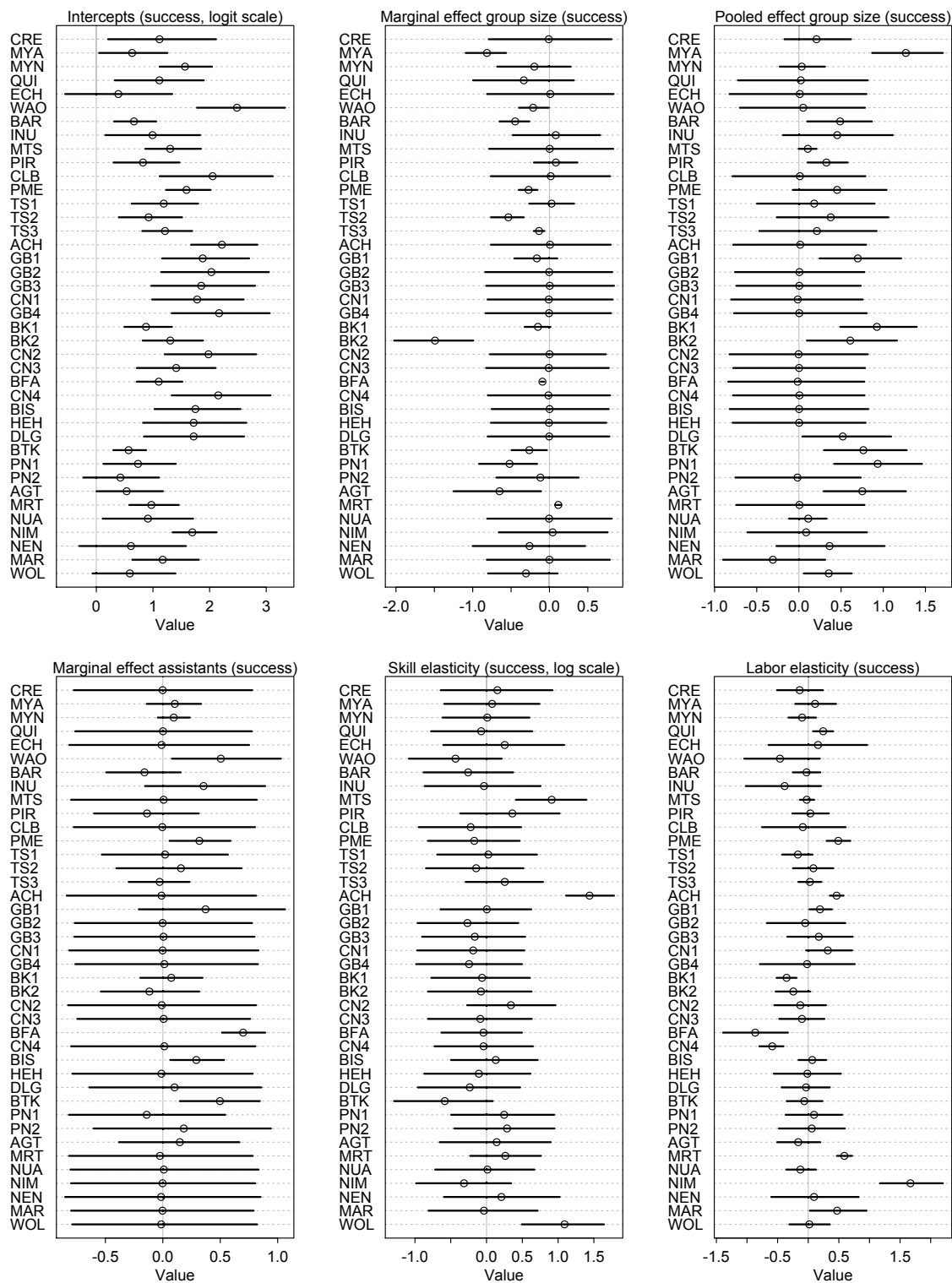


FIGURE S9. Marginal posterior distributions for production components (success). In the code, these parameters are named af [1], af [2], af [3], af [4], sef, and bhours [1], respectively. Note that marginal distributions centered on zero with standard deviation 0.5 correspond to the prior. In those cases, the society contained no information to inform the parameter.

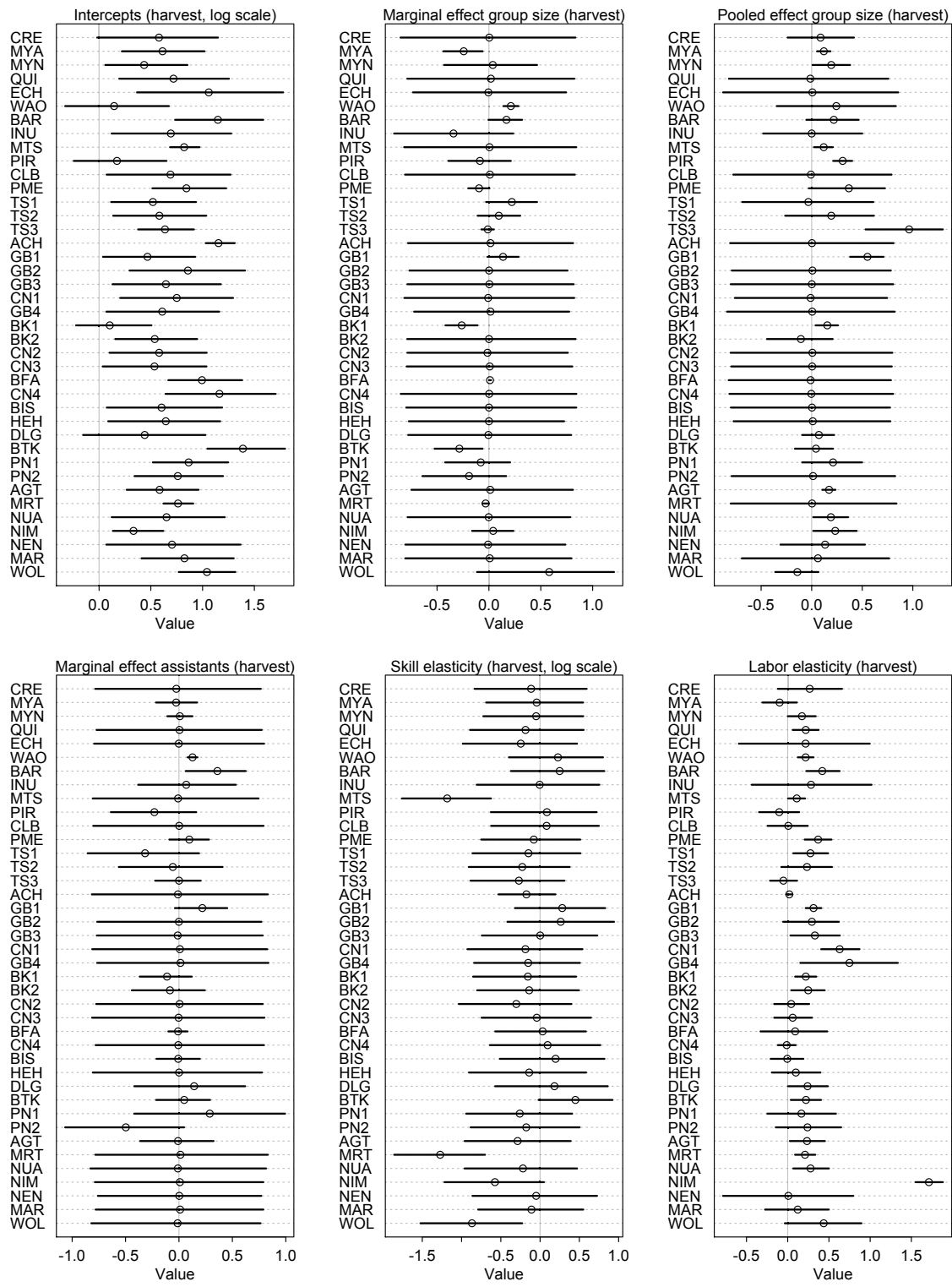


FIGURE S10. Marginal posterior distributions for production components (harvest). In the code, these parameters are named `ah[1]`, `ah[2]`, `ah[3]`, `ah[4]`, `seh`, and `bhours[2]`, respectively. Note that marginal distributions centered on zero with standard deviation 0.5 correspond to the prior. In those cases, the society contained no information to inform the parameter.

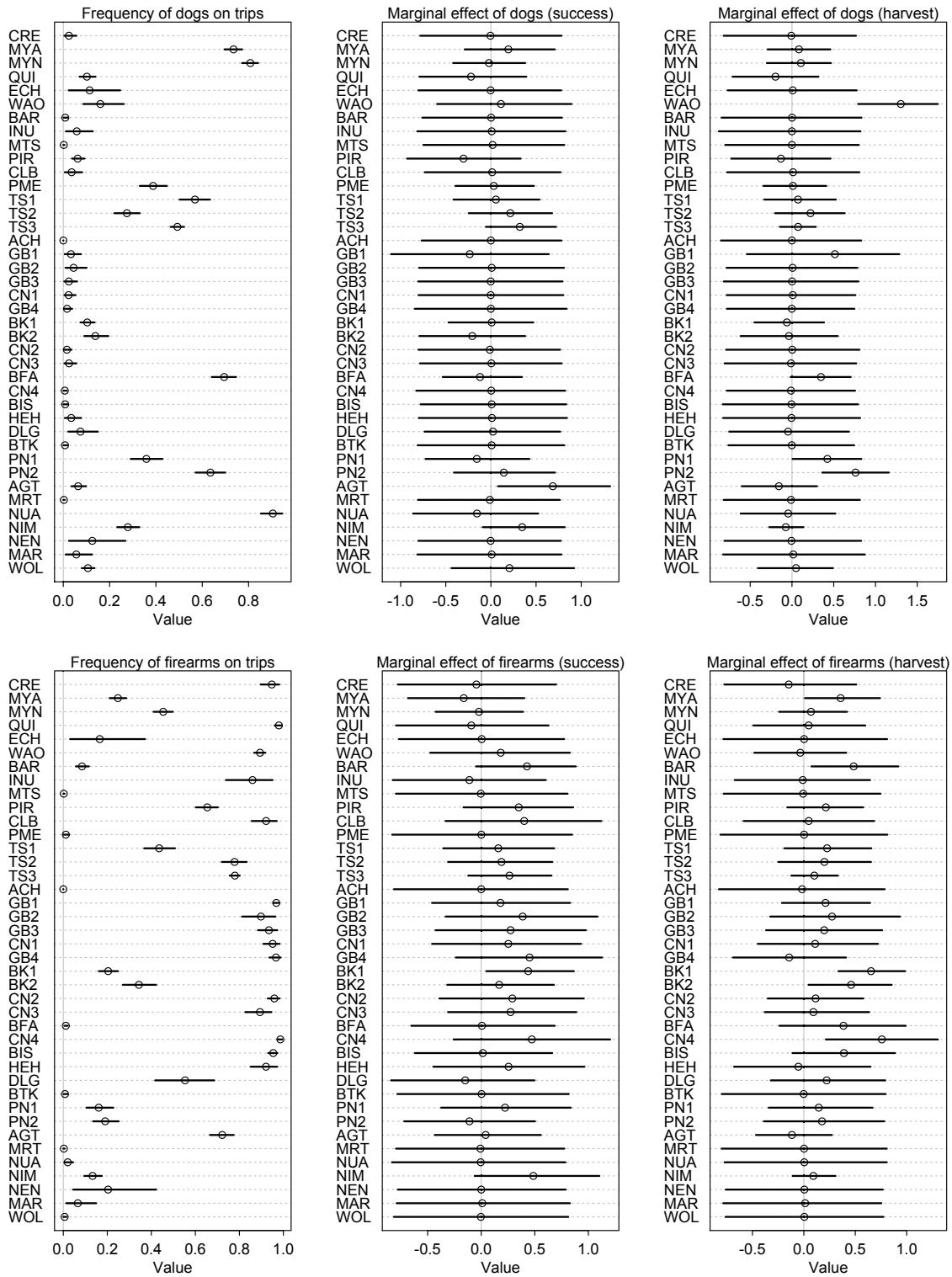


FIGURE S11. Marginal posterior distributions for dogs (top row) and firearms (bottom row). In the code, these parameters are named `dogs_mu`, `bdogs [1]`, `bdogs [2]`, `firearms_mu`, `bfirearms [1]`, and `bfirearms [2]`, respectively. Marginal distributions centered on zero with standard deviation 0.5 correspond to the prior. In those cases, the society contained no information to inform the parameter. Dogs are used at two sites, MTS and HEH, in which their use on trips was not documented. These missing data were averaged into the intercept and set to zero in this figure.

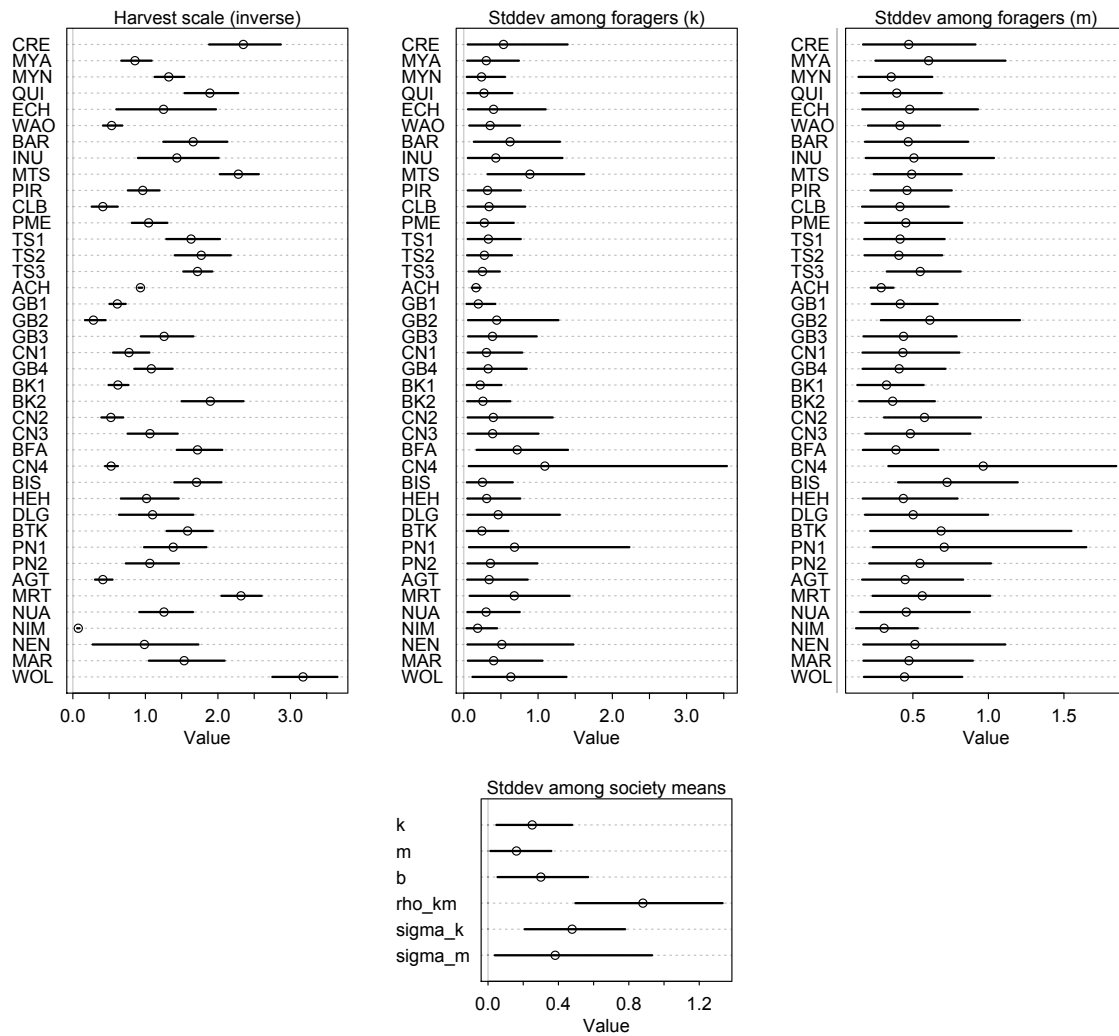


FIGURE S12. Marginal posterior distributions for dispersion and variance components. In the code, these parameters are named `hscale` (top-left), `sigmas_hunters[1]` (top-middle), `sigmas_hunters[2]` (top-right), and `sigma_societies` (bottom-middle). In the bottom-middle, k indicates the standard deviation among sites in mean skill growth, m the standard deviation among sites in mean skill decay, b the standard deviation in b across sites, ρ_{km} the standard deviation (on the latent scale) of the correlations between k and m across sites, and then σ_k and σ_m are standard deviations across sites of standard deviations among foragers in each site.

APPENDIX A

Detailed model code. The full code for the model is available in the accompanying R package and scripts (<https://osf.io/2kzb6/>). In this section, we explain the model block of the code, focusing on how the marginalization over missing values is accomplished.

The first portion of the model block defines local variables, used in calculations, and priors. The only unusual code here is the Jacobian adjustment applied to `lifehistmeans` [4] and `lifehistmeans` [5]. This adjustment allows us to apply the prior on the natural, instead of logarithmic, scale.

```
model{
  // temp variables
  real k[N_hunters];
  real m[N_hunters];
  real b[N_societies];
  vector[N_trips] lm_f;
  vector[N_trips] lm_h;
  real p;
  real mu;
  matrix[2,2] Sigma;
  vector[N_trips] trip_duration_merge;

  // priors
  // society-level life history means --- centered on global means
  // equivalent to:
  //vs~multi_normal(lifehistmeans,quad_form_diag(Rho_societies,sigma_societies));
  //see transformation in transformed parameters block
  to_vector(zs) ~ normal(0,1);

  lifehistmeans[1:2] ~ normal( 1, prior_scale ); // log k,m
  lifehistmeans[3] ~ normal( 1, prior_scale ); // log b
  lifehistmeans[6] ~ normal( 0, prior_scale ); // shifted logit rho_km
  // do prior for stddev k,m between [4,5] as normal on transformed scale
  // this allows us to define same prior for sigma_societies[1:2]
  exp(lifehistmeans[4]) ~ normal( 0 , prior_scale );
  exp(lifehistmeans[5]) ~ normal( 0 , prior_scale );
  // need Jacobian adjustments for these priors
  // log|d/dy exp y| = log|exp y| = y
  // see also section 33.2 of Stan reference manual
  target += lifehistmeans[4];
  target += lifehistmeans[5];

  sigma_societies[1:3] ~ normal( 0 , prior_scale2 );
  sigma_societies[4] ~ normal( 0.5 , prior_scale2 );
  sigma_societies[5:6] ~ normal( 0 , prior_scale2 );

  dogs_mu ~ beta(2,10); // weighted to stop mode switching in site 8
  guns_mu ~ beta(2,4);
```

```

ache_fix_rho ~ normal( 0, prior_scale );

afbar ~ normal(0, prior_scale );
ahbar ~ normal(0, prior_scale );
sigma_af ~ normal(0, prior_scale );
sigma_ah ~ normal(0, prior_scale );

for ( s in 1:N_societies ) {
  af[1,s] ~ normal(afbar,sigma_af);
  ah[1,s] ~ normal(ahbar,sigma_ah);
  for ( i in 2:4 ) {
    af[i,s] ~ normal(0,prior_scale);
    ah[i,s] ~ normal(0,prior_scale);
  }
  sef[s] ~ normal(0,prior_scale);
  seh[s] ~ normal(0,prior_scale);
  for ( i in 1:2 ) {
    b_hours[i,s] ~ normal(0,prior_scale);
    b_dogs[i,s] ~ normal(0,prior_scale);
    b_firearms[i,s] ~ normal(0,prior_scale);
    se_dogs[i,s] ~ normal(0,prior_scale);
    se_firearms[i,s] ~ normal(0,prior_scale);

    b_xday[s,i] ~ normal(0,prior_scale);
  }
} //s
hscale ~ normal( 1 , prior_scale );

// varying effects
// foragers --- these are zero-centered
// see translation to vh in transformed parameters block
to_vector(zh) ~ normal(0,1);

```

The next chunk of code handles imputation of missing ages and trip durations. For each missing age, there is a corresponding standard error of the age. This comprises a Gaussian prior for the error of each missing age. Combined with the prior for each missing age, this provides a way to average over the uncertainty. For each missing trip duration, similarly a parameter is used. Then a vector that merges observed and missing values is generated. The prior formed from each site's (standardized) trip durations constrains the imputed values.

```

// age imputation
for ( i in 1:N_hunters ) {
  if ( age_impute_idx[i] > 0 ) {
    if ( age_impute_table[i,1]==1 )
      age_err[age_impute_idx[i]] ~
        normal( 0 , age_impute_table[i,3] );
  }
}

```

```

}

// trip durations
for ( j in 1:N_societies ) trip_duration_mu[j] ~ normal(0,1);
trip_duration_sigma ~ exponential(1);
for ( i in 1:N_trips ) {
  if ( trip_hours[i]<0 ) {
    // missing
    trip_duration_merge[i] = trip_duration_imputed[hours_miss_idx[i]];
  } else {
    // observed
    trip_duration_merge[i] = log(trip_hours[i]);
  }
  // prior (when missing) or likelihood (when observed)
  trip_duration_merge[i] ~ normal( trip_duration_mu[trip_soc_id[i]] ,
                                  trip_duration_sigma[trip_soc_id[i]] );
}
}

```

The next short section computes hunter-specific and society-specific skill parameters. These are then reused in the likelihood calculations to follow.

```

// prep hunter effects so can re-use
for ( j in 1:N_hunters ) {
  k[j] = exp( lifehistmeans[1] + vs[forager_soc_id[j],1] + vh[j,1] );
  m[j] = exp( lifehistmeans[2] + vs[forager_soc_id[j],2] + vh[j,2] );
}
// prep b for each society, so only have to compute once
for ( s in 1:N_societies ) {
  b[s] = exp( lifehistmeans[3] + vs[s,3] ); // ensure positive with log link
}

```

The main loop of the model block comes next. This loop passes over trips, and then harvests within trips. The first chunk of code just prepares local variables. The `xdogsvec` and `xgunsvec` arrays exist to help us construct marginal log-probabilities when both dogs and firearms are unobserved (missing). The relevant code appears later down.

```

// likelihoods
lm_f = rep_vector(0,N_trips);
lm_h = lm_f;
// loop over trips and compute likelihoods
for ( i in 1:N_trips ) {
  real skillj;
  real sefx;
  real sehx;
  real ai;
  int hid;
  real avg_skill;
  vector[2] LLterms;
  vector[4] LL4terms;
  int xdogs;

```

```

int xguns;
int n_foragers_index;
int coopidx;
// prep binary tree for possible combinations of missing values
int xdogsvec[4];
int xgunsvec[4];
xdogsvec[1] = 1;
xdogsvec[2] = 1;
xdogsvec[3] = 0;
xdogsvec[4] = 0;
xgunsvec[1] = 1;
xgunsvec[2] = 0;
xgunsvec[3] = 1;
xgunsvec[4] = 0;

```

Next, when a trip has a pooled harvest, average skill for the entire group of hunters must be calculated. This is because we assume that production depends upon average skill in this case, where we cannot identify individual contributions. The `coopidx` variable tells us later which intercept parameter is needed, as the intercept in production differs depending upon pooled or individual harvests.

```

// compute avg skill (when needed)
avg_skill = 0;
if ( trip_pooled[i]==1 ) {
    // pooled harvest
    // compute average skill in foraging group
    for ( j in 1:n_foragers[i] ) {
        hid = forager_ids[i,j];
        if ( age_impute_idx[hid]==0 ) {
            // simple case, just fetch observed age
            ai = forager_age[i,j]; // from trip variables
        } else {
            // need some kind of imputation
            ai = forager_age[i,j] + age_err[age_impute_idx[hid]];
        }
        ai = ai/ref_age;
        skillj = exp(-m[hid]*ai)*pow(1-exp(-k[hid]*ai),b[trip_soc_id[i]]);
        avg_skill = avg_skill + skillj;
    }//j
    avg_skill = avg_skill/n_foragers[i] + 0.001;
    n_foragers_index = 1; // loop over just "one" forager
    coopidx = 3;
} else {
    // independent harvests
    n_foragers_index = n_foragers[i];
    coopidx = 2;
}

```

The big loop over individual foragers comes next. The loop begins by calculating individual forager skill, but only when harvest is not pooled. This code is structural the same as that used above to compute average skill, but it omits the averaging.

```
for ( j in 1:n_foragers_index ) {
  // if trip pooled, only one harvest (n_foragers_index==1)
  // otherwise loops over each harvest and predicts each

  if ( trip_pooled[i]==1 ) {
    skillj = avg_skill;
  } else {
    hid = forager_ids[i,j];
    if ( age_impute_idx[hid]==0 ) {
      // simple case, just fetch observed age
      ai = forager_age[i,j]; // from trip variables
    } else {
      // need some kind of imputation
      ai = forager_age[i,j] + age_err[age_impute_idx[hid]];
    }
    ai = ai/ref_age;
    skillj = exp(-m[hid]*ai)*pow(1-exp(-k[hid]*ai),b[trip_soc_id[i]]) + 0.001;
  }
}
```

Next we build “stem” expressions for each harvest log-probability. These stems contain all terms except those for dogs and firearms. Dogs and firearms must be added conditional on missingness. In that case, these stems are reused for each missingness state.

```
// failures production
lf_stem = exp( af[1,trip_soc_id[i]] +
               af[coopidx,trip_soc_id[i]]*(n_foragers[i]-1) +
               af[4,trip_soc_id[i]]*n_assistants[i,j] +
               b_xday[trip_soc_id[i],1]*trip_xday[i]
             ) *
           exp(trip_duration_merge[i])^b_hours[1,trip_soc_id[i]];
// harvests production
lh_stem = exp( ah[1,trip_soc_id[i]] +
               ah[coopidx,trip_soc_id[i]]*(n_foragers[i]-1) +
               ah[4,trip_soc_id[i]]*n_assistants[i,j] +
               b_xday[trip_soc_id[i],2]*trip_xday[i]
             ) *
           exp(trip_duration_merge[i])^b_hours[2,trip_soc_id[i]];
// failures skill elasticity
sef_stem = exp( sef[trip_soc_id[i]] );
// harvests skill elasticity
seh_stem = exp( seh[trip_soc_id[i]] );
```

Now we can do target updates. Different expressions need to be built, depending upon whether dogs, firearms, or both are missing. The simplest case is when both are observed. In this case, we just add the observed values to the stems, compute probability of failure, average harvest, and update. Note that -1 as the missingness indicator is chosen during

data initialization. Note that the code here considers the probability of a zero harvest, instead of the probability of a non-zero harvest. This is equivalent to the analytical model definition given earlier, even though the expression looks different.

```

if ( n_dogs[i,j] != -1 && n_firearms[i,j] != -1 ) {
  // dogs and guns both observed
  // use obs values to update base rates of dogs and guns
  n_dogs[i,j] ~ bernoulli(dogs_mu[trip_soc_id[i]]);
  n_firearms[i,j] ~ bernoulli(guns_mu[trip_soc_id[i]]);
  // build production functions with observed values
  lm_f[i] = lf_stem * exp( b_dogs[1,trip_soc_id[i]]*n_dogs[i,j] +
                          b_firearms[1,trip_soc_id[i]]*n_firearms[i,j] );
  lm_h[i] = lh_stem * exp( b_dogs[2,trip_soc_id[i]]*n_dogs[i,j] +
                          b_firearms[2,trip_soc_id[i]]*n_firearms[i,j] );
  sefx = sef_stem * exp( se_dogs[1,trip_soc_id[i]]*n_dogs[i,j] +
                        se_firearms[1,trip_soc_id[i]]*n_firearms[i,j] );
  seh_x = seh_stem * exp( se_dogs[2,trip_soc_id[i]]*n_dogs[i,j] +
                          se_firearms[2,trip_soc_id[i]]*n_firearms[i,j] );
  // compute failure probability and harvest mean
  p = 2*(1 - inv_logit( skillj^sefx * lm_f[i] ));
  mu = lm_h[i] * skillj^seh_x;
  if ( trip_harvests[ i , j ]==0 )
    // failure
    1 ~ bernoulli(p);
  else {
    // observed harvest
    0 ~ bernoulli(p);
    trip_harvests[ i , j ] ~ gamma( mu/hscale[trip_soc_id[i]] ,
                                   1/hscale[trip_soc_id[i]] );
  }
}
}

```

The next two cases are when either dogs or firearms are missing. In these cases, we need to marginalize over missingness states. This generates two log-probability terms in a mixture.

```

// now dogs missing, guns observed
if ( n_dogs[i,j] == -1 && n_firearms[i,j] != -1 ) {
  n_firearms[i,j] ~ bernoulli(guns_mu[trip_soc_id[i]]);
  // average over missingness
  // LLterms holds terms to mix over
  // LLterms[1] is where dogs == 0
  // LLterms[2] is where dogs == 1
  for ( nterm in 1:2 ) {
    xdogs = nterm-1;
    lm_f[i] = lf_stem * exp( b_dogs[1,trip_soc_id[i]]*xdogs +
                            b_firearms[1,trip_soc_id[i]]*n_firearms[i,j] );
    lm_h[i] = lh_stem * exp( b_dogs[2,trip_soc_id[i]]*xdogs +
                            b_firearms[2,trip_soc_id[i]]*n_firearms[i,j] );
    sefx = sef_stem * exp( se_dogs[1,trip_soc_id[i]]*xdogs +

```

```

                se_firearms[1,trip_soc_id[i]]*n_firearms[i,j] );
sehx = seh_stem * exp( se_dogs[2,trip_soc_id[i]]*xdogs +
                se_firearms[2,trip_soc_id[i]]*n_firearms[i,j] );
p = 2*(1 - inv_logit( skillj^sefx * lm_f[i] ));
mu = lm_h[i] * skillj^seh;
LLterms[nterm] = 0;
if ( trip_harvests[i,j]==0 ) {
    LLterms[nterm] = LLterms[nterm] + log(p);
} else {
    LLterms[nterm] = LLterms[nterm] + log1m(p);
    LLterms[nterm] = LLterms[nterm] +
        gamma_lpdf( trip_harvests[i,j] |
            mu/hscale[trip_soc_id[i]] , 1/hscale[trip_soc_id[i]] );
}
} // nterm
// do the mixture
// Pr(dogs==1)*Pr(harvest|dogs==1) + Pr(dogs==0)Pr(harvest|dogs==0)
// log_mix here is for numerical stability
target += log_mix( dogs_mu[trip_soc_id[i]] , LLterms[2] , LLterms[1] );
}
// now dogs observed but firearms missing
if ( n_dogs[i,j] != -1 && n_firearms[i,j] == -1 ) {
    n_dogs[i,j] ~ bernoulli(dogs_mu[trip_soc_id[i]]);
    // average over missingness
    // similar to above, but LLterms now average over missing guns
    for ( nterm in 1:2 ) {
        xguns = nterm-1;
        lm_f[i] = lf_stem * exp( b_dogs[1,trip_soc_id[i]]*n_dogs[i,j] +
            b_firearms[1,trip_soc_id[i]]*xguns );
        lm_h[i] = lh_stem * exp( b_dogs[2,trip_soc_id[i]]*n_dogs[i,j] +
            b_firearms[2,trip_soc_id[i]]*xguns );
        sefx = sef_stem * exp( se_dogs[1,trip_soc_id[i]]*n_dogs[i,j] +
            se_firearms[1,trip_soc_id[i]]*xguns );
        seh; = seh_stem * exp( se_dogs[2,trip_soc_id[i]]*n_dogs[i,j] +
            se_firearms[2,trip_soc_id[i]]*xguns );
        p = 2*(1 - inv_logit( skillj^sefx * lm_f[i] ));
        mu = lm_h[i] * skillj^seh;
        LLterms[nterm] = 0;
        if ( trip_harvests[i,j]==0 ) {
            LLterms[nterm] = LLterms[nterm] + log(p);
        } else {
            LLterms[nterm] = LLterms[nterm] + log1m(p);
            LLterms[nterm] = LLterms[nterm] +
                gamma_lpdf( trip_harvests[i,j] |
                    mu/hscale[trip_soc_id[i]] , 1/hscale[trip_soc_id[i]] );
        }
    }
}

```

```

    }//nterm
    // do the mixture
    target += log_mix( guns_mu[trip_soc_id[i]] , LLterms[2] , LLterms[1] );
}

```

Finally, both dogs and firearms could be missing. In this case, we need a mixture over four possible states.

```

// finally, both dogs and guns missing
if ( n_dogs[i,j] == -1 && n_firearms[i,j] == -1 ) {
    // L4terms holds combinations of possible values of dogs and guns
    //      dogs guns {probability at site k}
    // [1] 1      1      dogs_mu[j] * guns_mu[k]
    // [2] 1      0      dogs_mu[j] * ( 1 - guns_mu[k] )
    // [3] 0      1      ( 1 - dogs_mu[j] ) * guns_mu[k]
    // [4] 0      0      ( 1 - dogs_mu[j] ) * ( 1 - guns_mu[k] )
    for ( nterm in 1:4 ) {
        xdogs = xdogsvec[nterm];
        xguns = xgunsvec[nterm];
        lm_f[i] = lf_stem * exp( b_dogs[1,trip_soc_id[i]]*xdogs +
                                b_firearms[1,trip_soc_id[i]]*xguns );
        lm_h[i] = lh_stem * exp( b_dogs[2,trip_soc_id[i]]*xdogs +
                                b_firearms[2,trip_soc_id[i]]*xguns );
        sefx = sef_stem * exp( se_dogs[1,trip_soc_id[i]]*xdogs +
                               se_firearms[1,trip_soc_id[i]]*xguns );
        seh_x = seh_stem * exp( se_dogs[2,trip_soc_id[i]]*xdogs +
                                se_firearms[2,trip_soc_id[i]]*xguns );
        p = 2*(1 - inv_logit( skillj^sefx * lm_f[i] ));
        mu = lm_h[i] * skillj^seh_x;
        LL4terms[nterm] = 0;
        if ( trip_harvests[i,j]==0 ) {
            LL4terms[nterm] = LL4terms[nterm] + log(p);
        } else {
            LL4terms[nterm] = LL4terms[nterm] + log1m(p);
            LL4terms[nterm] = LL4terms[nterm] +
                gamma_lpdf( trip_harvests[i,j] |
                            mu/hscale[trip_soc_id[i]] ,
                            1/hscale[trip_soc_id[i]] );
        }
        // add leading factor for probability of combination of missingness
        if ( xdogs==1 )
            LL4terms[nterm] = LL4terms[nterm] + log(dogs_mu[trip_soc_id[i]]);
        else
            LL4terms[nterm] = LL4terms[nterm] + log1m(dogs_mu[trip_soc_id[i]]);
        if ( xguns==1 )
            LL4terms[nterm] = LL4terms[nterm] + log(guns_mu[trip_soc_id[i]]);
        else
            LL4terms[nterm] = LL4terms[nterm] + log1m(guns_mu[trip_soc_id[i]]);
    }
}

```

```
    }//nterm
    // do the mixture
    target += log_sum_exp( LL4terms );
}
```

In the end, the model block just loops over foragers j and trips i until all trips have been processed.

```
    } //j over foragers
  } //i over trips
} //model
```