Foraging complexity and the evolution of childhood

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Teaser: Different foraging proficiency schedules for hard and easy foods suggest childhood coevolved with our complex foraging niche.

Abstract

Our species' long childhood is hypothesized to have evolved as a period for learning complex foraging skills. Researchers studying the development of foraging proficiency have focused on assessing this hypothesis, yet studies present inconsistent conclusions regarding the connection between foraging skill development and niche complexity. In this paper, we leverage published records of child and adolescent foragers from 28 societies to (1) quantify how skill-intensive different resources are and (2) assess whether childrens proficiency increases more slowly for more skill-intensive resources. We find that foraging returns increase slowly for more skill-intensive, difficult-to-extract resources (tubers and game), consistent with peak productivity attained later in adulthood. Foraging returns for easier-to-extract resources (fruit and fish/shellfish) increase rapidly during childhood, with adult levels of productivity reached by adolescence. Our findings support the view that long childhoods evolved as an extended period for learning to extract complex resources characteristic of the human foraging niche.

1 Introduction

Human childhoods are characterized by slow physical growth, extended dependence on parents and alloparents for provisioning, and increased investment in brain growth compared to nonhuman primates (1, 2). Multiple hypotheses derived from life history theory have aimed to explain how this constellation of features was selected to maximize lifetime fitness. Following Charnov's dimensionless numbers model (3), which finds regular patterns of covariation between total life span and age at first birth across species, some researchers have suggested that human childhood is a by-product of our long total lifespans (4). Alternatively, the Embodied Capital Theory (ECT) posits that human childhood evolved alongside our increased reliance on the complex foraging niche typical for our species (5). Difficult-to-acquire, energy-packed resources compose a large proportion of human diets. The exploitation of these resources require high levels of coordination, strength, knowledge and/or other cognitive skills. ECT hypothesizes that these traits-collectively termed "embodied capital"—are acquired during a protracted development. Under the assumptions of ECT, the costs associated with low productivity in early life and high rates of parental provisioning are offset by high lifetime productivity.

Several lines of empirical research using data from contemporary subsistence societies have aimed to test one of ECT's key predictions: that early life productivity should be low, with children's foraging proficiency increasing with age alongside gains in knowledge, skill, and experience (6–12). Support for this prediction has been mixed. When considering overall caloric production, Kaplan et al. (5) found that among Hiwi, Ache, and Hadza, individuals only produce more than they consume in early to mid-adulthood. Yet, other studies have found that young children's foraging returns can exceed their daily caloric needs. One six-year-old Hadza forager reportedly produced 7000 kilocalories a day when collecting figs (9).Similarly, Savannah Pumé children aged 11-14 can return 7500 calories a day in fruit (13). Furthermore, Malagasy Mikea children can produce a substantial portion of their consumption, averaging 656 net kilocalories an hour when harvesting ovy tubers (14). In conflict with the expectation that more foraging experience should lead to greater foraging proficiency during childhood, time spent in boarding school (and thus away from foraging activities) did not negatively affect Hadza collection rates in an experimental task (8).

These mixed findings may be resolved by considering another of ECT's key predictions: that the difficulty of acquisition explains the age profile of production (5), with more difficult-to-acquire resources requiring longer investment in skill development. Yet few studies have explicitly tested this prediction. Moreover, these have overwhelmingly focused on hunting, showing that large game hunting returns peak in mid-adulthood, several years after peak strength (12). This suggests that accumulated knowledge and experience related to understanding the natural environment (e.g. tracking, animal behaviour), physical skill (e.g. aim, strength) and tool manufacturing (e.g. bows, poison) are fundamental to successful hunting (10, 15). Still, children can achieve high returns by specializing in hunting matched to their size, skill, and strength. For example, Australian Martu children hunt goanna lizards in rocky outcrops, where they can maximize their returns given their height, stride length, and walking speed (7). Beyond hunting, young Mikea foragers preferentially target

young ovy, whose tubers are small but shallow, and exploit patches more thoroughly than adults, in accordance with their smaller size and lesser strength. While Bird and Bird (6) found no effect of cognitive complexity on the age-specific production curves for various marine resources among the Australian Meriam, other authors qualitatively report that the timing at which foraging skills develop increases with task complexity. Both Hadza and Savanna Pumé children are described as becoming efficient in easier tasks, such as fruit collecting, before they effectively harvest tubers or hunt, which are more complex (13, 16, 17). Because much of this research is qualitative, from single populations, and single resources, it is currently hard to assess whether observed variation in children's foraging returns reflects cross-cultural differences in skill development, local foraging ecology, or study methodology.

Comparative analyses can help characterize how and why the life history of foraging varies across cultures. Data presented in Kaplan et al. (5) suggests that while Ache, Hiwi and Hadza overall production increases with age, these trajectories are not uniform. In their studies of child foragers, Hawkes, Blurton Jones, and colleagues argued that factors such as water availability, risk of getting lost, risk of predation, and availability of resources explained why Hadza children begin foraging so early whereas San children begin much later (16, 18–22). In the largest comparative study of hunting to-date, Koster et al. (12) found that in 40 societies, overall skill peaked in adulthood, though there was considerable inter- and intra-societal variation in age-specific returns. Because only 7% of observations in this study came from individuals younger than 20, and a mere 0.2% from children younger than 10, the ontogeny of hunting skill in early life remains poorly characterized. Further, we do not yet know how hunting skill development compares to that of other resources exploited by humans.

Indeed, although the human foraging niche may be generally more complex than that of other primates, the foods that foragers pursue are not uniformly difficult to collect. Complexity can vary along two major axes of strength and knowledge (13), and each task within the human ecological niche requires a specific set of competencies along these axes, which are acquired at variable timelines (23, 24). For example, to successfully collect fruit, a forager must have enough coordination to collect them and, in some cases, the agility and strength to climb tall trees (9), but also know where to find plants carrying ripe fruit. Collecting tubers requires yet more skill: underground storage organs (USOs) are usually embedded deep in hard substrate. A forager must have the knowledge to locate the tuber, the strength to excavate it, and the skill to make and use appropriate tools (8). Food items embedded in hard substratum, mobile prey, or food products requiring specialized technologies for the most part require high levels of both strength and knowledge for successful extraction (25, 26). To investigate whether complex resources are associated with slower learning curves, and thus the evolution of longer childhoods, research is needed to quantify variation in the ontogeny of foraging productivity according to resource type complexity.

In the present study, we aimed to test ECT's prediction that the development of foraging proficiency is slower for more complex resources. We operationalize foraging proficiency as age-specific foraging returns. We compiled a data set from published sources on foraging returns, totalling observations for 714 children and adolescents from 28 societies (see figure 1). We consider four resources differing in complexity: fruit and marine resources, which require less strength and individual knowledge to collect, and game and USOs (i.e. tubers), which require specialized tools, knowledge, and strength. Using these data, we model resource-specific foraging returns as a function of individual skill, a dimensionless latent variable that varies with age and sex (figure 2). Skill summarizes all traits relevant to foraging, thus conceptually referring to a combination of cognitive and physical "embodied capital" such as knowledge and strength. This allows us to 1) assess whether children's proficiency increases more slowly for more complex resources and to 2) quantify the skill-intensity for resources varying in complexity, i.e. how much underlying skill is needed to successfully forage a certain resource. Our approach can thus help resolve outstanding ambiguity regarding children's foraging proficiency and skill ontogeny.

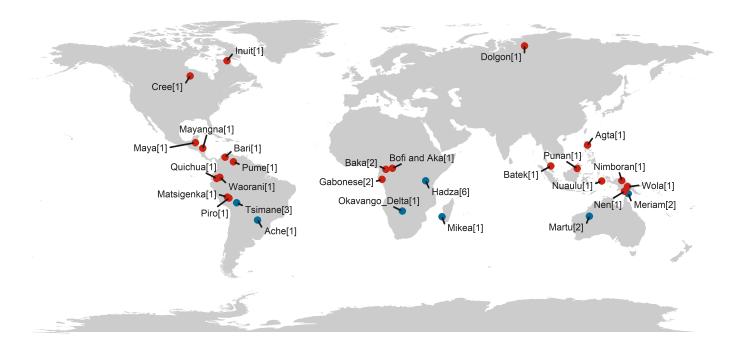


Figure 1: **Populations.** World map indicating the locations of study populations included in the present study. The number of data sets for each populations are in square brackets. The most represented community, the Hadza, appear in 6 studies. Populations for which data sets were sourced from the literature are in blue. Populations for which data sets were sourced from Koster et al. (12) are in red.

2 Results

Age specific foraging returns. We found that, in general, foraging returns increase steadily throughout childhood and adolescence (figure 3a). By age 5, the average child has achieved about 20% of the productivity they will have achieved by age 20. This value increases to approximately 50% by age 10. The largest increase in foraging returns happens between 10 and 20 years of age.

Resource-specific development of foraging proficiency. The general pattern of proficiency increase varies across resource type (figure 3b): game and USOs exhibit accelerating returns, and fruit shows diminishing returns with age. Fish/shellfish exhibit an intermediate pattern. The greatest gains happen early in life for fruit, while gains in game and tubers continue into adolescence and likely peak only in later adulthood (figure 3c).

Skill intensity of resources. Figure 4 shows the posterior distribution for η , which is the parameter indicating skill intensity. η provides an indication of how foraging returns relate to skill, that is, whether increasing skill results in diminishing or accelerating foraging returns. η is the elasticity of skill and controls its effect on returns, represented by the arrow that connects Skill to Returns in figure 2. The four types of resources analyzed here differ in how skill-intensive they are, with game and tubers requiring more skill, fruit requiring less skill, and fish/shellfish in between (figure 4, left). The maximum difference in skill intensity is between USOs and fruit: the right panel in figure 4 shows that values of η relative to USOs are greater than those of fruit in about 90% of the posterior samples, indicating with substantial confidence that extracting tubers is more skill-intensive than collecting fruit. Game shows a similar pattern, with 86% of posterior samples for η relative to game greater than η values for fruits. Note that there is considerable heterogeneity across studies within each category. In particular, 'game' resources span a wide array of foraging skill and return curves,

each implying distinct life history trajectories (figure 3b). Thus, we should be cautious in making strong claims about categorical differences between hunting and other types of foraging.

Sex differences. There are minimal gender differences in skill development, with skill appearing to increase slightly faster in early ages for males than for females (figure S2). Similarly, there were no strong resource-specific sex differences, apart from females showing more variation in the age-specific returns between resources, whereas males show similar patterns across resources (see figure S3 and S4). However, these findings should not be interpreted as evidence for no sex differences, given how uncertain our prediction intervals are. Instead, it may be that our data is of insufficient resolution to detect differences between male and female foragers—which are most likely smaller than differences between resource types.

3 Discussion

Childhood has been theorized to have evolved as an extended learning period for collecting complex resources. Yet, no studies to-date have explicitly modeled the association between resource complexity and children's productivity in a cross-cultural sample. Here, we empirically estimate how skill intensive different resources are and investigate age-specific returns for these resources. By testing predictions from the Embodied Capital Theory, our findings have important implications for current debates regarding the evolution of childhood, and point to several avenues for future research.

We found that by ten years of age, children in our sample achieved half of the productivity of 20-year-olds. Echoing research among Hadza, Mardu, Maya, BaYaka, Aka, and communities in the Okavango Delta (7, 9, 27–30), these findings suggest that children can be independent foragers well before maturity, given the right socioecological conditions. Still, in general, foraging returns continue to increase at least until adulthood for all resources, suggesting that individuals acquire embodied capital throughout the entire pre-reproductive stage (5).

The complexity of our species' foraging niche is reflected in our findings. For most data sets included in the present analysis, η is estimated to be greater than 1 (see figure S6). This means that gains in foraging proficiency are dependent upon considerable gains in skill. Within taxa, niche complexity and life history traits such as length of development are correlated (25). The foraging niches of other primates include a larger proportion of resources that are expected to have lower skill intensity. For example, chimpanzee are known to hunt small prey and eat nuts or tubers, but they are overall ripe-fruit specialists (31). While baboons are considered generalists, they still rely on fruit and leaves for most of their diets (32). Thus, while these species do collect complex resources, they do not specialize in them. Humans, on the other hand, preferentially target complex resources (5, 33), and this complexity is reflected across almost all sampled societies in the present analysis.

Our model estimated that tubers and game are more skill intensive resources to collect, compared to fish/shellfish and fruit. Children's productivity varied considerably by resource type: returns for more skill-intensive resources peaked later than those for less skill-intensive resources. In other words, children reached adult levels of proficiency for fruit early in life, whereas proficiency for tubers and game continued to increase into adulthood. These differences were better explained by variation in skill-intensity (figure 4) than by the timing of skill acquisition (figure S5). "Skill", a key parameter in our analysis, is an abstraction that captures differences in foraging ability with age and between individuals, but it has a non-linear relationship to actual returns. Some resources, like fruit, exhibit diminishing returns to skill, implying that even the best fruit collector will not produce much more than average, possibly due to constraints such as carrying weight and distance between patches. In contrast, resources such as game exhibit accelerating returns, with relatively low expected returns at low and moderate levels of skill. In sum, our findings suggest that children's foraging proficiency is dependent on skill acquisition, with foraging proficiency for more complex resources requiring longer periods of skill development. These findings support the view that complex resources require a longer investment in learning, and thus, in line with ECT, may have promoted the evolution of childhood.

Our novel analysis allowed us to explicitly estimate skill. This measure likely reflects various individual traits that contribute to skill, including somatic and cognitive traits such as coordination,

endurance, agility, wayfinding, traditional ecological knowledge, problem solving and planning, to name only a few. An implication of ECT is that cognitive more than somatic traits are the limiting factor when foraging complex resources. In their research with Mardu and Meriam, Bliege Bird and Bird (6, 7) find that foraging performances are largely constraint by size. However, knowledge was not explicitly measured in their analyses. Considering that size, strength, and knowledge tend to develop together (23), it remains unclear whether their findings are at odds with, or complementary to, predictions derived from ECT. Similarly, and because few studies consistently report individual measures for size, strength, and knowledge, our measure for skill does not differentiate between different types of embodied capital. Instead, our findings suggest that in order to target complex resources, children require high levels of skill, which they acquire through an unknown combination of learning and growing. Nonetheless, the difference observed across resource complexity is consistent with the coevolution of early life history traits and our especially complex foraging niche. We look forward to future studies, which collect data on various aspects of embodied capital in order to tease apart their relative contribution to foraging skill across resource types.

This paper has several limitations related to the comparability of the data we used. There were considerable differences in how data were collected, whether returns were presented as quantities or rates, and whether data were for individuals or for age classes. This could compromise some of our inferences, as data collected with different methods could be biased towards or against non-zero returns. However, figure S7 indicates that our model is able to predict the proportion of non-zero returns with sufficient accuracy. Further, across data sets, trip level traits such as travel time and group size are differently accounted for. Unfortunately, we could not address this problem statistically, as the relevant details of the data collection procedures (i.e., treatment of zero return trips) were highly variable and often not reported. Additionally, these study-specific parameters are highly correlated with resource type: with few exceptions, each study reports returns for only a single category of resource. This makes it difficult to confidently assess whether variation is due to true differences between resources or to unmeasured differences between populations or in study methodology. This issue is especially apparent for shellfish, where the large majority of the available data comes from one single research group (6, 23, 34). Our combined data set also contains few repeated measures, which made it impossible to model individual variation in the ontogeny of foraging skill.

Our analysis also highlights limitations inherent to the available literature. Over-reliance on cross-sectional data leaves us vulnerable to misinterpreting cohort effects for age effects. Hence, longitudinal data sets of foraging returns that span several decades are needed (12). Further, knowledge, strength, size, and cognition all likely vary independently and differently contribute to resourcespecific skill. For example, Bird and Bird (7) found that Mardu children's walking speed is a good predictor of goanna lizard hunting success. For Tsimane hunters, the ecological knowledge needed to directly encounter animals had the biggest effect on individual hunting returns (35). Moreover, available data mostly focus on either children or adult foraging returns, making it difficult to develop continuous measures of skill development through the whole lifespan. To better understand the resource-specific development of skill beyond the general estimation presented in the present paper, future studies should integrate ethnographic understanding of each population's subsistence strategies, as well as individual-level measures of traits which may contribute to skill. Future studies should also consider heterogeneity in complexity within resource types across regions, seasons, and based on available extractive technologies. For example, while we considered hunting more generally, prey types vary by size, seasonal abundance, distribution, and the availability of efficient hunting technologies. Future studies should consider this variation when reporting on hunting returns. Finally, as Kramer (36) points out, adults and children pool their energy budgets through labour specialization and food sharing (37). While much research into human social organization has focused on the gendered division of labour, the coordination of work between children and adults may be equally important (38-41). Social learning and social foraging can also scaffold children's participation in foraging, even if they haven't yet acquired all underlying skills. For example, children can help identify tuber vines, even if they are not strong enough to collect them themselves. Inversely, with the help of more experienced foragers, children can harvest ripe fruits even when they don't know where to find them. To fully understand variation in age-specific foraging returns, future studies should move beyond measuring only individual returns and towards accounting for how children coordinate their labour with other household and community members.

To conclude, we found that children's age-specific foraging proficiency varies with resource-specific skill intensity. In support of ECT, this finding is consistent with the view that long child-hoods evolved as an extended period to learn to exploit the most complex resources in our foraging niches. Our analysis also suggests that unmeasured factors related to individuals and their social and ecological settings may also contribute to variation in foraging returns across resource types and cultures (27). Such factors, including individual motivation, social networks, social foraging, and resource availability for the most part remain under reported in the existing literature, despite their importance to understanding how long human childhoods generally, and children's participation in foraging specifically, co-evolved alongside our species' propensity for cooperation and cumulative culture. In order to fully understand the developmental trajectories of children's foraging returns, and their articulation with ecological and social contexts in the present and throughout our evolutionary history, we call on researchers to consider these variables in their future research.

4 Materials and Methods

Study selection. We followed a systematic two-step protocol for locating relevant published articles, as summarized in figure S1. First, we queried major search engines (Google Scholar, JStor, PsycNet, Science Direct, Springer, Wiley) with the keywords 'children'&'foraging'&'returns' on September 26, 2019. This search produced 360 unique papers. After reading abstracts for eligibility, 133 papers were read in full. 35 papers were identified as potentially including data on foraging returns from children, according to two independent coders. Second, we endeavored to locate additional relevant texts. We searched through the bibliographies of papers with relevant data identified during our initial search. We also looked through the publication list of the first authors of these papers. We repeated these steps for all newly-identified relevant papers. This search method yielded a total of 40 papers potentially containing data on children foraging returns.

We screened these studies against our inclusion criteria: (1) the paper reported original data on foraging returns from children and/or adolescents. Time allocation studies, secondary analyses, and reviews were not eligible for inclusion; (2) the paper contained individual-level data or group-level means and variances; (3) the paper reported data for multiple pre-reproductive individuals or age groups. Reports of returns for single pre-reproductive age groups were excluded; (4) the data was presented as continuous quantities, e.g. kcal/day, g/h. Ranges were not eligible. For example, Kawabe (42) reports number of animals (1 to 5 or more than 5) by species killed across childhood. This study was not included in the present analysis. Finally, (5) we included data for individuals and age groups 20 years and under. If the age range of an age group crossed 20 years, this age group was excluded.

To identify studies that used the same data in separate analyses published in different papers, we compiled metadata for each paper. Data sets were considered overlapping if they were collected in the same population, time period, and for the same set of resources. Age ranges, reported data collectors, unit of measure (e.g. kcal/h) and methods of data collection (e.g. naturalistic or experimental) were also examined. See table S1 for more details on metadata for the selected papers. In cases where reports of children's foraging returns were duplicated, we retained the paper with the most detailed information, such that individual returns were preferred over group returns, and reports with specific ages were preferred over those focused on age classes. We also included child hunting return data available in the cchunts package from Koster et al. (12). Two papers contained data present in the cchunts package and were hence discarded. A total of 38 papers which contain 58 data sets produced a sample of 714 individuals and group measures from 28 societies on five continents (1-6 studies per society—mean: 1.39, SD: 1.03, see figure 1).

Coding. Data presented in tables were extracted by transcribing the values. Data presented in figures were extracted using the metadigitalize R package (43). Two coders independently extracted each type of data. Values were compared and averaged to account for potential coder error. We included data for individuals and age groups 20 years old and under. This was due to the

fact that research focusing on children foraging often does not report adult foraging returns, and considering age groups that span both adolescence and adulthood would complicate interpretation. Hence, if the age range of an age group crossed 20 years, this age group was excluded. Data from the cchunts R package present individual level hunting returns. Of these, we selected all the observations for individuals below 20 years of age, which represent 70% of our data. We assigned a targeted resource to each data set based on information present in text and figure captions of the papers. Most papers contained data referring to a single resource, e.g. hunting returns for game, or fish and shellfish. In cases where a paper contained different resources types, we unpacked the data, treating data points relative to different resources as different outcomes. If data points could not be attributed to specific resources, they were categorized as mixed, as were data relative to eggs and honey. These 'mixed' data contributed to the estimation of posterior values for the overall estimates, but not the specific resource comparisons. We followed Johnson and Bock (44), Lancaster et al. (24), Schuppli et al. (25), and Kramer (13) in categorizing resource complexity according to the degree to which strength and knowledge were required for successful extraction. In this framework, foods which are sessile and can be simply collected (e.g. fruit) require less strength and knowledge for collection, whereas those that need to be extracted from a hard substrate (e.g. USOs) and food that moves and needs to be hunted down (namely, game) require high levels of strength and knowledge for collection. We thus defined game and USOs, e.g. tubers, as more complex, and fruit and fish/shellfish as less complex. Note that because it is rarely reported in the publish literature, we were not able to account for variation in game size, though we acknowledge that there may be substantial differences in skill development for small and large game. Note as well that shellfish is here considered a collected resource, as we did not account for the complex processing phase. All data points are represented in figures S8-S12.

Statistical model. Following recent studies on the ontogeny of subsistence knowledge and ability (12, 29), we employed a dynamical model of foraging that allowed us to estimate how foraging skill accumulates with age, and how skill (a latent variable) relates to observed returns (which vary for reasons other than forager skill).

We used a hurdle model to describe both the probability of acquiring any return at all and probability of harvesting a certain amount of resources. Assume that individuals go on foraging trips in which they successfully acquire some return (y > 0) with probability p, or come home empty-handed (y = 0) with probability 1 - p. Further assume that non-zero returns follow a lognormal distribution. Observed foraging returns are thus mapped onto a hurdle model where:

$$f(y) = \text{Bernoulli}(1-p)$$
 if $y = 0$ (1)

$$f(y) = p[\text{LogNormal}(\mu, \sigma)] \quad \text{if} \quad y > 0$$
 (2)

Previous studies of human foraging returns have found that both the probability of a zero-return and the quantity of returns depends on forager skill (S), which varies across the lifespan. As a directed acyclic graph, this can be conceived of as age $\to S \to p$ and $S \to \mu$ (see figure 2). Koster et al. (12) modeled the relationship between age and S as a concave downward function to account for senescence among older adults. However, our focus was on the returns of foragers below age 20-more than a decade earlier than the estimated peak of foraging skill—so we did not model senescence. Otherwise, we used the same functional form as Koster et al. (12) and Lew-Levy et al. (29) to describe change in latent foraging skill with age:

$$S(age) = [1 - \exp(-k \times age)]^b$$
 (3)

Where k is the constant rate of growth in foraging skill and b is an elasticity parameter that determines the proportional change in skill. Skill itself has nonlinear effects on foraging success. Depending on how "difficult" the subsistence task is, skill may be more or less important for actual foraging productivity, which we model with an additional elasticity parameter η . $\eta < 1$ indicates diminishing returns (decreasing differentials of returns with increasing skill), while $\eta > 1$ indicates accelerating returns (increasing differentials of returns as skill increases). Comparison of η thus offers empirical estimates of skill-intensity for different types of resources (e.g., fruit vs game). k, b, and η were assumed to be positive, which means that skill is strictly increasing with age and that

higher skill always has a positive effect on foraging returns. Finally, we add the log-linear α , which acts as an intercept for foraging returns, independent of age.

$$\mu = \log(S^{\eta_{\mu}} \alpha_{\mu}) \tag{4}$$

$$p = 2[\log i t^{-1} (S^{\eta_p} \alpha_p) - \frac{1}{2}]$$
 (5)

Figure 5 shows prior distributions of skill and corresponding returns. We employed weakly regularizing priors, as described in the Supplementary Information, so that multiple possible shapes of the correlation between both skill and returns with age are possible, allowing sufficient flexibility to comfortably fit any effect of age.

In order to untangle the effect of age from that of other factors, our model was multilevel, which allowed us to accommodate variation across individuals, sex, resource type, and study. We allowed the parameters k, b, η , and α to vary among and between studies (i.e., if a single study had multiple outcomes) and resource type using random effects.

$$\log(\alpha) = \alpha_0 + v_{[\alpha_0, \text{outcome}]} + v_{[\alpha_0, \text{resource}]} + \alpha_{[\text{sex}]} + \alpha_{[\text{sex}, \text{outcome}]} + \alpha_{[\text{sex}, \text{resource}]}$$

$$\log(k) = k_0 + v_{[k_0, \text{outcome}]} + v_{[k_0, \text{resource}]} + k_{[\text{sex}]} + k_{[\text{sex}, \text{outcome}]} + k_{[\text{sex}, \text{resource}]}$$

$$\log(b) = b_0 + v_{[b_0, \text{outcome}]} + v_{[b_0, \text{resource}]} + b_{[\text{sex}]} + b_{[\text{sex}, \text{outcome}]} + b_{[\text{sex}, \text{resource}]}$$

$$\log(\eta) = \eta_0 + v_{[\eta_0, \text{outcome}]} + v_{[\eta_0, \text{resource}]} + \eta_{[\text{sex}]} + \eta_{[\text{sex}, \text{outcome}]} + \eta_{[\text{sex}, \text{resource}]}$$

We also model correlations between the random (varying) effects v to account for the possibility that studies where the base rate of skill acquisition is higher may have lower age-independent returns. To account for repeated measures of participants in some studies, we also included a random intercept for skill across individuals.

We accounted for measurement error in forager age, which can lead to deflation of parameter estimates, i.e. attenuation bias, by replacing the extracted ages, which were given as either point estimates or age intervals, with a Gaussian measurement error model.

We highlight that all model parameters are estimated jointly, from a combination of 8 chains with 6000 iteration steps each.

All analyses were run in R (version 4.2.0) and all models were fit using the RStan package (Stan Development Team 2020), which fits Bayesian models using Hamiltonian Markov Chain Monte Carlo. Markov chain convergence was assessed using standard diagnostics (number of effective samples, the Gelman-Rubin diagnostic, and visual inspection of trace plots). More details on the model can be found in supplementary section 1.2.

We used posterior samples drawn from our model to predict foraging returns given different combinations of age, resource type, and sex. These predictions are dimensionless quantities of productivity that are only interpretable in relative terms (as opposed to, for example, a rate with dimensions like kilocalories per hour). As such, we cannot say whether children in one society are more skilled than another, or whether girls are more productive than boys. We can only determine how the shape of the age trajectories vary. While modeled as a continuous measure, we quantified age-specific pattern by assessing foraging relative to the return quantity predicted for a 20 year old (the oldest age included in our data-set). This takes the form:

 $\frac{\text{model prediction at age } x}{\text{model prediction at age 20}}$

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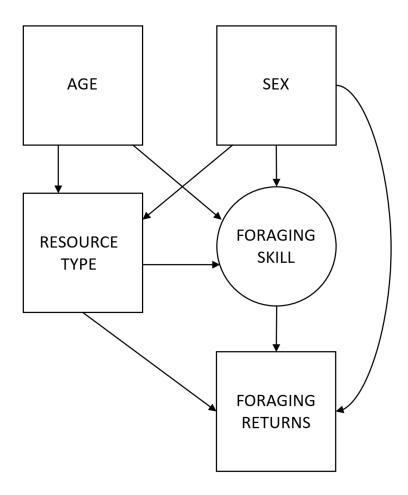


Figure 2: Directed Acyclic Graph. This DAG illustrates the proposed causal associations between the main factors investigated in this analysis. Age and sex affect the probability of choosing a resource. Skill levels also depend on age and sex. Returns vary across resources and depend on skill. Thus, all effects of age pass through skill (the sum of all age-varying traits that influence returns), excluding the influence that age has on the choice of resource (i.e. children perform different activities at varying ages).

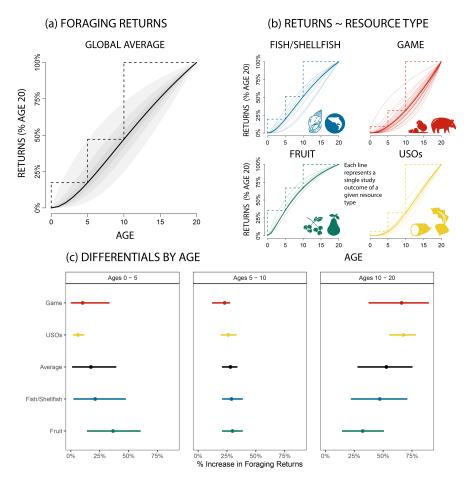


Figure 3: Foraging returns.(A)Predicted change in foraging returns with age, averaging over variation between studies, individuals, sex, and resource type. The x-axis shows age, while the y-axis is an unit-free measure of the proportion of increase compared to the maximum value (predicted returns at age 20). Solid line is the posterior median prediction, shaded intervals depict the 30th, 60th, and 90th percentile credible intervals. Dashed lines highlight arbitrary age differentials across childhood. (B) Predicted change in foraging returns by resource type, with thick lines denoting the average posterior median and thin lines denoting the median for each unique study outcome for that resource type. All curves are scaled by their maximum value (predicted returns at age 20). The shape of the curves illustrates how productivity increases with age. (C) Percentage increase in foraging returns across childhood, covering the intervals denoted by the dashed lines in A-B. Points indicate posterior median, bars indicate 90% HPDI.

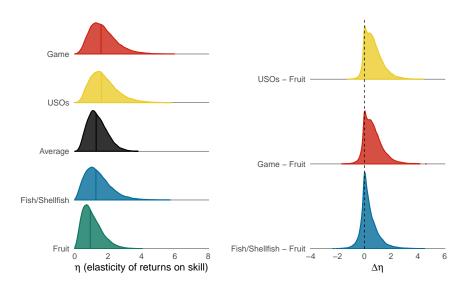


Figure 4: **Skill intensity of resources.** Left: Posterior distributions for the elasticity of foraging returns on skill (η) for each resource type. Higher values indicate that returns are more dependent on skill. Right: Contrast between the elasticity of USOs, game, and fish/shellfish vs. fruit resources, showing how much more skill intensive these resources are (posterior probability η USOs $> \eta$ fruit = 0.89, η game $> \eta$ fruit = 0.86.)

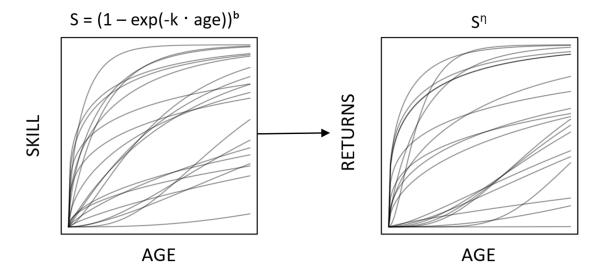


Figure 5: **Combined priors.** Curves depict possible curves for skills and foraging returns given the weakly regularizing priors in the model.

1 Supplementary Information

1.1 Data sets and metadata

In figure S1 we summarize the literature selection process that produced our sample. Table S1 shows the main metadata referring to the datasets included in the analysis. Those for which the Code of Paper includes the string cchunts are published in the R package with the same name, associated to the paper from Koster et al. (12). These were compiled by Koster, who "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" (12).

Following inclusion of data from this source, we screened the data we extracted from published papers to remove repeated data sets. In particular, data relative to the Ache of Paraguay extracted from Walker et al. (15) have not been used because they are already present in the "Hill_Kintigh" data set included in the cchunts package.

Tsimane data extracted from Gurven et al. (10) are a repetition of those included in the cchunts data ("Trumble_Gurven"). Only the latter were used in the analysis.

Data collected by Bliege Bird and Bird among the Martu in Western Australia come from both a 2005 study on children foraging (7) and from the dataset in the cchunts package (12). The 2005 paper reports data from individual of both sexes between 5 and 14 years old hunting goanna lizards in the rocky outcrop not far from the camp. These data were collected by the authors between 2000 and 2002. The cchunts data were collected between 2002 and 2010, are relative to individuals aged 7 to 79 and partially exclude female contributions ("This data set includes observations of female foragers when they were accompanied by men on trips, but not women on foraging trips that did not include male foragers"). The two data set are thus not fully overlapping, but there is the possibility that some data are present in both sets. In particular, 14 foraging returns collected in 2002 from individuals below 14 years old are present in the cchunts data set and could hence have been included in Bird and Bird (7). Looking in detail at these subsets, they do not appear to be repetitious (a 9 years old boy present in the cchunts dataset does not appear in the Bird and Bird (7) study, for example, and none of the younger individuals' returns reported here appear in cchunts).

Table S1: **Metadata for included datasets.** These are relative to each source of foraging returns data included in the analysis. The first 11 datasets have been extracted from published papers, the remaining were part of the cchunts package. As sample size we report the total number of observations for foraging returns, with the total number of foragers under 20 years included in our analysis in parentheses.

Data	Population Years	Resource (Unit)	Ages Sample Size
Bird_2005 (7)	Mardu 2000-2002	game (kcal/hr)	4- 14 157 (22)
BliegeBird_1995 (34)	$\begin{array}{c} {\rm Meriam} \\ {\rm 1993} \end{array}$	fish, fruit, mixed (g/min)	3-14 $12(12)$
BliegeBird_2002a (6)	Meriam 1993-1998	$\mathrm{fish} \ \mathrm{(kcal/hr)}$	4-75 196(42)
BlurtonJones_1989 (16)	Hadza 1985-1986	USO, mixed, fruit (g/hr)	2- 20+ 70 (29)
BlurtonJones_2002 (8)	Hadza 1997	$\overline{\mathrm{USO}}$ $(\mathrm{kg/hr})$	6-75 79 (46)
BlurtonJones_1997 (21)	Hadza 1986- 1989	USO, fruits (kcal/hr)	2-18 61 (61)

Table S1 continued from previous page

Table 5.	Continued from		F 14
Bock_2005 (23)	Bugakwhe, et al	fish	5- 14
()	1994	(kcal/hr)	16 (16)
Crittenden_2013 (9)	Hadza	mixed	3-17
C1100cHdcH_2019 (0)	2005	(kcals/day)	34 (34)
Froehle_2018 (28)	Hadza	mixed	5- 14
F10eHle_2018 (28)	2005	(kcal/trip)	9 (9)
TI 1 1007 (00)	Hadza	USO, fruits	3-17
Hawkes_1995 (22)	1988	(g/hr)	20 (17)
	Mikea	USO	NA
Tucker_2005 (14)	1997- 2003	(kcal/hr)	254(37)
	Piro	game	15-70
Alvard_cchunts (45)	1989-1991	(kg/trip)	42(5)
	Bari	game	12-55
Beckerman_cchunts (46)	1970-1972	(kg/trip)	18(9)
Bird_Bird_Codding_cchunts	Mardu	(0/ -/	7-79
~	2000-2010	game	
(47)		(kg/trip)	77(21)
Coad_cchunts (48)	Pouvi, et al	game	15- 69
, ,	2004-2010	(kg/trip)	70(7)
Duda_cchunts (49)	Baka	game	16- 69
(15)	2012-2013	(kg/trip)	57(6)
Ellen_cchunts (50)	Nuaulu	game	10-70
` '	1970	(kg/trip)	37(8)
$Fernandez_Llamazares_$	Tsimane	game	15-70
cchunts (49)	2012-2013	(kg/trip)	29(4)
E 1 (71)	Waorani	game	16- 77
Franzen_cchunts (51)	2002	(kg/trip)	48(4)
G 11 1 1 (40)	Baka	game	16- 75
Gallois_cchunts (49)	2012-2013	(kg/trip)	80(9)
	Punan	game	16- 61
Gueze_cchunts (49)	2012-2013	(kg/trip)	35(2)
	Agta	game	13- 66
Headland_cchunts (52)	1962-1984	(kg/trip)	44(7)
Healey_Nen_PNG_cchunts	Nen	game	18- 46
Preliminary fieldwork	2013	_	
Fremimary neigwork	Ache	(kg/trip)	7(2)
Hill_Kintigh_cchunts (53)		game	11- 75
- , ,	1980-2007	(kg/trip)	147(37)
Koster_cchunts (54)	Mayanga	game	8- 63
(01)	2004-2013	(kg/trip)	52(17)
Kramer_Greaves_cchunts (55)	Pume'	game	11- 65
	1990-2006	(kg/trip)	23(9)
Lupo_Schmitt_cchunts (56)	Bofi, Aka	game	6- 60
Eupo-Semmer-cenums (90)	1999-2002	(kg/trip)	59(20)
Pacheco_cchunts (57)	Maya	game	16- 60
	2011-2012	(kg/trip)	59(10)
Dongou Adam 1 (50)	Nimboran	game	16- 67
Pangau_Adam_cchunts (58)	2005-2006	(kg/trip)	26(1)
Ready_cchunts (59)	Inuit	game	12- 55
	2013-2014	(kg/trip)	15(4)
	Tsimane	game	16- 91
Reyes_Garcia_cchunts (49)	2012-2013	(kg/trip)	37(2)
	Wola	game	10- 45
Sillitoe_cchunts (60)	1977	(kg/trip)	27(10)
	1911	(rg/ trip)	21(10)

Table S1 continued from previous page

Siren_cchunts (61)	Quichua 1999, 2008	$_{ m game} \ m (kg/trip)$	19- 59 2(1)
Trumble_Gurven_cchunts (10)	Tsimane 2002-2011	game (kg/trip)	7- 82 172(53)
Van_Vliet_et_al_Gabon_cchunts (62)	Ba-Kota et al 2006-2007	$_{\rm game}^{\rm game}$ $({\rm kg/trip})$	15- 45 19(3)
Venkataraman_et_al_cchunts (63)	Batek 1975-1976	$_{\rm (kg/trip)}^{\rm game}$	9- 50 27(11)
Winterhalder_cchunts (64)	Cree 1975	$_{\rm (kg/trip)}^{\rm game}$	15- 59 16(4)
Yu_et_al_cchunts (65)	Matsigenka 2004-2007	$_{\rm (kg/trip)}^{\rm game}$	8- 52 69(18)
Ziker_cchunts (66)	Dolgan 1993- 1997	$_{ m game} \ m (kg/trip)$	15- 66 26(3)

1.1.1 Excluded datasets

Several papers that passed the first rounds of selection (i.e. appeared to report original data on children foraging returns) were not included in the analysis for a variety of reasons.

Some were subsequently found not to report relevant data (19, 67). Others did not include enough data on forager ages (11, 68–70). Kramer (71) does not include data relative to foraging, and Kramer (72) estimates returns from time allocation data, which is not consistent with the other data sets. Several papers reported data in formats that did not allow them to be extracted for analysis, such as failing to report errors around mean return per age class (5, 73), or including smoothed loess curves (74–76). Kawabe (42) reports ranges for individual returns (e.g. "more than 5 specimens killed"). Finally, a number of papers use the same data. In these cases, we included only the data sets for the latest or most informative paper. Bird and Bird (77), Blurton Jones (78), Pollom et al. (79), Walker (80), for example, present data which are best extracted from other papers.

1.2 Statistical model

1.2.1 Integrating individual-level data with study-level summary statistics

Our data included a mix of individual-level returns (e.g., a forager brought back y kilograms of fish) and summary statistics, such as the mean and standard deviation of returns for age classes (e.g., children of ages 5-10 collect tubers at a certain average rate). The challenge was to synthesize two distinct types of data: individual-level observations drawn from $f(y|\mu,\sigma)$ and group-level averages $\mathbb{E}[y|\mu,\sigma]$.

When returns were given as summary statistics (i.e., mean and standard error), we modelled them using a measurement error model:

$$\mu_{[\mathrm{Obs}]} \sim \mathrm{Normal}(\mathbb{E}[y|\mu, \sigma], \sigma_{\bar{\mu}})$$

Where $\mu_{[\text{obs}]}$ is the group-level mean, $\sigma_{\bar{\mu}}$ is the standard error of that mean, and, following our generative model defined in the main text, $\mathbb{E}[y|\mu,\sigma] = p(\exp(\log(\mu) + \frac{\sigma^2}{2}))$.

Finally, there was some variation in the number of measures available for individuals, and some studies have multiple measurements from the same forager, in which case we included a random effect on skill to account for non-independence of these data points. However, lack of longitudinal data meant that it was not possible to estimate individual differences in the life history parameters.

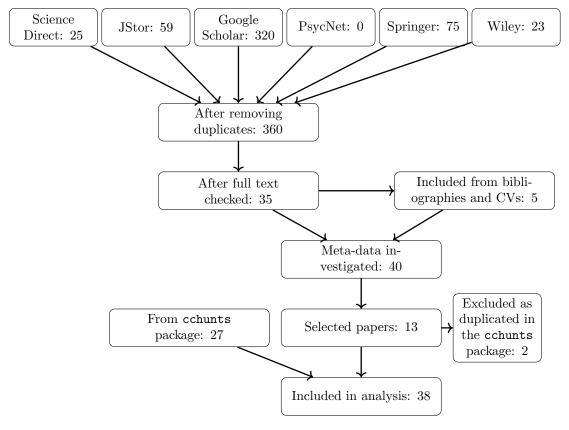


Figure S1: Process of paper selection.

1.2.2 Priors

We employed regularizing priors for all parameters to reduce over-fitting and facilitate model convergence. Specifically, we assigned a Normal(0,1) to fixed effects (e.g., intercepts), an Exponential(1) for the random effect standard deviations and LKJ(2) for the correlations between random effects. Moreover, we fixed to zero the starting values for several parameters, as this can be helpful (and in some cases, necessary) for the model start sampling. However, after many iterations of warm up there is no dependence on starting values, unless the model is badly mis-specified or suffers from a multimodal posterior. We used standard MCMC diagnostics and found that all population parameters had Rhat < 1.01 and an effective sample size > 1000.

1.3 Dealing with uncertainty

Uncertainty in age: Forager age was not reported exactly in any study. Most frequently, authors reported an integer age for each child. In other cases an interval of possible ages was given (e.g., 4-7). We modelled age using a Gaussian measurement error model:

$$age_{obs} \sim Normal(\mu_{age}, \sigma_{ag\bar{e}obs})$$

Uncertainty in sex: In cases where sex of the forager was not reported (or was given as a summary statistic), we average over sex differences in proportion to how often males and females appeared in a given study using Stan's log_mix() function.

1.4 Additional figures

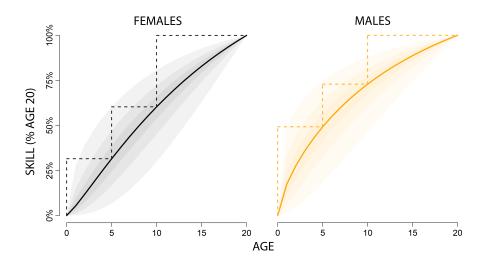


Figure S2: **Predicted change in foraging skill by sex**. Values averaged over variation between studies, individuals, and resource type. The x-axis shows age, while the y-axis is an unit-free measure of the latent variable.

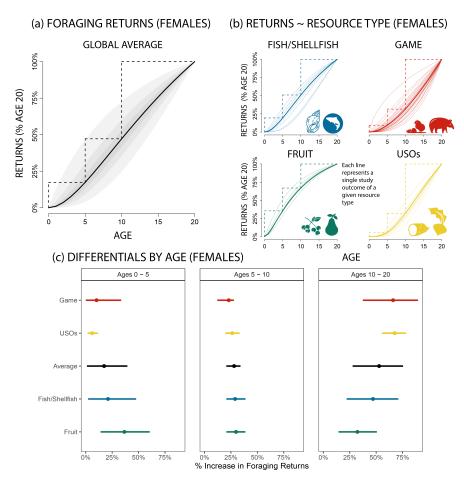


Figure S3: Foraging returns for females only. (A)Predicted change in foraging returns with age, averaging over variation between studies, individuals, and resource type. The x-axis shows age, while the y-axis is an unit-free measure of the proportion of increase compared to the maximum value (predicted returns at age 20). Solid line is the posterior median prediction, shaded intervals depict the 30th, 60th, and 90th percentile credible intervals. Dashed lines highlight arbitrary age differentials across childhood. (B) Predicted change in foraging returns by resource type, with thick line denoting the average posterior median and thin lines denoting the median for each unique study outcome for that resource type. All curves are scaled by their maximum value (predicted returns at age 20). The shape of the curves illustrates how productivity increases with age. (C) Percentage increase in foraging returns across childhood, covering the intervals denoted by the dashed lines in A-B. Points indicate posterior median, bars indicate 90% HPDI. This figure is similar to figure 3, but focuses only on females.

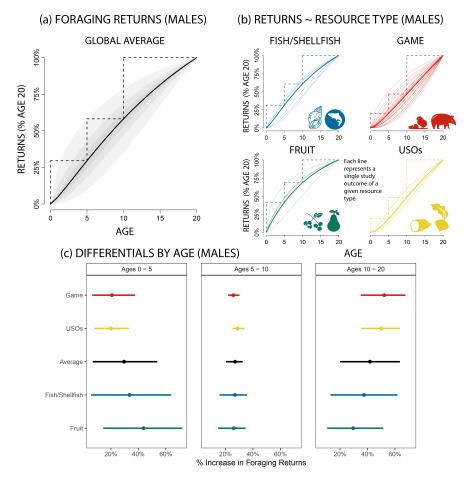


Figure S4: Foraging returns for males only. (A)Predicted change in foraging returns with age, averaging over variation between studies, individuals, and resource type. The x-axis shows age, while the y-axis is an unit-free measure of the proportion of increase compared to the maximum value (predicted returns at age 20). Solid line is the posterior median prediction, shaded intervals depict the 30th, 60th, and 90th percentile credible intervals. Dashed lines highlight arbitrary age differentials across childhood. (B) Predicted change in foraging returns by resource type, with thick line denoting the average posterior median and thin lines denoting the median for each unique study outcome for that resource type. All curves are scaled by their maximum value (predicted returns at age 20). The shape of the curves illustrates how productivity increases with age. (C) Percentage increase in foraging returns across childhood, covering the intervals denoted by the dashed lines in A-B. Points indicate posterior median, bars indicate 90% HPDI. This figure is similar to figure 3, but focuses only on males.

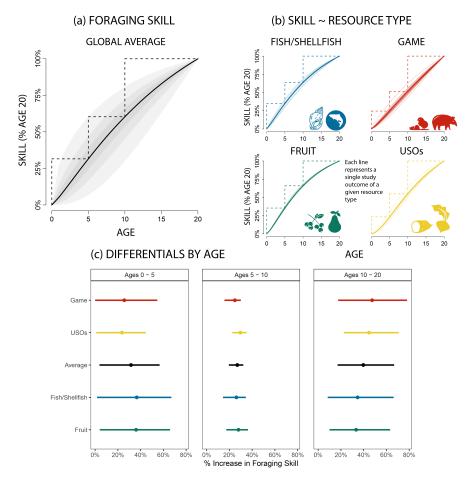


Figure S5: Foraging skill. (A)Predicted change in foraging skill with age, averaging over variation between studies, individuals, sex, and resource type. The x-axis shows age, while the y-axis is an unit-free measure of the proportion of increase compared to the maximum value (predicted returns at age 20). Solid line is the posterior median prediction, shaded intervals depict the 30th, 60th, and 90th percentile credible intervals. Dashed lines highlight arbitrary age differentials across childhood. (B) Predicted change in foraging skill by resource type, with thick line denoting the average posterior median and thin lines denoting the median for each unique study outcome for that resource type. All curves are scaled by their maximum value (predicted returns at age 20). The shape of the curves illustrates how skill increases with age. (C) Percentage increase in foraging skill across childhood, covering the intervals denoted by the dashed lines in A-B. Points indicate posterior median, bars indicate 90% HPDI. This figure is similar to figure 3, but describe underlying foraging skill instead of returns.

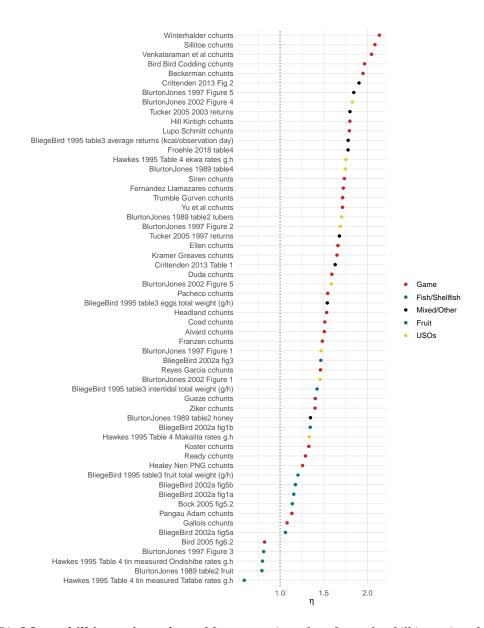


Figure S6: Mean skill intensity values. Mean posterior values for η , the skill intensity of foraging, by outcome. Each individual dataset (either present in the cchunts package or extracted from a single figure/table) is represented here, color coded for resource.

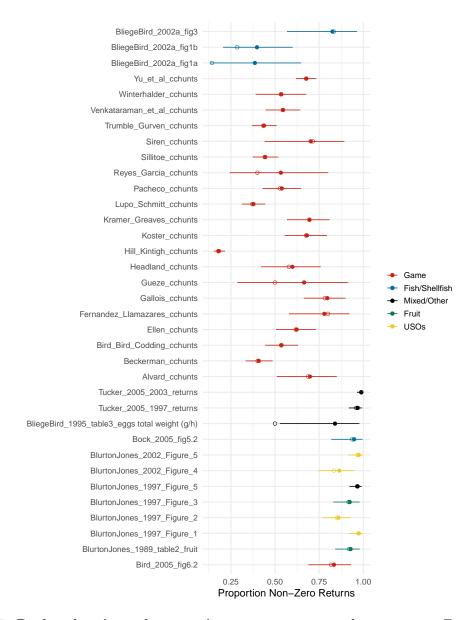


Figure S7: Real and estimated proportion non-zero returns by outcome. Empty circles show real proportion of non-zero returns by outcome, mean and 95 percentile intervals of posterior distribution of estimated proportion of non-zero returns are indicated by full circles and bars. The model predicts with sufficient accuracy the proportion of non-zero returns.



Figure S8: Fish data. Data points for all datasets reporting fish and shellfish data.

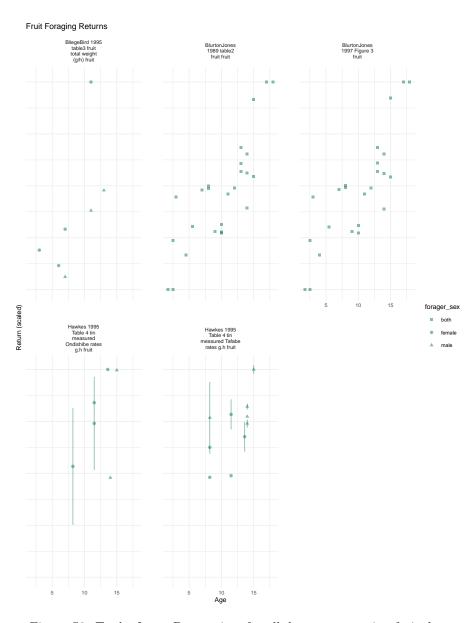


Figure S9: Fruit data. Data points for all datasets reporting fruit data.



Figure S10: Game data. Data points for all datasets reporting game data.

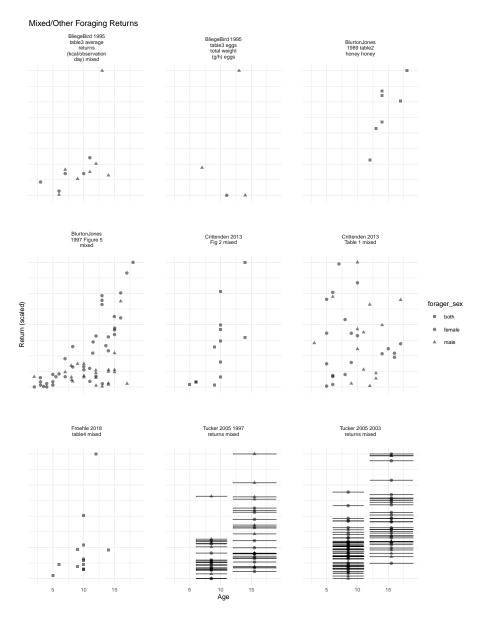


Figure S11: \mathbf{Data} from other resources. Data points for all datasets reporting data for other kinds of resources.



Figure S12: Tubers data. Data points for all datasets reporting tuber data.