Foraging Efficiency and the Importance of Knowledge in Pemba, Tanzania: Implications for Childhood Evolution.

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September 12, 2022

Abstract

Childhood is a period of life unique to humans. Childhood may have evolved through the need to acquire knowledge and subsistence skills. In an attempt to evaluate the importance of learning for the evolution of childhood, previous research examined the increase with age of returns to foraging across various resources. Any increase could be due to increases in knowledge or other factors such as body size and strength. Here, we first estimate age-specific foraging returns for two different resources. We then model the relative importance for foraging of ecological knowledge, grip strength and height in a population of part-time children foragers on the island of Pemba, Tanzania. We use anthropometric measures, such as height and strength, and estimates of ecological knowledge for more than 250 and 90 individuals respectively, in association to behavioral observations for 63 individuals across 372 foraging trips. We find slower increases in foraging returns with age for trap hunting than for shellfish collection. We do not detect any effect of individual knowledge on foraging returns, potentially because relevant information can be shared within foraging parties. We also find positive effect of individuals' height on shellfish collection. This is the first study providing accurate estimates of individual traits' contribution to foraging performance, which is important to evaluate evolutionary hypotheses for the emergence of childhood.

1 Introduction

Humans have special life histories, that is, how individuals trade off growth, maintenance, and reproduction along the life course (Jones, 2011; Kaplan, 1997; Leigh, 2002). Across the animal kingdom, larger bodies are often associated with longer lifespans and later reproduction, under the assumption that it pays off to invest in growth for longer periods as long as enough benefits are provided by bigger size during adult life (Charnov, 1989). For example, larger bodies are associated with higher fertility and mortality reduction, a main driver of life history evolution (Kingsolver and Pfennig, 2004). But other traits can be acquired during development and result in low mortality and high fitness, and thus they have the potential to influence life history traits. In particular, encephalization, i.e., investment in brain growth, is thought to be at the basis of the slow down of primate and human life histories. But how would encephalization benefit humans? Kaplan et al. (2000) suggested that several human life history traits coevolved with our reliance on complex ecological niches. In what they call Embodied Capital Theory (ECT), they propose that during a long pre-reproductive period, young humans acquire somatic and especially cognitive traits (the 'embodied capital') that allow them to extract from the environment resources requiring high levels of skill, but that also yield high caloric returns. Once adults, humans can then reduce mortality risk and provide for larger families with high quality food. Alternative hypotheses explain the evolution of long childhoods and slow lives as a consequence of a general elongation of life span, where the selective pressure is on survival to older ages (Hawkes et al., 1998), or by inclusive fitness benefits linked to cooperation and resource sharing within human reproductive nuclei (Kramer and Ellison, 2010).

Predictions from these three alternative hypotheses have been addressed in numerous ways. For example, an association between encephalization and environmental complexity has been found when modelling the cost of brain tissue as a function of environmental and social challenges (González-Forero et al., 2017). Similarly, a cross-species analysis of niche complexity and life history found that reliance on foods that require high levels of cognitive skills predict slow development in primates (Schuppli et al., 2016). Alternative investigations can test evolutionary hypotheses for the evolution of human life history relying on data on contemporary hunter-gatherer societies, tackling one or more predictions associated with the embodied capital model. Many researchers looked at how foraging proficiency varies with age, under the ECT-driven assumption that learning to forage imposes a trade-off between current and future production. Late age at peak foraging, consistent with ECT, has been found in various studies focusing on hunting (Gurven et al., 2006; McElreath and Koster, 2014; Walker et al., 2002), including in a large cross-cultural comparison (Koster et al., 2020). Other studies, on the contrary, find early development of foraging skills in other resources, especially fruits and shellfish (Bliege Bird et al., 1995; Blurton Jones et al., 1989; Crittenden et al., 2013), which appears in contrasts with the current vs. future production trade-off assumption previously listed. But foraging skill acquisition will vary with complexity of the task, so that findings of no strong age effects Bliege Bird and Bird (e.g. 2002) may be specific to easy tasks. Indeed, Pretelli et al. (2022b) find that, across cultures, more complex resources require more skill and longer acquisition times.

Finally, researchers tackle the difference between types of 'embodied capital'. For example, Bock (2002) suggests that the need for both somatic and cognitive embodied capital establishes a ratchet mechanism where foraging itself promotes the acquisition of these traits, which in turn improve individuals' ability to forage, a system he defines 'punctuated development model'. In support of the necessity for a combination of cognitive and somatic skills for the development of foraging skills, Bock (2005) finds that arm strength is a predictor of return rates in canoe fishing for boys on the Okavango Delta, in Botswana, while it is not for girls' basket fishing returns rates. Similarly, Bird and Bliege Bird (2005) find that height, as a proxy of stride length, is an important predictor of foraging returns, suggesting that somatic characteristics are an important limiting factor for foraging proficiency among Western Australian Mardu children. Bird and Bliege Bird (2005) interpret their finding as inconsistent with ECT, although they provide no parallel test of the impact of different cognitive skills.

Here, we address we address the challenges of testing the embodied capital models listed above using novel data coming from a part-time foraging population on the island of Pemba, Zanzibar, Tanzania. We first characterize age specific foraging returns, focusing on the comparison across two different types of resources varying in complexity. Second, we measure the relative contribution to foraging returns of one cognitive trait, i.e., ecological knowledge, and two somatic traits, i.e., height and strength, operationalized as grip strength. In doing this, for the first time, we compare the importance of the two types of embodied capital across the two examined resources using individual-level measures for all traits. Finally, we discuss more at large other aspects of human behavior associated to foraging.

2 Materials and Methods

2.1 Research Location

Data collection was carried out on the island of Pemba, Tanzania. The island is part of the Zanzibar archipelago and is located in the Indian Ocean, about 50 km off the coast of east Africa (see map). Pemba's climate is tropical, with two wetter and two drier seasons brought by alternating monsoonal winds.

Bantu-speaking people have been living on the island since at least 600 A.D. (Fleisher and La Violette, 2013). Around the turn of the millennium, its inhabitants lived in wattle-and-daub villages and 'stone-towns', with coral-rag mosques and multi-store houses (LaViolette et al., 2018). They cultivated rice, coconuts and cotton (Walshaw, 2010), and were engaged in long-distance maritime trade that encompassed the whole Indian ocean (Fleisher et al., 2015). At the end of the 15th century, the Portuguese crown took control of the island, only to lose it to the Omani sultanate at the end of the 17th century (Prestholdt, 2018). Although under increasing control from the British, up to the establishment of a protectorate in 1890, the Busaidi sultans remained the formal rulers of the Zanzibar archipelago until 1964, when a revolutionary movement removed them from power and promoted the unification of Zanzibar to mainland Tanganika, thus forming modern Tanzania.

Pemba is known in Arab texts as al-Jazra al-khadr, or the Green Island, because of its thick forest cover and fertile soils. The primary forest has now been largely replaced by crops, including clove trees, which are the main cash crop on Pemba. The island is poor of larger wild fauna, but there are several endemic species of birds, bats, and other smaller animals. Many of these live in the forest of Ngezi, the largest patch of rainforest that still stands in the north-western corner of the island. The village where data were collected is located in this area, between Ngezi forest and the coast.

2.2 Subsistence and foraging around Ngezi forest

People in the village subsist mainly on agriculture, fishing and the products of the forest, which respectively represent 40.6%, 9.7% and 33% of total income for the average family in this ecozone (Andrews and Borgerhoff Mulder, 2022). Hunting and gathering are a secondary source of food and are carried out primarily by children and young adults, although the foods thus produced regain importance in case of famines (Walsh, 2009). The present study focuses on two main forms of foraging: shellfish collection along the coast rimmed with mangroves and snare hunting in the forest or in the *shambas* surrounding the village (this was the most common form of hunting recorded, accounting for 80% of all observed foraging trips).

Shellfish are collected by girls of various ages, sometimes including adult women and often accompanied by younger boys–sons or younger brothers. At low tide, groups of foragers walk on the exposed sandy bottom searching and collecting different kinds of shellfish, crabs, and occasionally other animals such as small octopuses. Shellfish need to be located, which requires good eyes and some experience, then extracted from the sandy bottom, often with the help of a knife and some strength. Crabs are often also embedded in the sand, but usually escape when extracted, so that a good deal of agility is necessary to capture them. Moreover, stride length is considered a good predictor of shellfish encounter rates (Bird and Bliege Bird, 2002).

Hunting is almost exclusively practiced by groups of boys, mostly before reproductive age, and involves the use of snares, slingshots, baited traps, or gluey sticks targeting birds of various sizes and small mammals, as well as dogs to pursue monkeys or other animals that pose a threat to crops. Young hunters in Pemba are also known to hunt bats, especially the endemic Pemban Flying Fox, *Pteropus voeltzkowi* (Walsh, 1995). In this paper, we focus on trapping with snares. Snares are built using wooden sticks and common sewing threads on the forest floor. Traps are placed along wildlife paths within the forest proper, often close to marshes, or in the casuarine forest closer to the sea, with the aim of capturing ground-dwelling birds including Hadada Ibis (*Bostrychia hagedash*) and the Water Thick-knee (*Burhinus vermiculatus*), or small mammals such as the endemic Pemban Blue Duiker (*Philantomba manticola sundevalli*). Hunting with snares requires understanding the ecology of prey species and tracking skills, in order to appropriately place the traps, as well as dexterity to mount the traps, plus a baseline of strength to bend the long elastic stick that provides momentum to tighten the loop of the snare (see 5.1 for more details on these subsistence activities).

2.3 Data collection

Demographic data: With government approval for research (IMMZ/07/17/25, ethic approval provided also by Max Planck Institute Ethics Council, application number 2019_05), IP visited all households in the village in June 2019. An overview of the project was presented, in order to obtain informed consent, and basic demographic and household-level data were collected for each family unit. A total of 94 households were surveyed and the village census counted 576 individuals in 2019.

Ecological knowledge data: A survey instrument was developed during focus groups, in collaboration with adult members of the village and with the Department of Forestry and Non-Renewable Natural Resources in Pemba. Between July and August 2019, IP used the survey thus developed to interview 93 individuals aged 5-26, plus a 56-year-old man. For the present study, knowledge was measured from answers to the freelist section of the interview, where individuals were asked to name all living creatures that could be encountered in and around the village, forest, or beach and sea. For more information on this method, see (Pretelli et al., 2022a).

Anthropometric data: Anthropometric data, namely height, weight and grip strength, were collected multiple times for individuals offering themselves for measurement, including during demographic interviews, knowledge interviews, and other impromptu situations. Height was measured for 284 individuals, weight for 304 and grip strength for 258 individuals.

Behavioral observations: Between February and December 2020, children planning a foraging trip were invited to inform IP or BMK so that behavioral observations could be carried out. A value of 1000 TSH (about the equivalent of 0.40$) was paid to the group to promote the communication of upcoming trips–an amount sufficient to buy a few candies or a couple of pencils, but also enough to ensure that the researchers could observe foraging trips. For each trip, we recorded the following information: group composition, start and end time from a location in the village, time of arrival and departure from destination of the trip (i.e., the shore where shellfish are collected, or the area in the forest where traps are mounted), and GPS track of the movement of the group.

Moreover, each participant in shellfish collection trips was provided with a small bucket which content was weighted at the end of the trip in order to measure individual level returns. Time and height of low tide was recorded on the day of each foraging trip from the website Tide Charts (https://www.tideschart.com/Tanzania/Pemba-North/Micheweni/Konde/). 40 individuals participated in 37 shellfish collection trips, which gave a total of 158 person-trips. Of these, 70% are relative to female foragers, and 8-39 is the age range for person-trips data (mean 16.32).

Additional trap-level information was recorded during foraging trips that involved installing and checking traps in the forest, including who installed each trap, when a trap was installed, checked and dismantled, whether a trap captured something and, if so, the weight of the prey. 56 individuals participated in snare hunts and, of these, 23 individuals installed a total of 678 snares during 335 foraging trips. The outcome measure considered in the analysis is whether a snare has captured something between foraging trips, which yielded a total of 4091 data points. All observed hunters were males, aged 7 to 26, and the mean age of the individuals installing traps was 15.23.

2.4 Causal framework

The directed acyclic graph in figure 1 shows the factors that are believed to influence foraging. The first step in our analysis is a description of how foraging varies with age, for which we look at the total effect of age and include only age as a predictor of foraging at the individual level. But age itself does not 'cause' foraging, rather its total effect is mediated by time-varying covariates, such as knowledge or somatic characteristics. In addition to these measurable traits, several other unmeasured or unmeasurable time-varying traits, including, for example, ability with a knife or patience, influence foraging, and are designed in the DAG with the letter U. For the second step in our analysis, we take into consideration the separate effects of ecological knowledge, as measured by our survey instrument, and anthropometric measures, namely height and grip strength. Additional somatic traits that have not been measured might influence foraging returns; hence, we include an additional unknown variable O. Note that the effect of these other unmeasured traits is likely captured by age, strength or height. Both somatic and cognitive traits are correlated with age, and thus with each other, but controlling for age in this model makes them conditionally independent. In this way, we can estimate their effect with the same statistical model. Moreover, we include in all models trip-level covariates such as duration and, in the case of shellfish collection, tide height. Note that these variables are not confounders on the path of age, but are concurrent causes of foraging success and could introduce biases if not controlled for. Finally, with the exception of tides, this causal structure holds for both types of foraging considered here, even though the factors might act in different ways. For example, the duration of shellfish collection trips stands for the number of 'time units' during which people forage and has a monotonically increasing effect on foraging, whereas duration in the trap model is the time between one inspection of a trap and the following, which has a non monotonic effect.

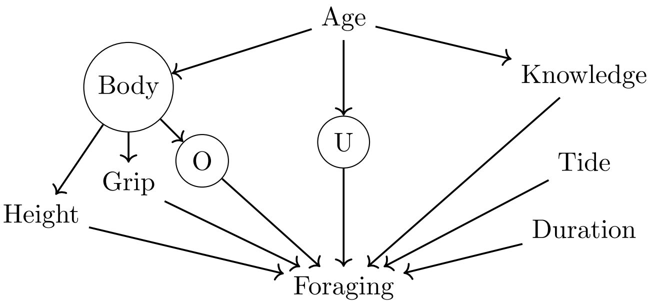

Figure 1: DAG describing relationships between analyzed variables.

2.5 Analysis

Most recently, foraging returns have been modeled as hurdle models, modeling separately (i) the probability of success (i.e., non-zero returns) and (ii) the amount of returns (e.g. grams or calories collected) for a certain trip (Koster et al., 2020; Lew-Levy et al., 2021; McElreath and Koster, 2014; Pretelli et al., 2022b). In the case of the present study, however, the two types of foraging can be analyzed with just one of the two parts of a hurdle model. This is because, for hunting with traps, we mainly model the probability that each trap has of collecting anything at all, i.e. the first part of a hurdle model, given that the weight of the captured animal is most likely independent of the modeled traits. For collecting seashells, the second part of the hurdle model is sufficient, because children always obtain something–hence no need to model zero returns separately.

Mathematically, the amount of shells collected by children is a lognormally distributed quantity, where the mean of the underlying normal distribution is μ and the standard deviation is σ. Whether a trap captures something between being checked one day and the following check is a Bernoulli distributed outcome, with probability p. .

$$R \sim \text{Lognormal}(\mu, \sigma) \tag{1}$$
$$S \sim \text{Bernoulli}(p) \tag{2}$$

μ and p are modeled in parallel, so that the effect of age and other individual level traits can be compared. Appropriately transformed, both are a combination of a general intercept, α, an equation including the effects of individual-level traits, designed by ϕ, and an equation for trip-level traits, designed by ψ.

$$\mu = \log(\alpha\, \phi_i\, \psi_f) \tag{3}$$
$$p = 1 - \exp(-\alpha\, \phi_i\, \psi_f) \tag{4}$$

The first parameter in the equations defining p and μ is α, which simply scales all other parameters and allows them to fit to the data.

ϕ_i is calculated for each individual i and includes individual level random effects, ι_i, and a series of factors that are tied together in a production function akin to a Cobb-Douglas. In particular, age a is scaled by parameters β and γ so that its effect on foraging can grow in a flexible, sigmoidal function before leveling off at 1 (see figure 8). Knowledge k, height h and grip strength g are included only in the second part of our analysis and are scaled by exponents ζ, η and θ, respectively, as it is the norm in Cobb-Douglas functions. This structure allows us to incorporate some basic biological assumptions in the model: for example, in the absence of any knowledge, height, or grip strength, foraging cannot happen. For more details, refer to Supplementary Information, section 5.2.

$$\phi_i = \iota_i\, (1 - \exp(-\beta\, a_i))^{\gamma}\, {k_i}^{\zeta}\, {h_i}^{\eta}\, {g_i}^{\theta} \tag{5}$$

Moving on to ψ_f, this parameter includes all information relative to f, i.e., the foraging trip, for shellfish, or trap, for the snare data. These include a time scaling parameter, ξ which moderates the effect of the duration d of a foraging trip, for shellfish, or of duration of exposure, i.e. how many hours passed since a trap was checked last, for trap-hunting. Collecting shellfish is also influenced by the depth of the tide t, so that ψ for this kind of data includes the effect of average height of the tide during the foraging trip, multiplied by τ.

$$\psi_f = {d_f}^{\xi} \exp(t_f \tau) \tag{6}$$

Other aspects of the models include the estimation of ecological knowledge from answers to freelists using an Item Response Theory model (see Pretelli et al. (2022a) for more details on this tool) and the imputation of missing data for knowledge, height and grip strength according to each individual's age and sex (see section 5.2.2).

We used weakly informative or informative priors for all parameters, reported here for the parameters listed above (see section 5.2.1 for the remaining parameters and for a visual description of the joint distribution of the prior in figure 13).

$$\begin{aligned}
\alpha &\sim \text{Half-Normal}(0,1)\\
\beta, \gamma, \sigma &\sim \text{Exponential}(1)\\
\iota, \zeta, \eta, \theta, \xi, \tau &\sim \text{Normal}(0,1)
\end{aligned}$$

Hamiltonian Monte Carlo engine Stan (Stan Development Team, 2021) was used to estimate the posterior distribution for each parameter using CmdStan. Posterior distributions were processed in R 4.0.3 (R Core Team, 2021), with the help of the Statistical Rethinking R package, version 2.13 (McElreath, 2020). Our models were validated with simulated data to ensure that they could recover the simulated parameters (see 5.2.3) and, for all analyses, visual inspection of the trace plots, Gelman-Rubin diagnostic, and the effective number of samples indicate model convergence.

Parameter estimation in the Bayesian framework does not return point estimates, but rather a posterior distribution of possible values for a parameter. Hence all the figures in the result section try to convey information relative to the whole posterior distribution, when possible. All code necessary to reproduce these analyzes is available on GitHub (https://github.com/lalla-ilaria/Children_foraging_returns).

3 Results

Fit to data. Before discussing the inferences from our results, we must point out some differences between the types of data we analyze. The grey points in figure 2, panels A and B, show our raw data, i.e. kg of unprocessed shellfish or success of trap respectively, as a function of age of participant. A first visual inspection of these data reveals that, despite having received substantially more sampling effort (335 foraging trips observed over 11 months, with a total of 1158 person/trip), trap-hunting yielded relatively low-definition data: only 23 participants actually built traps during these trips, the age range does not cover adult individuals, with the oldest man in the sample only 26, and traps have overall a small success rate (29 out of 678 traps captured anything, giving only 31 data points for success). In contrast, the data set for shellfish collection is relatively well defined from childhood to early adulthood, with sparser but still helpful data up to mid-adulthood (141 person/trips within ages 8-19, plus 20 trips up to age 39). This difference has consequences for the precision with which we can make inferences relative to the two types of foraging: shellfish data provide clearer and more reliable estimates than trap-hunting across all of our results. For example, we can see this by the higher precision with which our models define age trajectories for shellfish data in figure 2, panels A and C, compared to the less confident estimates relative to trap-hunting, in panels B and D. Despite this, both models do a good job of predicting outcomes that match the observed data, as we can infer by the extent by which the predicted outcomes–colored points–match the observed data–gray points–in figure 2, panels A and B. So, keeping in mind that results are less confident for trap-hunting, we can look at central tendencies in the posterior distributions and proceed to describe our results.

Variation with age. Our first target of inference is how foraging returns varies with age, for which the two types of foraging we analyze show very different patterns (see figure 2, panels C and D). While, on average, a 10 years old individual collecting shellfish has reached 75% of the maximum foraging returns, a 10 years old boy who goes hunting with traps has achieved only about 15% of the maximum success rate individuals can be expected to achieve. In general, foraging returns increase at a much faster rate for shellfish collection than for trap hunting.

Knowledge, strength, height. As a second step, we aim at partitioning the relative contribution of cognitive versus somatic traits for foraging. These are represented by ecological knowledge and by height and grip strength, respectively. We find a positive effect of height on foraging for shellfish collection (Figure 3, panel A), and slightly negative effects of grip strength on shellfish collection, as well as of ecological knowledge on trap-hunting. On the contrary, knowledge appears to have no effect on shellfish collection. Finally, the effect of grip strength and height on trap hunting is unclear, given that the model is mostly recovering the priors we imposed on the model, although if any, their effect is likely to be limited (see Figure 13).

Other predictors: time and tide. In addition to individual-level traits, we considered trip-level traits for shellfish collection, that is, duration of the foraging trip and average level of the tide during the trip, and duration of exposure of a trap for the trap-hunting data, that is, how much time passed between two consecutive observations of the same trap. These trip level factors appear to be the most important predictors for shellfish collection data. Longer trips yield significantly more shellfish, as each unit of time increases total shellfish production. Moreover, there is a strong positive effect of the average water level on returns, with higher returns associated with a more extreme low tide. Duration of exposure does not appear to have a strong effect on the probability that a trap captures a prey. This might be a feature of a most likely non-linear effect: not enough time and no prey would encounter the trap, but too long an interval increases the possibility that the prey is spoiled or stolen.

4 Discussion

In this study, we aim at measuring the relative contribution of cognitive and somatic traits for foraging returns. This is important for assessing the significance of hypotheses for the evolution of human childhood. We also replicated existing studies testing these same hypotheses and brought together a variety of approaches that characterized three decades of research on the subject. To do so, we collected novel data, including behavioral observations for two different types of foraging, associated to a variety of anthropometric and demographic measures, and also, for the first time, to an explicit measure of ecological knowledge. We built on existing literature (e.g. Koster et al., 2020; Pretelli et al., 2022b) to develop a statistical model based on explicit causal assumptions, which helps us tackle the question of why humans spend so long as prereproductive individuals.

Our first result, in agreement with previous studies, is an early-age increase of foraging returns for shellfish collection, and, on the contrary, late development of foraging skills for trap-hunting. This is overall in accordance with ECT, as foragers take longer to become proficient hunters, an activity that is deemed to require a more complex set of skills.

However, we do not find that ecological knowledge positively affects shellfish collecting or trapping returns. This is one of the predictions of ECT, as individuals who spent longer time learning about the environment are expected to have higher foraging return rates. Several limitations inherent to our data set could explain this finding. For example, we do not include foraging types such as big game hunting, which is considered to require both ecological knowledge and skill. In addition, the types of foraging we target are only two of the many in which Pemba children engage, while our measure of individual level knowledge is non-specific and includes information relative to medicinal plants, pelagic fish, pests, etc. Moreover, our data are observational and, as such, do not randomize knowledge of individual foragers, potentially introducing biases. For example, we may be observing

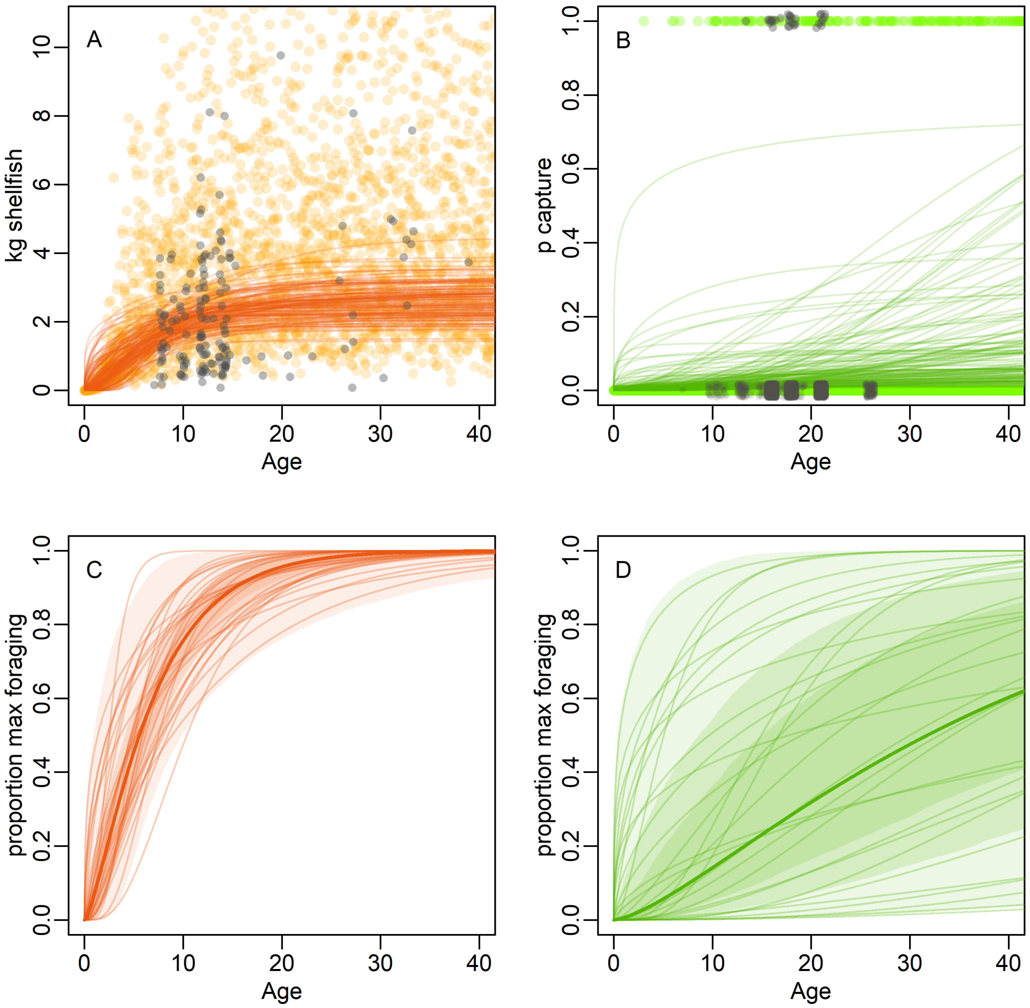

Figure 2: Panels A and B show, for shellfish collection and trap-hunting respectively, i) raw data, in grey, i.e. kg of unprocessed shellfish or success of trap, as a function of age of participant; ii) curves showing 150 posterior predictions for expected outcome values, by age, as predicted by the models, i.e. average amount of shellfish an individual of a certain age is expected to collect in a fixed amount of time–orange lines in panel A, or the probability that a trap set by a boy of a certain age has of capturing any prey–green lines, panel B (note that the results presented here refer to an 'optimal' counterfactual where only the best hunter and shortest time are involved–so that the pattern of age variation is more evident. Refer to figure 12 for the average value); iii) actual outcomes predicted by the model, in colored points, i.e. simulated kg of shells per trip or success of traps. Panels C and D show the age component of this variation, stripped of the effect of other predictors, i.e. the average value of ϕ for each age. Considering ϕ, which is a dimensionless variable defining the total effect of individual characteristics, allows comparison between the two types of foraging, despite the different scales at which the actual outcomes are measured. Shaded areas in panels C and D show the 30th, 60th and 89th percentiles, and the overlying curves show 30 samples drawn from the posterior distribution of parameters. The results presented in this figure are given by a model that includes only individual level random effects and an effect of age to define ϕ–refer to equation 5.

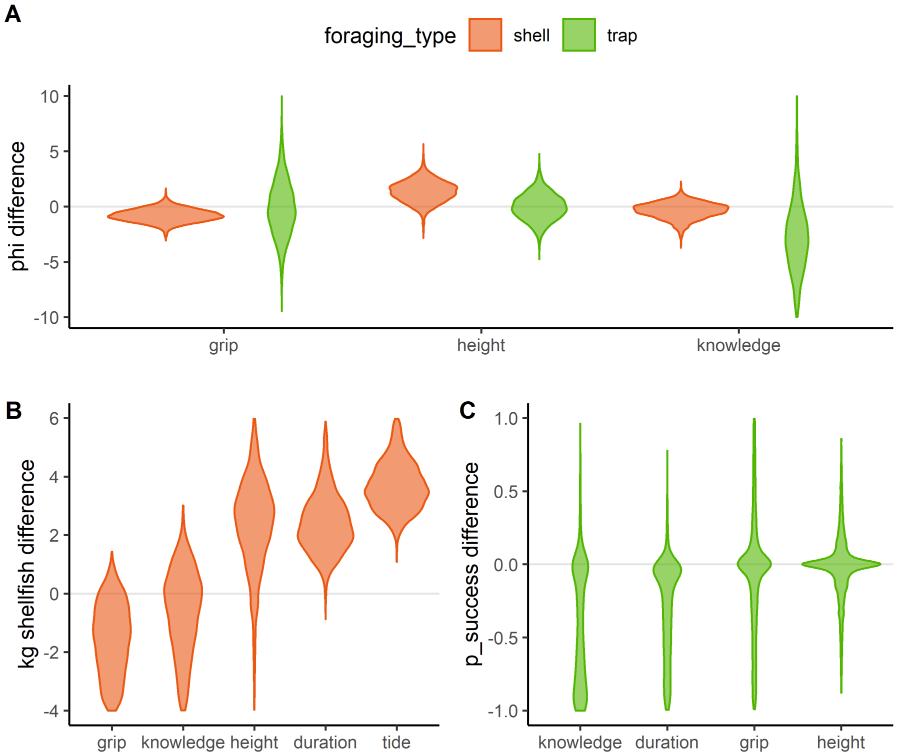

Figure 3: Panel A shows the effect of grip, height and knowledge on returns. This is defined as the distribution of the difference between counterfactuals of ϕ with maximum and minimum values of each trait in the sample, for both shellfish data, in orange, and traps, in green. This is the difference in ϕ between two hypothetical foragers who differ only in one of the traits, keeping the rest constant. Panels B and C show the effect at the outcome level of each of the main predictor in the sample, excluding age. This is defined as the difference in average amount of shellfish produced in two counterfactual conditions where all variables are kept at mean value apart from the one under evaluation, for which maximum and minimum values are contrasted. See SI section 5.2.4 for more information on how these values are calculated.

only the most knowledgeable individuals foraging, so that we cannot pick up a positive effect of having learned about the environment.

Still, it is important to note that all activities considered are performed socially. With median group size of 3 and 4 foragers respectively, both trap hunting and shellfish collection are almost always carried out in groups. This means that whatever knowledge is necessary for these activities, this can often be shared within the group as long as at least one individual possesses it. For example, when boys go on a trip to build traps, they generally take responsibility for building one trap each, but also keep sharing information and offer counseling. Trap building, then, becomes a discussion between individuals building several traps at the same time, coordinating and suggesting to move the location of the trap or to grab a different stick. For shellfish collection, we might be observing something that has been suggested for the harvest of fruits as well: knowledge is necessary during these activities in order to locate high-yield patches and, maybe more importantly, to know when these seasonal resources will be available. In the case of shellfish collection, additional temporal variability is given by the tidal cycles. Tide level is important for shellfish collection because it influences how many resources are available. Even though this activity is always carried out at low tide, there is considerable variation in how much the water retreats, as minimum yearly tides are observed only when certain astronomical conditions are met. This has implications for shellfish gathering, not only because the lower the tide, the larger the exposed area of sandy bottom, but also because the areas that are exposed less often are also less exploited and likely to yield higher returns. Hence, given that tides are the best predictor for foraging success, it is important to know when a tidal minimum is going to happen. But, as long as one person per group has this information, everyone else will enjoy the benefits of foraging at low tide. This means that, although ecological knowledge of foraging individuals does not appear to promote higher returns, the knowledge available to foragers and shared within the group can nevertheless be relevant for the foraging success of all participants.

Concerning other types of ‘embodied capital’, one interesting result is the positive effect of height on shellfish collection. This replicates previous findings of Bird and Bliege Bird, e.g.2002, who argue that, in accordance with predictions of Optimal Foraging Theory (Winterhalder and Smith, 2000), encounter rate is one of the main determinants of shellfish collection efficiency. When foraging for sessile organisms, the rate of encounter is related to the speed of the forager, which, for humans, is usually correlated with height and stride length. Optimal Foraging Theory also predicts a shift in the prey set foragers target as the encounter rate with favored preys changes. In our data, for example, we observe a smaller size of adult’s prey-set, which only include two or three types of shellfish, while children and teenagers collect up to eight or ten different types (see figure 6). Finally, the apparent negative effect of grip strength could be explained by features in the data. In particular, we have very few data points relative to adult men, who have higher strength but lower foraging returns than a woman of the same age, maybe because of different motivation behind the foraging and gender specified roles. For both grip strength and height, the data are not sufficient to reveal a clear pattern in the case of trap hunting.

One more aspect to consider is the underrepresentation of adults in our sample. This can be a feature of our data collection procedures, which explicitly targeted younger individuals. But ethnographic understanding supports the idea that adults do not forage nearly as much as children and teenagers do. In particular, for trap hunting, we are aware of only one adult man who occasionally practices the activity. This might be due to the fact that hunting in the forest is restricted by law and adults might either refrain from hunting because of legislation or might fail to report it to researchers. But also, hunting with traps has very low success rates, and relatively high costs in terms of time. Simply put, most adult men might have better things to do. Shellfish collection, on the contrary, can be a reasonably profitable activity: when the tide is low, the average forager is expected to collect more than 3 kg of unprocessed shellfish in a 3 hour-long trip. Still, adults are underrepresented in our sample. This might be due to the fact that adults, according to our models, do not have higher return rates than teenagers, and they might prefer to delegate collecting shellfish to their children, when possible.

Overall, although our results do not explicitly support ECT, they are also consistent with several other non-exclusive possibilities: long pre-reproductive periods might be exclusively driven by skills for the most difficult resources, or those where the skills of all foragers are relevant, e.g. communal hunting. Selection could also act through composition of the foraging parties and specialization: if each type of foraging requires at least one highly skilled forager, individuals who take a long time to acquire specialized knowledge contribute to certain types of foraging trips, and also get the benefits of participating in other foraging activities led by other specialized individuals. ECT may also have favored the emergence of traits such as selective imitations and attentiveness to other individuals' level of skill, or, more generally, social foraging may weaken the strength of selection for embodied capital.

In conclusion, we find that complexity of resources influences age trajectories in foraging returns, but also that returns are not improved by individual level ecological knowledge. However, once again, we remark on how complex human subsistence and its study are. Many different elements contribute to the foraging success in each type of hunting or gathering. These often vary during the lifetime of foragers due to development or aging, but also due to societal and technological changes, complicating the analysis of longitudinal foraging data, which themselves are fundamental to addressing time-varying questions. Moreover, societies perform multiple types of foraging, and, in order to appropriately address each of them, it is important to have an exhaustive ethnographic understanding of the subsistence strategies and how they vary across the lifetime, socioeconomic status, etc. Finally, inferences that can be generalized to the whole human species require cross-cultural analyses that additionally complicate the goal of keeping into account these ethnographic details. Although satisfying tests for hypotheses on the evolution of childhood are yet to come, here we pave the road for future studies clearly estimating the contribution of individual level traits to foraging success. This will help us understand the processes leading to the evolution of childhood.

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5 Supplementary materials

5.1 Ethnographic notes on hunting and gathering in Pemba

5.1.1 Trap hunting details

Hunting is a secondary activity in the village, either with the goal of obtaining additional meat to integrate in the foragers' diets, or to capture animals that pose a treat to crops. It is mainly done by young adult males. By practicing hunting, young adults interact with their environment and gain skills and knowledge that allow them to determine the best techniques, mechanisms and seasons to hunt various species. In particular, some factors influence hunting activities in the village.

Mechanisms used in hunting. Some mechanisms are unique for hunting specific species, for example bats are hunted by using *Msoo*, a long spiky stick that is shaken among nesting bats. This technique cannot be used for hunting any other species, like ibises. Glue is a flexible technique used to hunt several species of birds like Tongo, Sauti, Green pigeons and horn-bills, but it is not used for hunting bats. In this paper we focus on the use of snares.

Season of hunting. There is seasonal variation on optimally targeted species, which include ibises, duikers and green pigeons. The best season for hunting ibises is at the end of dry season, when the marshy areas in the forest tend to dry and are visited by these birds to find food, such as earth worms. Duikers are normally hunted during the rainy season, because they are more weary of predators and more sensitive to the smell of human bodies. During the wet season, human smell tends to be cleared by the rain in the area around where traps are built. Green pigeons are hunted around the time when one of their favorite foods, the fruits of palm trees (*misinduzi*), ripen. This species is hunted with the use of gluey sticks, snares and other types of traps.

Required skills. Setting up traps requires body strength, especially to build traps for duikers, which require stronger components. Ecological knowledge can help determine the paths the duikers take in the forest, and tracking skills help to recognize the footprints of duikers on the forest floor.

Snares construction and maintenance. Traps are built and activated as described in figure 4. They are then usually checked at regular intervals, as shown in figure 5. Sometimes, undesirable preys are captured in the traps, for example monkeys or mongooses. In this case, the animal is freed, usually unscratched, if rather unhappy. In other occasions, instead, mongooses or other predators might find a captured prey before the hunters do, and thus spoil the meat. It can also happen that the prey frees itself or that other people find it in the forest before the person who placed the trap. Finally, the trap can be triggered, but fail in capturing the prey, for example because it is badly placed. In all these cases, the trap is considered unsuccessful. Traps are deployed for periods of time ranging from a few days to about a month, and are often purposefully dismantled, although they might be forgotten for a while (see figure 5).

5.1.2 Shellfish collection

Fishing is one of the primary source of income in the village where data were collected. A large number of different techniques is employed in fishing, with shellfish collection and crab-fishing being quite common.

Shellfish collection is practiced mainly by females, both young and adults. There are two main elements to this technique: collection and extraction. Collection of shellfish involves the moving along the intertidal zone during the low tide and collection of the shells that do not live within the sandy substratum, such as those called *korong'onjo.* Shells which are usually embedded in the sand need to be extracted, digging by hand or with the help of a knife. These species include *Panga, Pangansole, Kombe, crabs, Kijinu* and *Maringapau* just to mention few.

Crab fishing in the village can be both a source of income and also contribute to family diets directly, and is sometimes practiced by younger or adult males. Crabs are normally extracted either in the exposed intertidal zone or among the roots of mangroves. Crabs differ in term of size, with larger and smaller ones. The bigger ones have great value and can be sold at a good price, while the smaller ones are often used as (delicious) stew. Fishing of bigger crabs requires skills, knowledge

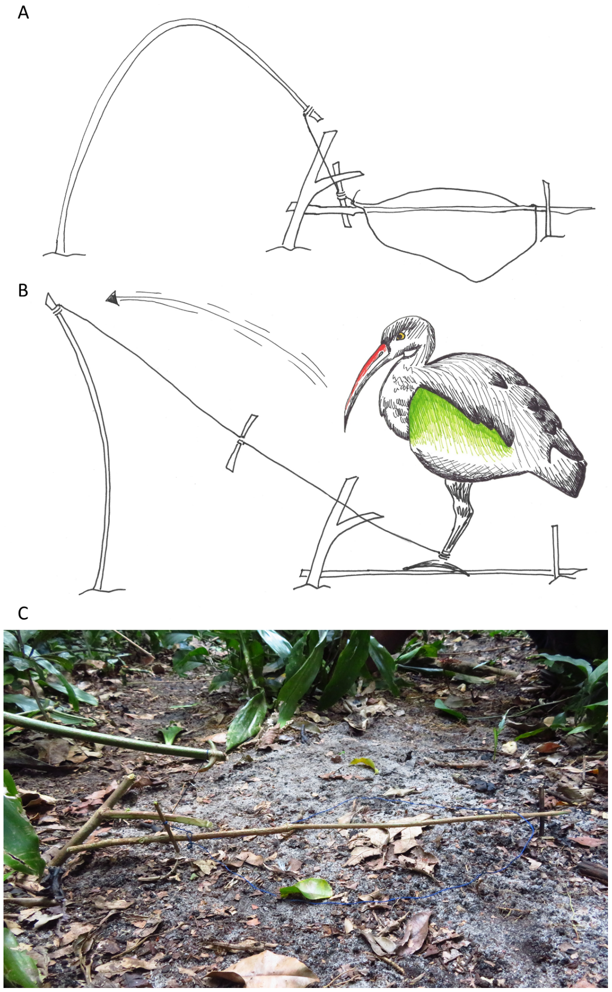

Figure 4: Traps are placed on the forest floor, along paths or where there are signs of animal passage–panel C. The mechanism acting as trigger is composed of two vertical sticks infixed in the ground, one of which features a branching opening at a wide angle, plus a longer stick placed horizontally between the two. On top of the horizontal stick is placed a common sewing thread, tied into a slipknot and tied to a long flexible branch, also infixed in the ground at some distance. Along the thread is tied a smaller piece of wood that blocs the trap once it's activate. Once all these elements are in place, activation happens by bending the long elastic stick so that the small piece of wood can be fixed behind the long horizontal stick and the branching of the smaller one infixed in the floor. This way, the horizontal stick is blocked at a certain distance from the floor. Once the prey steps on this long horizontal stick, it unblocks the piece of wood, allowing the long flexible branch to spring free from the bent position it was forced into. In doing this, the branch pulls the thread, which slipknot closes around the leg of the prey like a snare.

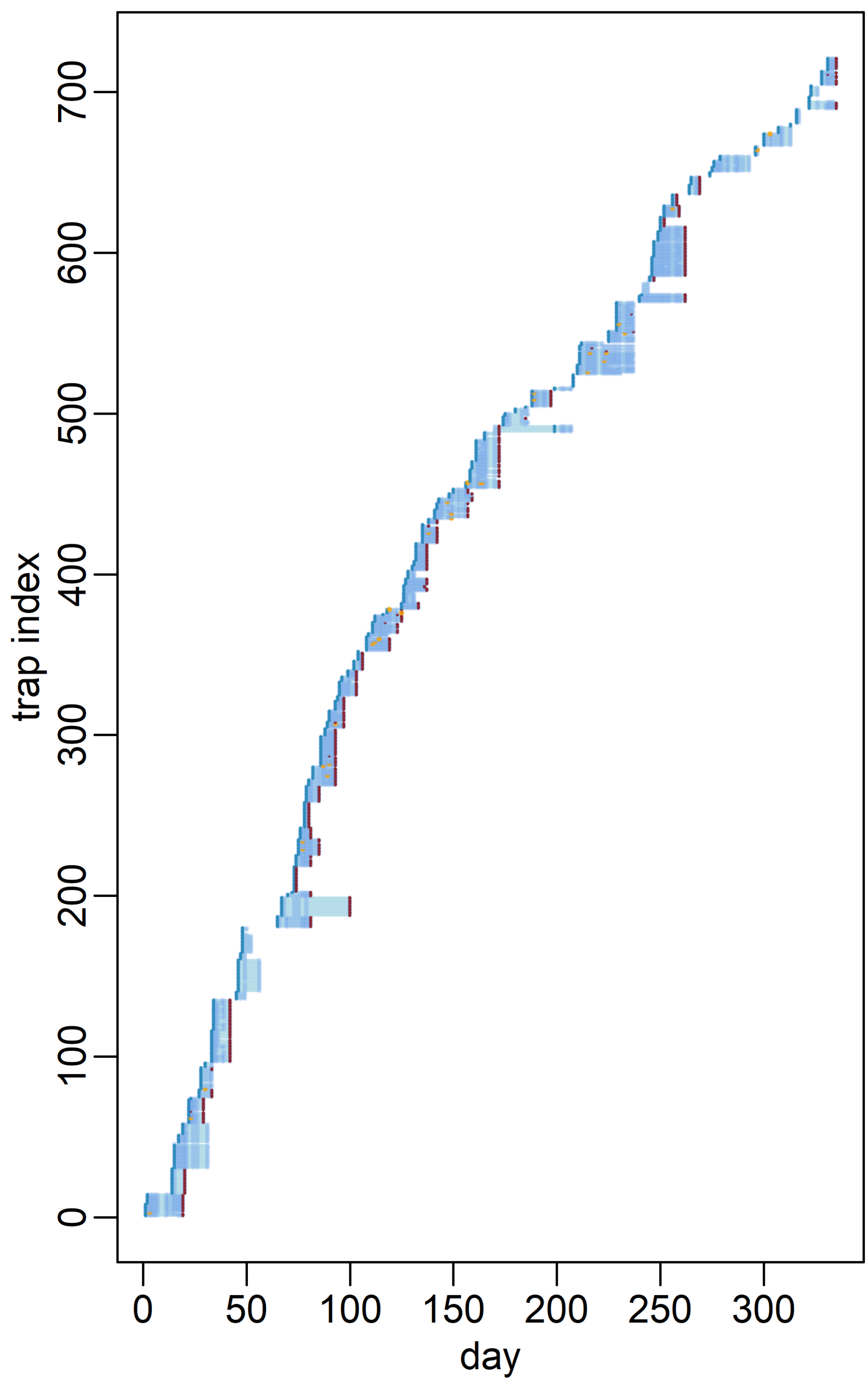

Figure 5: Exposure of all traps. Each trap occupies a row, while the position of the line marks when the trap was deployed, starting from the first of February 2020, when the first traps were built. Dark blue dots mark the building of the trap, dark red ones mark the active dismantling of the trap (note that some traps were not actively dismantled), while yellow dots mark the days when a trap captured something. Along the line, light color indicates that the trap has not been monitored, darker colors indicate that the trap has been checked.

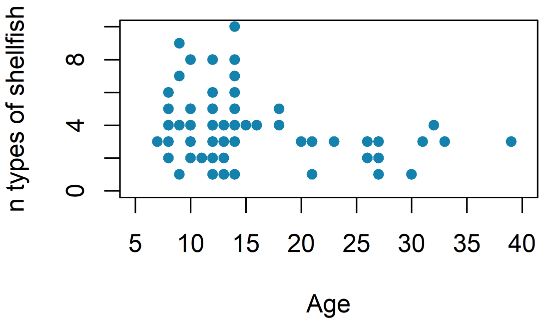

Figure 6: Number of different types of shellfish collected as a function of forager's age.

and strength because normally these species are found in muddy areas among the mangrove roots, so that tools like hoes and iron hooks must be used.

Several factors are thought to influence the collection and extraction of shellfish. These include:

Tide level. Lower the tide level are associated to larger catches and collection of larger specimens (see section 5.1.3).

Age of the forager. Younger individuals are thought to be less proficient foragers. Some shellfish types need strength to be extracted, for example *Panganole, Kimai* or *Mwamize* and some *Maringapau.*

Season. Season also influences shellfish collection or extraction in the village. During the dry season, shellfish like *Panga* are more available than during the rainy season, because the specimens that are exposed to atmospheric water tend to die. Hence there is lower availability of *Panga* during the rainy season compared to the dry one.

Nature of floor in the shellfish areas. Some areas are covered by slimy mud, while others are rocky and have a lot of spikes and very sharp shellfish like *Panga.* It is difficulty to collect and extract shellfish in these areas because most foragers are barefooted and risk getting cut on the coral rag.

5.1.3 Tide

For each foraging trip that was carried out on the shore or around it, information on tides have been recorded. In particular, time of low tide closest to the foraging trip, and minimum height of tide at that time. From these information we calculated the average tide height encountered during the trip. This has been accomplished by defining a function describing the tide height during the foraging period and calculating its average via grid approximation. A Gaussian kernel distance can imitate the behavior of tidal bulges, so that we can estimate height of tide while children forage, and hence calculate a value summarizing the average height of the tide during this period.

First, we need to estimate the width of the Gaussian function by modelling a curve that imitates average behavior of tidal bulges (see figure 7). Tides follow the movement of the moon around the Earth at regular time intervals, for example a minimum low tide happens on average 6 hours and ten minutes after and before the high tides immediately preceding and following it. Water height does not change linearly between high and low tide, but rather follows a curvilinear shape which can be approximated by the Gaussian function. For fishing/diving/surfing purposes, people approximate tide height using the rule of twelfth: divide the total tidal range, i.e. the difference between high and low tide, by twelve; in the first hour after low tide, the water will rise of a twelfth of the total tidal range; in the second hour water rises of two twelfths, of three twelfths in the third and fourth hour, and then starts decreasing to two and one twelfths in the fifth and sixth hour respectively. This means that after three hours, water levels will be about in between high and low tide. So the width (defined as the square of the standard deviation σ^2) of the Gaussian curve should be such that

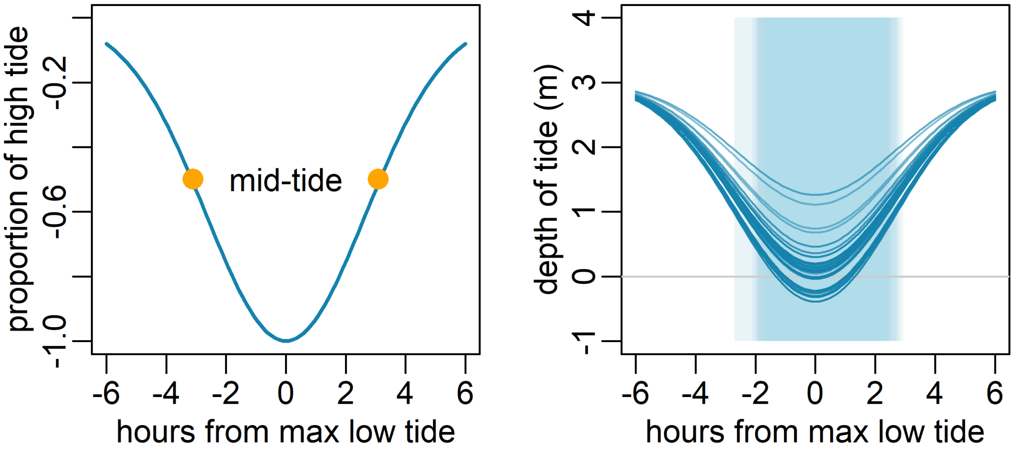

Figure 7: On the left, Gaussian curve parameterized so that it imitates the behavior of tidal bulges. On the right, curves showing estimated tidal levels during and around the shellfish foraging trip. The duration of each trip, relative to the minimum tide, is shown by the shaded areas. Note that the vast majority of trips are carried out while the tide is lowest.

the curves reach half of the distance between the minimum and the maximum (-0.5 in our plot) at about three hours. Note that the Gaussian distance kernel is defined by the function $-(x-y)^2/\sigma^2$. This function is defined between zero and one, which we invert here between zero and -1 so that it looks like low tide in a tide chart. The x axis below are hours from minimum tide.

Once the shape of the curve is identified, we re-scale the curve so that it maps onto the actual values of tides, i.e. what in the plot above is -1 becomes the low tide, and zero is high tide. Tide height is highly variable by day, for both high and low tide. We recorded values for low tide each day of data collection involving the sea, but we did not collect high tide. Hence, we cannot properly calculate this curve, and only provide an approximation using an arbitrary high tide value established by checking tide charts for the site of study (i.e. +3.00 m). We then can draw inverted Gaussian functions per each foraging trip, where the minimum is the recorded value for low tide and the maximum is an arbitrary high tide value.

The shaded area shows the time where the foraging trips happen, relative to minimum tide. They largely overlap the minimum level of water.

We can calculate the average value of these functions within the foraging period via grid approximation to get a different estimate of the impact of tide on foraging. This is very correlated to low tide values, with some differences. Mainly, long foraging trips include more time around low tide, and hence are ‘penalized’.

5.2 The statistical model

5.2.1 Model structure and priors

As described in the main text, our models employ separately the two components usually combined in a hurdle model to represent the probability of a trap capturing something and the kg of shellfish collected, respectively. These values are influenced by both forager and trip level factors, combined in the values ϕ and ψ respectively.

For the first section of our results, e.g. those represented in figure 2, ϕ depends on individual age only, with form:

$$\phi_i = \iota_i \left(1 - \exp(-\beta \, a_i)\right)^{\gamma} \tag{7}$$

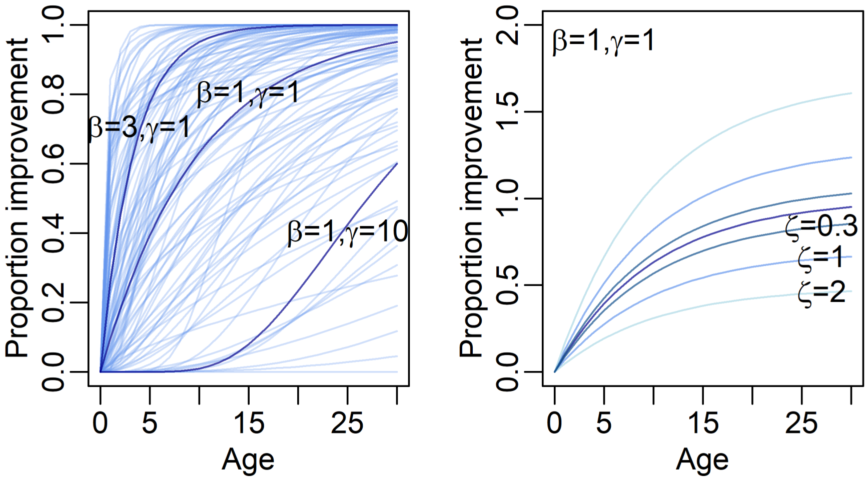

Figure 8: On the left, 100 lines showing possible relations between age and foraging according to the priors used in the models. Darker lines show specific combinations of β and γ parameters. In the models using only age as an individual level predictor, this is the only relation between age and foraging returns. When including other individual level traits such as height or knowledge, this relation changes, as shown on the right. Given β and γ equal to 1, individuals with higher knowledge will have on average higher returns than individuals with average knowledge, and lower if their knowledge is lower, as long as the effect of knowledge remains positive. How much higher and lower depends on the value of ζ, the exponent of knowledge, for which values of 1, 2, and 3 are shown here.

This allows the relation between age and foraging returns to take many functional shapes, increasing more or less steeply, earlier or later in life. Figure 8, left panel, shows what happens as values for β and γ change, as well as some samples extracted from the priors used in the models.

For the second section of the results, e.g. those represented in figure 3, ϕ depends on age, ecological knowledge, grip strength and height as described by function 5. Adding the effect of a trait means that the curves shown in figure 8, left panel, move 'upwards' or 'downwards' so that at each age, foragers who have higher or lower than average values for a certain trait will also have higher or lower values of ϕ and foraging returns.

Figure 8, right panel, shows, for different values of the exponent of a trait, e.g. ζ, the expected values of ϕ for individuals who possess higher or lower amounts of a certain trait.

5.2.2 Missing data

Our analysis focuses on a total of 63 individuals, considering both gatherers of shellfish and hunters. But different data collection procedures guided the collection of anthropometric and knowledge data, so that we did not have these kind of data for all of our focus individuals. In particular, we did not have knowledge data for about half of the focus individuals, and missed information on height and weight for a handful of individuals. In order not to limit our inference to complete case analysis, we adopted a data input procedure to estimate individual level measures for knowledge, grip strength and height of the individuals for whom measurements were missing. To do so, we used 94 measures of knowledge and more than 200 for the anthropometric data to define age and sex specific expected values, from which we sampled individual measures to replace the missing data.

We model each trait (i.e. ecological knowledge, height and grip strength) as a normally distributed quantity, with mean ν, which depends on age and sex of individuals.

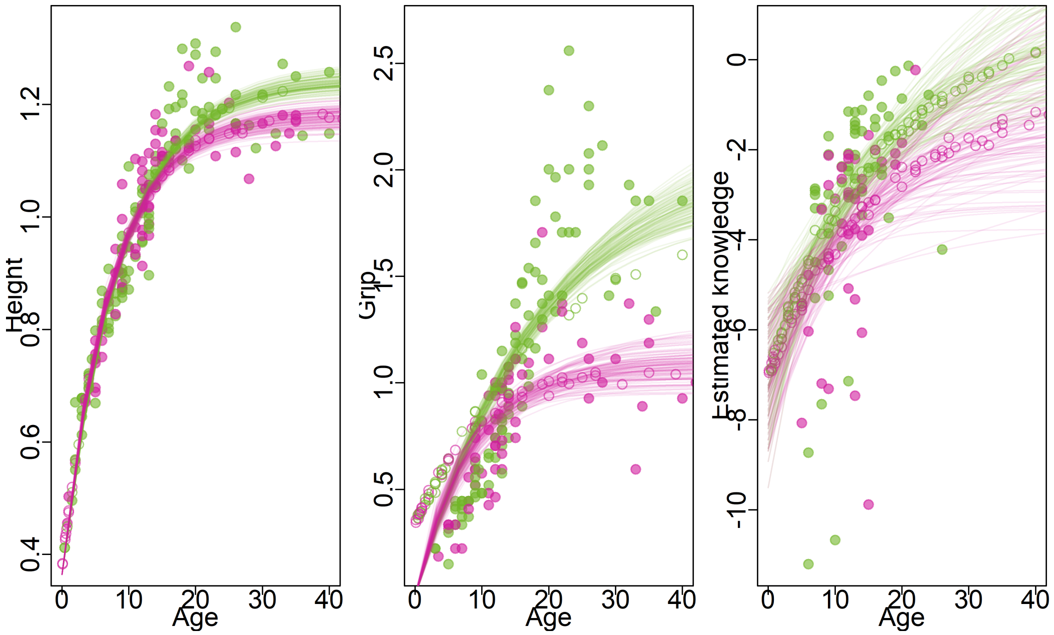

Figure 9: Available data as filled points, missing data as empty points. The model estimates average traits for individuals whose data are missing, taking into account their age and sex.

$$trait \sim \text{Normal}(\nu, \sigma) \tag{8}$$

$$\nu = \omega + \kappa_s * (1 - \exp(-\lambda_s\, a)) \tag{9}$$

Where ω represents the intercept of the function (i.e. the value of the trait at birth, which is zero for grip strength, 50 cm for height and a parameter estimated by the model for knowledge), a is age of individuals, and κ and λ are parameters that define the form of the function. The priors for these parameters are Exponential(1) across all traits.

This functional form allows the model to fit relatively well to the data and to sample measures of knowledge, grip strength and height from the average values for an individual of a certain age and sex (see figure 9).

5.2.3 Model validation

A model such as the one we developed for the present paper requires careful considerations in the development phase, as well as repeated testing before drawing conclusions from the results. In particular, to validate this model we first produced simulated data according to the assumed generative process, we then fitted the model to the simulated data and then we observed if the model can recover the parameters through which the data were generated. We find that the model tends to recover the relative order of the simulated parameters, thus confirming that it can pick up signals present in the data (see figure 10).

In this process, we can also test the performance of the model to different sample sizes. We find that the model works very well for sample sizes as low as 30 individuals for both shellfish and trap hunting, but that it is sensitive to the number of successes in the trap hunting data. In particular, its sensibility decreases at low proportion of successes, although it still recovers the order of the simulated parameters.

Using simulated data, we can also verify the ability of the IRT section of the model to recover knowledge estimates from freelist data, as well as ascertain that the missing data are correctly recovered (see figure 11).

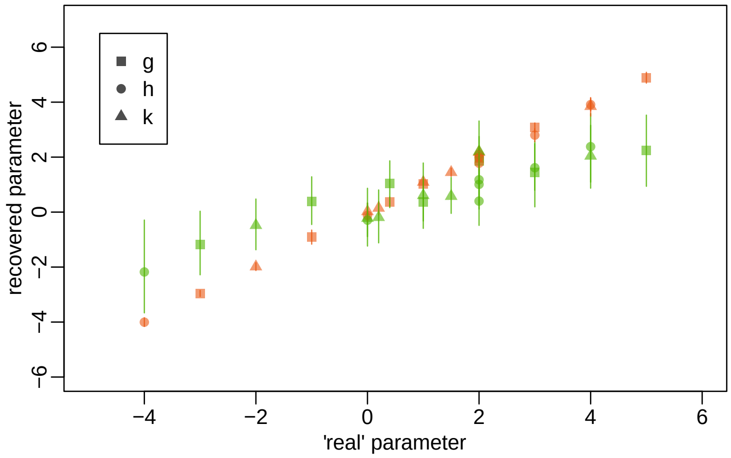

Figure 10: Recovered parameters vs parameters used in the simulation. The model does a great job of recovering parameters for shellfish data, in orange, and is overall capable of picking up the signal even for the trap data, in green.

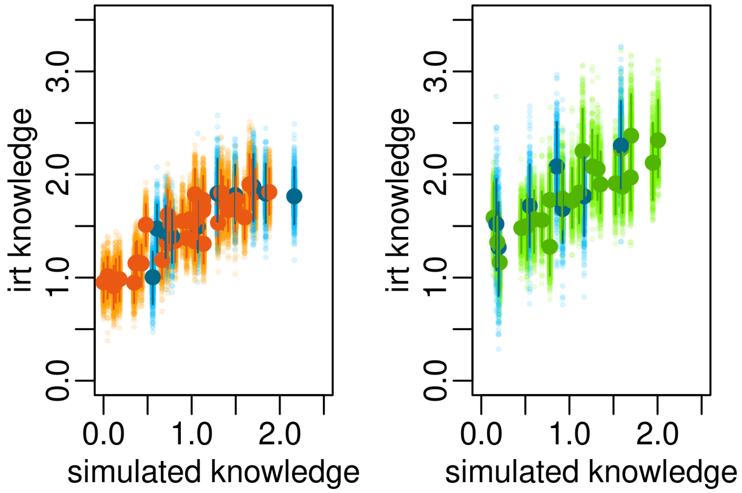

Figure 11: Simulated values for knowledge versus those recovered with IRT model. The IRT is very well able to recover the 'real' values of knowledge, i.e. the simulated ones. In orange and green knowledge values for the individuals for whom the model has access to simulated freelist data, in blue the individuals whose data are missing and whose knowledge is inputed.

5.2.4 Calculating counterfactuals

Figure 3 is difficult to interpret. The plots show distribution of a difference, i.e. a contrast, measured between counterfactual situations where all traits are kept constant apart from one.

What does this mean? A conterfactual is a statistical measure that estimates the outcome variable given a specific value of the data, in other words it calculates how many kg of shellfish/the probability of success of a trap built by an individual of a certain age, strength, height and knowledge. Varying the measure of these traits, we can estimate an outcome value of an hypothetical individual of average height and strength, who exhibit ecological knowledge equivalent to that of the most knowledgeable individual in the sample, at 20 years of age. We can then calculate the same value for another hypothetical individual, identical to the first, but exhibiting ecological knowledge equal to the lowest value in our sample. We can then subtract this value from the first, and obtain a contrast, i.e. the difference, on the outcome scale, between kg shellfish/ probability of success of two incredibly knowledgeable and un-knowledgeable hypothetical individuals.

These kind of measures, considering alternatively ecological knowledg, height, grip strength, duration of a trip and tide level as well, are shown in panels B and C of figure 3, for shellfish and trap data respectively.

In order to compare the relative effect of knowledge, height and strength between the two different types of foraging, we can compare the contrast of our counterfactuals not at the outcome level, but one step before, when we calculate ϕ. ϕ is an abstract value that summarizes the effect of individual level traits for foraging returns. We can then calculate counterfactual values of ϕ for hypothetical individuals varying in knowledge, grip strength and height and compare them between the foraging types, as these values are dimensionless and should not be dependent on the dimension of the outcome variable.

Differently from effect sizes, counterfactuals are often expressed in a scale that is understandable to the reader (e.g. kg of shellfish, while our ϕ difference refers to a measure *within* the model mechanics and is more difficult to understand). Moreover, as the effect of various factors is usually not independent, counterfactual estimation allows to consider them jointly, thus providing a more reliable estimate of real world variation.

Finally, considering counterfactuals allows to express results in more interesting ways, for example we can calculate how much shellfish an average forager of a certain age would collect at low tide, during a 3 hour long trip. Or, we can estimate age effects for a specific forager, using the individual level random effect of one single individual, as we did in figure 2. This way we can see the variation in the age estimates for trap hunting, which are barely visible in figure 12, showing the variation in trap success along the ages for the average forager.

Because a counterfactual takkes into consideration the whole joint combination of parameters in a model, which are sometimes transformed in non-intuitive ways, it is worth comparing the posterior counterfactual contrasts to the prior ones. Figure 13 shows the same results as figure 3, but comparing the posterior values of the contrasts to those expected by the model before seeing the data. The model's priors imply an expectation of no difference between short and tall people, for example. But having updated the posterior on the base of the available data, the model predicts that taller people will bring back more shellfish (the distribution is slightly above zero). On the contrary, the model does not update much its beliefs about the effect of height or grip strength for trap hunting, suggesting that the data do not provide enough information to reliably estimate these parameters.

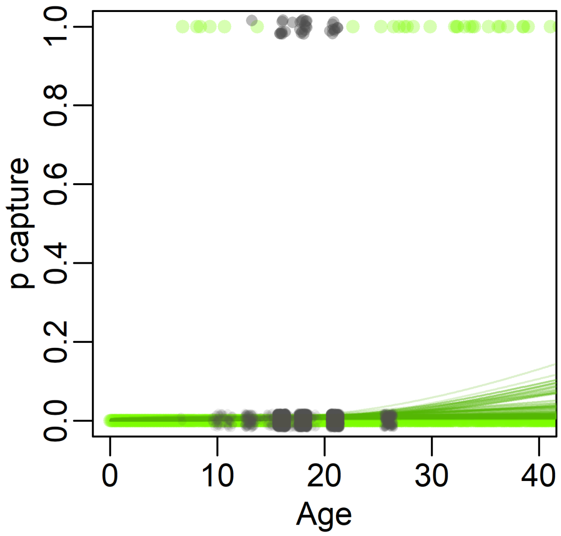

Figure 12: Plot equivalent to figure 2, panel B, but using the mean value for all foragers and mean time.

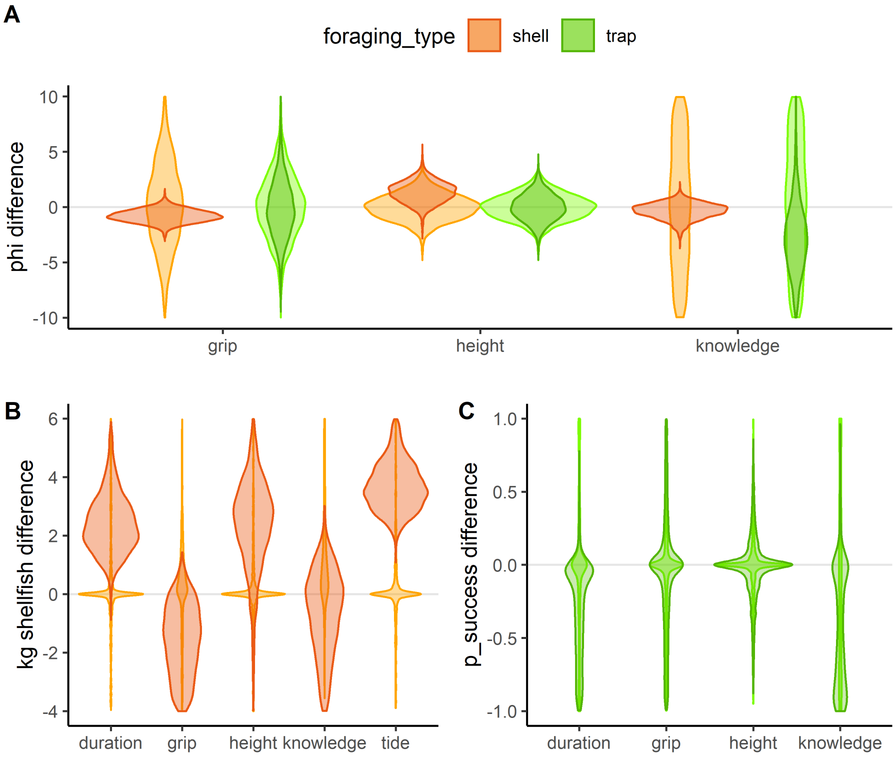

Figure 13: Same results as those presented in figure 3, but overlaying the posterior distributions, in darker colors, to the prior distributions, in lighter colors.