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Author for correspondence:
Michael D. Gurven
e-mail: gurven@anth.ucsb.edu

The optimal timing of teaching and learning across the life course

Michael D. Gurven†, Raziel J. Davison† and Thomas S. Kraft

Integrative Anthropological Sciences Unit, Department of Anthropology, University of California Santa Barbara, Santa Barbara, CA, USA

MDG, 0000-0002-5661-527X; RJD, 0000-0002-6752-826X; TSK, 0000-0002-0634-9233

The evolutionary biologist W. D. Hamilton (Hamilton 1966 *J. Theor. Biol.* **12**, 12–45. (doi:10.1016/0022-5193(66)90184-6)) famously showed that the force of natural selection declines with age, and reaches zero by the age of reproductive cessation. However, in social species, the transfer of fitness-enhancing resources by postreproductive adults increases the value of survival to late ages. While most research has focused on intergenerational food transfers in social animals, here we consider the potential fitness benefits of information transfer, and investigate the ecological contexts where pedagogy is likely to occur. Although the evolution of teaching is an important topic in behavioural biology and in studies of human cultural evolution, few formal models of teaching exist. Here, we present a modelling framework for predicting the timing of both information transfer and learning across the life course, and find that under a broad range of conditions, optimal patterns of information transfer in a skills-intensive ecology often involve postreproductive aged teachers. We explore several implications among human subsistence populations, evaluating the cost of hunting pedagogy and the relationship between activity skill complexity and the timing of pedagogy for several subsistence activities. Long lifespan and extended juvenility that characterize the human life history likely evolved in the context of a skills-intensive ecological niche with multi-stage pedagogy and multigenerational cooperation.

This article is part of the theme issue 'Life history and learning: how childhood, caregiving and old age shape cognition and culture in humans and other animals'.

1. Introduction

Humans everywhere take a long time to attain adult-level proficiency in a broad range of productive activities. This applies not only to industrialized economies where schooling, apprenticeship and on-the-job training can span over two decades, but to contemporary hunter–gatherers who represent the best analogue of foraging livelihoods and lifestyles more typical of our ancestral past [1,2]. Peak productivity in hunting and extractive foraging tasks often extends into the 30s and 40s [3–5]. This delayed proficiency is a conundrum because it imposes costs on others to subsidize growth and meet daily needs. It has been posited that such costs can be overcome if mortality is sufficiently low, and delayed development results in high adult production surplus [2]. Humans are unique among animals in obtaining tremendous surplus production in adulthood, a result that has been linked to large brain size and a complex foraging niche [6–8], coupled with a longer pre-adult life stage to attain skill proficiency. The rate at which proficiency is obtained in a skills-intensive ecology is therefore paramount to understanding the evolution of the human life history, yet much is unknown about how complex foraging skills are learned or the factors limiting proficiency gain. What role do teaching, instruction and other forms of pedagogy play in the development of proficiency? If the rate of skills acquisition is central to determining productivity over the life course, and postreproductive individuals play a key role in transferring skills, then natural selection could favour the evolution of postreproductive lifespan. Patterns of social transmission may therefore relate to species-typical life history.

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†Joint first author.

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Here, we first briefly synthesize the role of pedagogy in animal and human subsistence societies, and explore its potential relevance for explaining derived features of human life-history evolution. If teaching is so beneficial, why is it claimed to be rare in many species, and even among many human groups? We then present a formal framework for considering the contribution of pedagogy to biological fitness in humans, with relevance for other social animals. We introduce a modelling framework that links pedagogy with a faster rate of skills acquisition. Given costs to teachers and benefits to pupils, we model optimal ages for teaching and learning that facilitate maximal lifetime production. We consider how multigenerational pedagogy might shape production profiles and the efficiency of cooperation. Though the evolution of teaching is an important topic in behavioural biology and in studies of human cultural evolution, there are few formal models of teaching (e.g. [9,10]). We outline predictions and provide some preliminary tests among subsistence human populations to help understand age profiles of pedagogy in broader ecological context. We show that benefits of pedagogy vary by an activity's skill complexity, and that optimal teacher and pupil ages depend on both skill complexity and potential trade-offs with direct production. Low teacher costs combined with opportunities for pupil skill gain may help explain why teaching is more common for some activities and in some species than others.

(a) Human life-history evolution

Though the life expectancy of human hunter–gatherers ranges from 25 to 40 years, approximately 50–65% survive to age 15 and live an additional 40 years; moreover, the 25–35% who survive to the postreproductive age of 50 years can expect to live an additional 15–20 years [11,12]. The modal age of adult death in contemporary hunter–gatherers with no or minimal access to healthcare is about seven decades, suggesting that a long postreproductive period is characteristic of our species. The existence of a substantial postreproductive life stage is an evolutionary conundrum, yet postreproductive lifespans have also been observed in some cetaceans, elephants and insects [13]. The traditional force of selection derived from W. D. Hamilton [14] is central to understanding the evolution of ageing [15], but it considers fitness only in terms of direct reproduction. Adaptive explanations for a long postreproductive life therefore emphasize indirect fitness-relevant contributions made by older adults [2,16].

(b) Information as fitness-relevant transfer

As human subsistence shows relatively late ages of proficiency, children and adolescents rely heavily on food transfers from older adults to meet their daily nutritional needs [17]. The modern version of G. C. Williams' Grandmother Hypothesis was itself based on observations showing children to be ill-equipped to find and extract roots in the woodland savannah, whereas older women were highly productive and also engaged in protective childcare [18]. We propose that another type of transfer affects kin fitness: information. Information helps reduce uncertainty by communicating something novel or relevant [19]. The evolution of complex communication suggests that information transfer can provide myriad benefits, but here we focus on its potential to enhance the speed at which individuals obtain and master complex foraging skills. Unlike food, information is not zero-sum, may be difficult to exclude others from, and can be broadcast in a variety of ways, such as one-to-one, one-to-many or many-to-one. Information reliability can be a concern, especially when there is distrust, and/or when environmental change is frequent [20]. Especially if pedagogy is tailored toward kin, then the potential for pedagogical transfers to generate positive fitness value at postreproductive ages could help explain the evolution of longevity in some species. Given age schedules of production and consumption along with certain reasonable assumptions about the nutritional dependence of fertility and survival, one could amend Hamilton's influential 'force of selection' [14] to estimate indirect fitness contributions made through pedagogical investments (see electronic supplementary material, §S1).

2. Pedagogy and skills acquisition

(a) Non-human animals

Most reported instances of social learning in non-human animals pertain to foraging strategies [21]. Observation and imitation are two primary ways to learn from others' experience that do not require any explicit instruction or teaching, and account for most social learning in non-humans. Teaching, however, has a more restrictive definition in behavioural biology [22]; it requires modifying one's behaviour in order to help facilitate learning. Learning that occurs without teachers altering their behaviour would be considered an incidental byproduct. A key requirement of teaching is that skill development should occur more quickly with it than without [22,23]. Though sophisticated cognitive abilities (e.g. theory of mind) might help attune one's actions to the needs and changing performance of a student, the strongest evidence for teaching in the animal literature suggests that such abilities may not be necessary [23]: adult meerkats provide safe opportunities for young pups to learn how to handle dangerous scorpion prey in ways that increase their hunting skills [24], pied babblers help nestlings learn to associate certain purr calls with feeding opportunities [25], and rock ants take slower, longer routes to food when accompanied by naive followers in ways that improve their food search abilities [26]. All three species are highly social, consistent with the expectation that teaching is a form of cooperation, especially when teaching is costly. We report 28 species where potential teaching has been observed (compiled by Thornton & Raihani [27]), including orcas, hamadryas and olive baboons, and a number of avian species (figure 1). Though not an exhaustive list, figure 1 illustrates that the potential for teaching exists widely among taxa.

(b) Hunter–gatherers

Even if the prevalence of animal teaching is underestimated, it is widely accepted that cases of animal teaching are very specific, whereas human teaching is common and generalizes across many domains [28]. Studies in Western populations have tested the existence of specialized cognitive abilities oriented towards pedagogy, including attentional cues, high-fidelity imitation, over-imitation and mental state attribution [29,30]. The ability of humans to transmit information with high-fidelity figures prominently in theories about the evolution of cumulative culture, innovation and technology advancement and human uniqueness [31–33]. However,

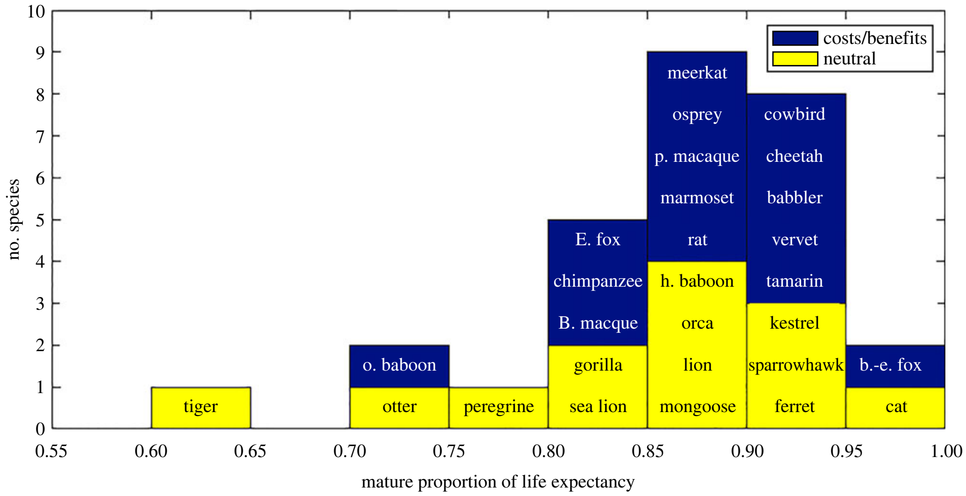

Figure 1. Animal species with suspected pedagogy. Cases of suspected pedagogy among 28 animal species catalogued in the Appendix of [27], shown as a function of proportion of the lifespan spent in adulthood after sexual maturity; o. baboon, olive baboon; B. macaque, Barbary macaque; E. fox, European fox; p. macaque, pigtailed macaque; h. baboon, hamadryas baboon; b.-e. fox, bat-eared fox. Blue and red bars refer to species that do versus do not show evidence of teacher costs or pupil benefits, respectively. Life-history information taken from University of Michigan Museum of Zoology Animal Diversity Web (https://animaldiversity.org/, see electronic supplementary material, table S3). (Online version in colour.)

there is a long-standing claim that teaching is rare in hunter–gatherers (typified by Lancy [34] and MacDonald [35]). At issue is the definition of teaching [32]. Formal classroom-like instruction with elaborate lesson plans is indeed absent in other species and most subsistence societies, but many other forms of knowledge transfer are possible [36–38]. For example, reinforcement in the form of positive evaluative feedback (e.g. a smile), or negative feedback (e.g. displeasing comment or sound), and 'natural pedagogy', where teacher cues (e.g. eye gaze, pointing) can focus a student's attention to a particular task [29]. Teachers may assign tasks or chores [39], demonstrate actions, monitor, supervise and correct poorly executed actions, especially during instances of 'opportunity scaffolding' whereby pupils are monitored after being given tools [37]. Social transmission without teaching occurs when students copy behaviours of others through mimicry and imitation, or emulation. By 'pedagogy', we refer to all of these types of teaching, even where there may be no cost to teachers (as teacher cost is a variable we manipulate in our model).

The explicit study of learning in hunter–gatherers is limited but growing, with the first volume synthesizing the literature published recently [33]. Given that most of human existence was spent living as hunter–gatherers, the evolution of pedagogy and its associated psychological capacities [29] may be uniquely informed by studies of foragers [40]. Social learning helps individuals adapt to environmental conditions, and can lead to cultural diversification. Though we focus on food production, pedagogy has also been studied with respect to ritual, mythology, morality and norm socialization [38]. Understanding the conditions that favour different types of transmission and a psychology oriented towards social learning is necessary to understand both human evolution and contemporary patterns of cultural and behavioural change.

3. A model of optimal pedagogy

(a) Overview

We present a model linking human subsistence strategies, pedagogy and population demographic rates to identify conditions where teaching is favoured, and to predict optimal ages of teaching and learning. Given population vital rates that determine a stable age structure and age profiles of production and consumption, we calculate net production across the life cycle. Surplus production enables transfers from prime-age foragers to dependents. While adolescents may be competent at acquiring some foods, recognized 'experts' in hunting, extractive foraging and other complex domains are usually older adults [1,35], suggesting complex skills mastery takes decades and could benefit from pedagogy. Our model enables teachers to boost the rate of pupil skill acquisition at some cost to their own productivity. In our steady-state framework, the pupil later becomes a teacher and the optimal strategy maximizes lifetime food production over the same life course by balancing the costs of teaching with the benefits of learning. Production can be largely strength-dependent (high-strength) or skill-dependent (high-skill). These axes determine the shape of the production function for different activities. The effects of pedagogy are stronger in high-skill settings, as instruction leads to an earlier age of skill mastery, resulting in higher lifetime production. Teaching is favoured when the expected future production gains of the pupil more than offset any production losses due to teaching, after accounting for mortality attrition. Using the population-level effects of teacher–pupil pairing at different ages, we identify optimal age combinations under which aggregate population production is higher with teaching than without. When teaching efficacy improves with skill, and when declining production reduces opportunity costs (given somatic ageing), teaching by older adults is favoured. Younger, less skilled peers are also expected to teach when their productivity is relatively low.

(b) Model construction

Baseline production (P_x) at age x combines effects of physical strength (S_x) and knowledge or skill (K_x) [*sensu* 41] as a standard Cobb–Douglas production function (electronic supplementary material, figure S1 and table S2):

$$P_x = S_x^{\alpha} K_x^{\beta}. \tag{3.1}$$

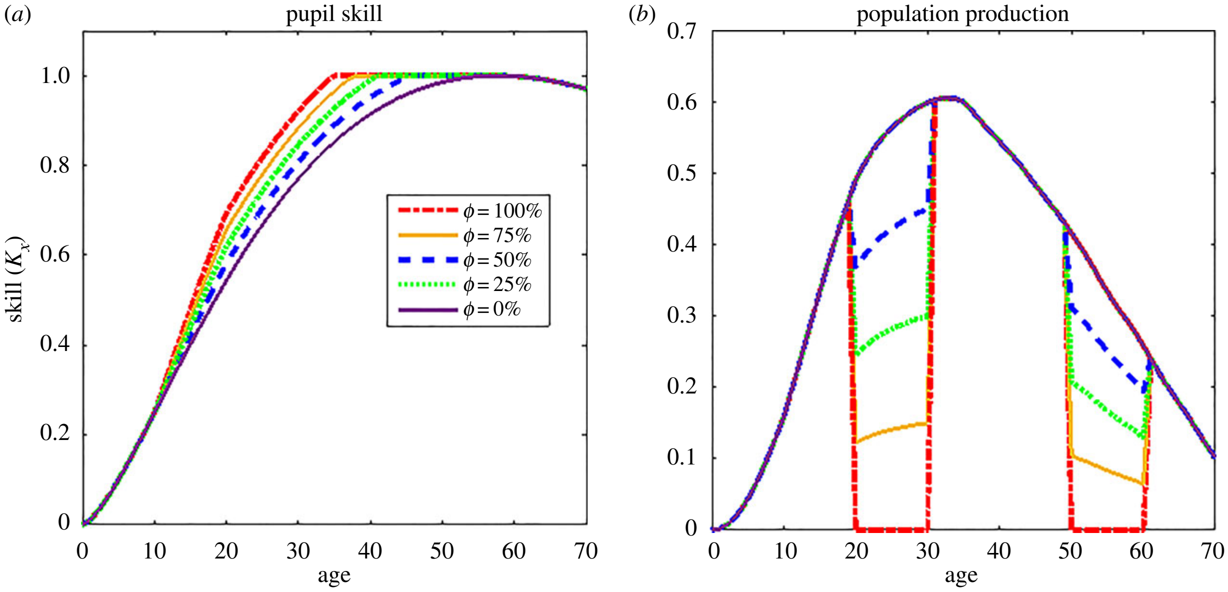

Figure 2. Skills ontogeny reflecting pupil boost (θ) and teacher handicap (φ). (*a*) *Pupil benefit*: a pupil at age 10 is taught for 10 years and increases rate of skill acquisition by the boost ($0 \le \theta \le 1$), thereby reducing age at skill mastery. (*b*) *Teacher cost*: A teacher suffers a loss in production during the 10 years of teaching by a proportion φ of baseline production. Notice for a given φ that absolute production loss is lower when teaching occurs later in life (e.g. when $b = 50$ instead of when $b = 20$). Inset values show the lost production across the 10 years of teaching, where 1.0 represents 1 year of peak production. (Online version in colour.)

Here, α and β modulate the relative importance of strength versus skill, respectively, in determining production (electronic supplementary material, figure S2). For humans, strength increases relatively rapidly with age, peaks in the mid-20s, and then declines slowly, whereas skill increases slowly, peaks in late adulthood, then declines slowly to reflect cognitive ageing (electronic supplementary material, figure S1a). Population age structure is defined by the stable age distribution predicted under constant age-specific survivorship (l_x) and fertility (m_x) schedules. We assume average survivorship and fertility age schedules of hunter–gatherers from Gurven & Davison [42].

We add pedagogy by allowing teachers to improve skills of younger individuals at some potential cost to their production. A pupil receives instruction at age a, until age $a + t$ or until skill mastery is achieved. Pedagogy increases annual pupil skills acquisition rates ($\mathrm{d}K/\mathrm{d}x$, $K_x = 1$) by a factor θ (pupil boost) (figure 2). The extent of pupil boost is affected by the availability of teachers ages b to $b + t$ reflected in survivorship l_{x+q}, where q is the age difference between students and teachers ($q = b - a$). We let teacher efficacy increase with skill, so θ is further discounted by the skill of the teacher (K_{x+q}) relative to mastery. Thus, skills ontogeny reflects baseline skill (K_a) in the absence of pedagogy plus the pupil boost (θ) applied to baseline skills acquisition rates ($\mathrm{d}K_x/\mathrm{d}x$), depreciated by teacher survivorship (l_{x+q}) and teacher skill (K_{x+q}) across the ages a to $a + t$:

$$K^*_{a<x<a+t} = K_a + \theta \sum_{y=a}^{x-1} l_{y+q}\, K_{y+q}\, \frac{\mathrm{d}K}{\mathrm{d}y}. \tag{3.2}$$

A teacher instructs for a maximum of t years from ages b to $b + t$ at annual cost φ ($\varphi = 0$ reflects no cost, or 100% baseline production, $\varphi = 1$ indicates that production is reduced to zero) (figure 2; electronic supplementary material, table S3). Production during this period of instruction is

$$P^*_{b_{\le x<b+t}} = (1 - \varphi) S_x^{\alpha} (K_x^*)^{\beta}, \tag{3.3}$$

where K_x^* is skill at age x accounting for the pupil boost to skills ontogeny. Because we cap skill at mastery ($K_x = 1$), pedagogy fosters earlier mastery (at age $x_{K\max}$), thus increasing the duration, but not the level, of maximum skill. After instruction ends at pupil age $a + t$, skills ontogeny reflects residual benefits of the pupil boost but skills acquisition thereafter returns to the baseline rate ($\mathrm{d}K_x/\mathrm{d}x$). In the electronic supplementary material, we also explore the effects of pupil preparedness, whereby some minimal level of skill is necessary to benefit from teaching, thus delaying the optimal age of students until pupil skill increases (electronic supplementary material, figures S3 and S4).

The costs and benefits of pedagogy reflect the trade-off between φ-handicapped teacher production and θ-boosted pupil skills over a single, optimal life course; pedagogy is favoured by conditions where survival-discounted lifetime production ($P_{\mathrm{L}} = \sum_{x=0}^{T} P_x l_x$) with the pupil–teacher arrangement exceeds baseline production ($P_{\mathrm{L}}^* > P_{\mathrm{L}}$). For a subsistence activity with strength requirements α, skill requirements β, teaching handicap φ and pedagogical boost θ, we identify the boundary thresholds of pupil age, teacher age, and teaching duration ($a^{\dagger}$, $b^{\dagger}$, $t^{\dagger}$) favouring pedagogy, and the optimal pedagogical arrangement (a^*, b^*, t^*) that maximizes lifetime production. Below we highlight some features of our model applied to hunter–gatherers, but provide MATLAB code so that others can make modifications or apply the model to other species or contexts (available at https://osf.io/38624/).

(c) Model results

(i) Benefits of pedagogy

Low survivorship to older ages limits the availability of older teachers and increases the likelihood a teacher will die before instruction is complete. Thus, solely from the pupil's perspective, mastery can be attained sooner and more reliably by having middle-aged teachers because they are more available (electronic supplementary material, figures S3 and S4), despite having lower skill than older teachers. Optimal age for pupils

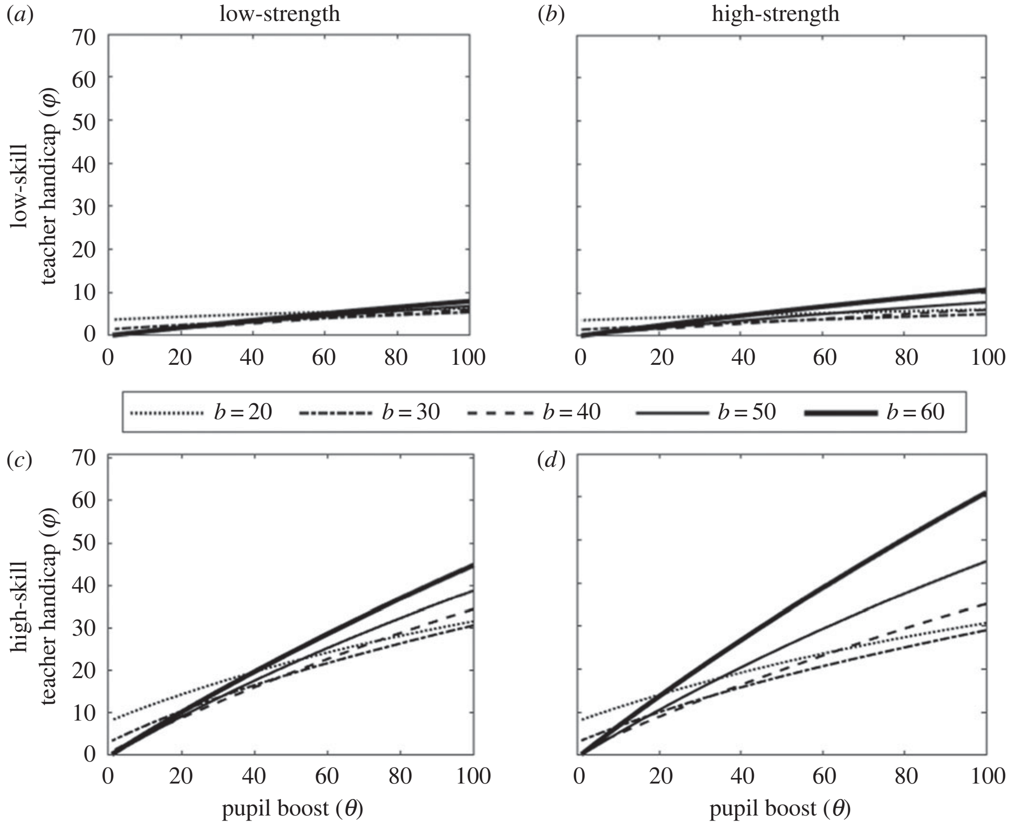

Figure 3. (*a–d*) Boundary analysis for optimal pedagogy. Break-even isoclines indicate maximum teacher handicaps (φ) and minimum pupil boosts (θ) for which pedagogy yields higher lifetime production ($P_{T*} > P_T$ lies in the bottom right corner of each panel). Shown for subsistence activities with low- versus high-strength requirements (columns) and low- versus high-skill requirements (rows). Different lines show boundary conditions for different ages of teacher onset (*b*, legend), assuming pupils begin instruction at age 10 ($a = 10$) and continue for 10 years ($t = 10$).

to begin learning is when the rate of skill acquisition $\mathrm{d}K_x/\mathrm{d}x$ is maximal (age 7 in electronic supplementary material, figure S3 top row), but is more delayed if learning itself requires having some skill threshold, as we expect for more difficult tasks (age 21 in electronic supplementary material, figure S3 bottom row).

(ii) Costs of teaching

Lifetime production suffers if high producers are handicapped by teaching, so higher teacher handicaps favour young and old teachers with lower opportunity costs (figure 3).

(iii) Costs and benefits combined

We consider break-even thresholds where pedagogy increases lifetime production beyond baseline ($P^*_\mathrm{L} > P_\mathrm{L}$) across four subsistence regimes, permuting high/low-skill × high/low-strength requirements of production. These can also be viewed as separate activities in a single subsistence economy, each varying in its reliance on strength and skill. For example, bow hunting and honey collecting may often be characterized as high-strength/high-skill, fruit gathering may be low-strength but low- to high-skill depending on context, hook-and-line fishing may be low-strength/medium-skill, water fetching may be low-skill/high-strength where water sources are readily available, but more high-skill in desert environments.

In a low-skill setting, teaching is only favoured when teacher handicaps are very small and pupil boost is very high (figure 3*a*,*b*). Young adults are more likely to teach when pupil boost is low. Higher strength requirement reduces early- and late-age productivity and so makes teaching less favourable for strong, unskilled youths, but more worthwhile for skilled older adults with declining strength (figure 3*b*,*d*). For low-skill activities, where there is only minimal increase in lifetime production from pedagogy under low teacher handicap ($\varphi \leq 5\%$), we expect only high-efficiency (high θ) pedagogy by the oldest adults, and no pedagogy if teaching is costly ($\varphi > 10\%$) (figure 4).

Teaching is more favourable in high-skill settings (figure 3*c*,*d*), and results in greater total production over the life course (figure 4; electronic supplementary material, figure S5). As long as teacher handicap is not too high, and pupil boost is sufficient, teaching is favoured across adult ages. For high-strength/high-skill activities, teaching by older adults is most favoured. Younger students may benefit from peer-aged teachers, but older students require older teachers, consistent with multi-stage teaching over the life course (electronic supplementary material, figures S5 and S6).

(d) Predictions

The following three predictions are inspired by our modelling exercise:

1. Skill-intensive niches show greater opportunity for pupil boosts in production, and greater net effects on lifetime production. Costly teaching is expected to be more favourable in species with complex foraging niches and is expected for more skill-intensive (high-skill) activities.
2. Teaching should be more common in long-lived species where pupil boosts early in life can yield production dividends throughout later life, thus offsetting costs

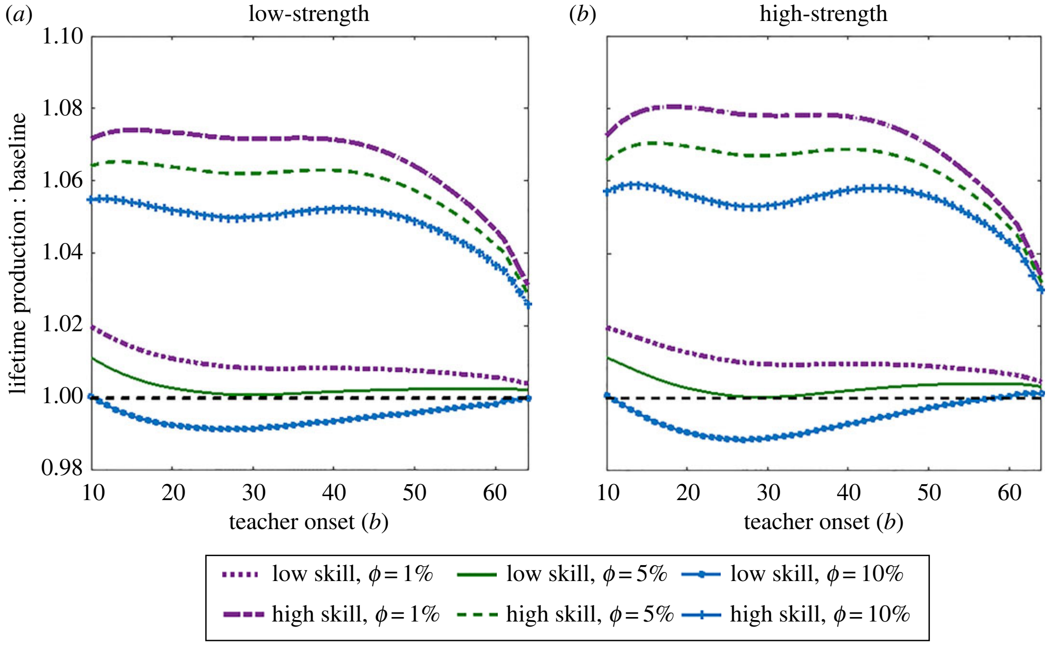

Figure 4. Lifetime production effects of pedagogy. Lifetime production (P_{T*}, *y*-axes) is shown for activities differing in strength and skill requirements, across a range of ages of teacher onset (*b*, *x*-axes) and with teacher handicaps (φ) ranging from 1 to 10% with a strong pupil boost ($\theta = 100\%$) and early pupil onset ($a = 10$). Solid lines show results for low-skill activities and dashed lines show results for high-skill activities. Bold dashed black line is the break-even threshold ($P_{T*}/P_T = 1$). (Online version in colour.)

borne by teachers. Teaching should be especially important for species with late maturity, which often reflects a relatively long period of child dependence.

(3) Teacher–pupil pairings should maximize pupil learning while minimizing teacher costs, which may explain why evidence for direct instruction is relatively rare. Also, economies of scale favour one-to-many instruction, which magnifies teacher effort to simultaneously impact multiple pupils (increasing P_T by applying the pupil boost θ to a wide range of ages, and also effectively increasing θ by boosting skills acquisition in multiple pupils simultaneously). Language certainly makes teaching less costly, as does the existence of pedagogical cues and context-sensitive psychology, but language requirements for communicating the complex information required for cooperative foraging may also delay optimal pupil onset and peak production as youths develop the necessary vocabulary and detailed working knowledge. 'Natural pedagogy' should be most evident to help facilitate information transfer at lower cost in complex skill-intensive settings.

Additional relevant predictions from our model are not necessarily unique to it, as others have connected complex skills with costly teaching and multi-stage teaching, or reflected on the cooperative nature of teaching (e.g. [9,20,27,43]):

(4) In our model, the potential for free-riding is not a concern because fitness interests were coincident in our single life cycle approach to optimization. In real populations, teaching should be more common when the fitness outcomes of teachers and pupils are more tightly linked, e.g. through kinship, food sharing, cooperative foraging, and cooperative breeding. Lower inclusive fitness effects or low fitness interdependence should favour only low-cost teaching.

(5) Though we model a steady-state teacher–student dyad, in complex ecologies characterized by a multifaceted skill set, we expect multiple teachers at different ages. This is consistent with 'two-stage' or 'multi-stage teaching' [40,44,45], first to foster basic skill proficiency and then to develop and refine expertise. Also, if some tasks require more knowledge or skills to be an effective learner, then ages for pupil training in skill-intensive tasks should be older than those for low-skill activities.

4. Preliminary tests of model predictions

We assess a few of our predictions in new analyses of existing data. While limited in scope, they help illustrate the kinds of tests that will be needed to better explain variability in teaching behaviour.

(a) Non-human animals

Social learning appears to be common in animals, despite costly teaching being rare [23]. If juveniles of precocial species are largely self-sufficient soon after birth, potential pupil benefits from pedagogy may be minimal. Teaching costs may also be high in the absence of complex communication abilities. For the 28 species with reported pedagogy shown in figure 1, the majority (21 or 75%) are carnivores or omnivores, and seven are frugivores, insectivores or granivores. This observation is consistent with teaching being more useful where feeding strategies are more complex. Teaching may also be more common where the potential pedagogical gains persist over a longer time period. Though the sample in figure 1 includes mostly short-lived species (median life expectancy $e_0 = 16.2$ years), 57% above the median e_0 include evidence of either teacher costs or pupil benefits versus 50%

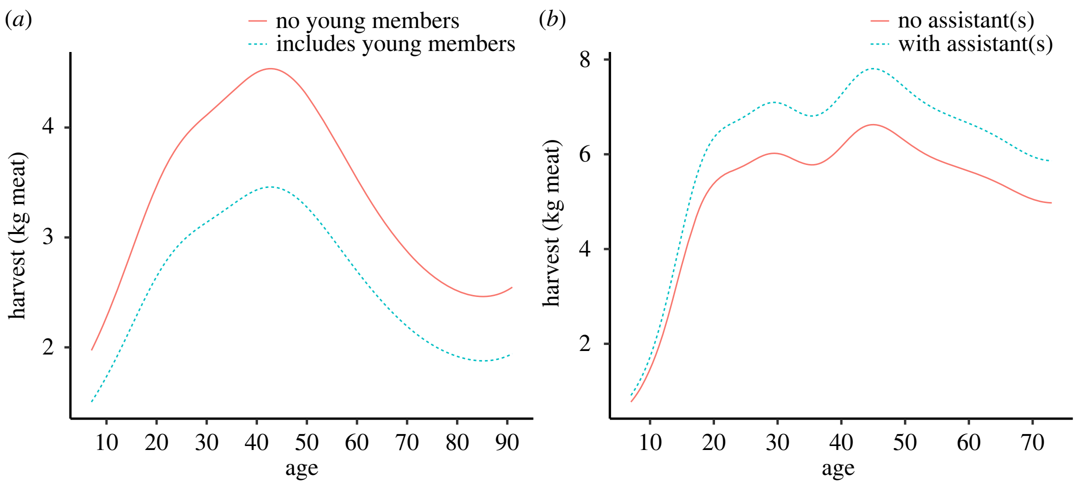

Figure 5. Hunting returns with and without the presence of one or more young (less than 20 years old) cooperative foraging group members (*a*) or younger 'assistants' (*b*). Lines represent predicted means based on multilevel models (see the electronic supplementary material for details). Statistical assessment for differences between groups in both panels are reported in the text. Note that panels (*a*) and (*b*) have different *x*-axes because there were no observations of assistants accompanying hunters older than 73 years. (Online version in colour.)

below the median e_0. Though suggestive, this difference is not statistically significant (one-tailed Welch's t-test: $t = 1.71$; $p = 0.31$). Species with documented teacher costs or pupil benefits also trend toward spending more of their lifespan in post-mature adulthood (figure 1, $t = 1.73$, $p = 0.13$). While not a definitive test based on a random sample, this last observation is consistent with the prediction that pedagogy is favoured by a longer period over which to reap the gains of early learning, and because of greater availability (i.e. survival) of potential teachers. Teaching should also be more prominent among cooperative breeders, where joint fitness interests are high, and where all benefit from group-wide sharing if juveniles transition earlier to independence [27]. These features are central to human fitness, where successful childrearing requires cooperative breeding and where kin groups share food extensively, and also may explain why teaching has been observed in tandem-running ants, social bees, meerkats, pied babblers and callitrichids.

(b) Human hunting and teacher costs

Hunting proficiency takes longer to achieve than many other subsistence activities, with production efficiency peaking around 30–45 years [3–5,35]. Certain tasks like hitting a target and identifying spoor may be learned early and quickly [4], but effective search, pursuit and capture take longer to learn. Juveniles learn about animal behaviour and biology well before they start hunting, gaining vicarious experience from hundreds of hours of stories heard around the campfire (low-cost, one-to-many teaching by elders). Child pretend play often mimics adult subsistence tasks, especially when actually performing those tasks would be dangerous or risk resource loss [46,47]. Such play behaviour often transitions into increasing participation in the actual work activity. Children often only start 'apprenticing' in adolescence with older male relatives, consistent with the need for pupil preparedness prior to direct instruction. While on-the-job learning accompanying experienced hunters involves much observation and passive learning through direct experience, we suspect that experienced hunters may alter their behaviour in ways to help convey skill development. But does such potential teaching come at a cost to hunters?

Our model generalizes to any subsistence task, but we focus our two empirical tests of teaching costs on hunting for two reasons. First, as a high-skill activity, hunting is expected to show strong evidence of teaching, and with a notable cost to production. Second, to our knowledge, extensive cross-cultural data on gathering and other subsistence activities suitable for such tests do not exist. Here, we use a recently published database that includes more than 23 000 records of 1800 individuals from 40 locations [5]. In the first test, we examined cases of cooperative foraging trips that included primary group members less than 20 years old ($n = 953/3145$ person-hunts). In the second test, we examined cases in which one or more non-productive 'assistants' (less than 20 years old) accompanied primary foragers on hunting trips ($n = 424/4706$ person-hunts). The difference between these cases lies in an explicit distinction in the dataset between primary foragers and assistants, who were defined as individuals on hunting trips 'to whom harvested biomass cannot be credited'. For each we constructed a binary variable of *potential* teaching, with the expectation that controlling for other variables, hunting returns would be reduced by the presence of young foragers or non-productive assistants. Following [48], we tested for such an effect by specifying a multilevel lognormal hurdle model of hunting returns as a function of teaching (indicated by the presence of young group members or assistants) and age (modelled with a smoothing spline). In all models, we adjust for potential confounders, including type of technology, foraging party size, hunting trip duration, and use of dogs, and include individual- and population-level random intercepts (see electronic supplementary material, §S2 for further details).

In accordance with our predictions, we found that inclusion of a young forager (less than 20 years old) in a hunting group substantially decreased expected harvest size ($\beta = -0.26$, 95% CI = [−0.44, −0.11]; figure 5*a*). For a peak-age forager hunting in a group of two, for example, having a young companion is predicted to reduce harvest by 23% (1.2 kg). However, *contra* predictions, our second analysis of assistants found no effect of inclusion on hunting outcomes ($\beta = 0.16$, 95% CI = [0.01, 0.31]; figure 5*b*).

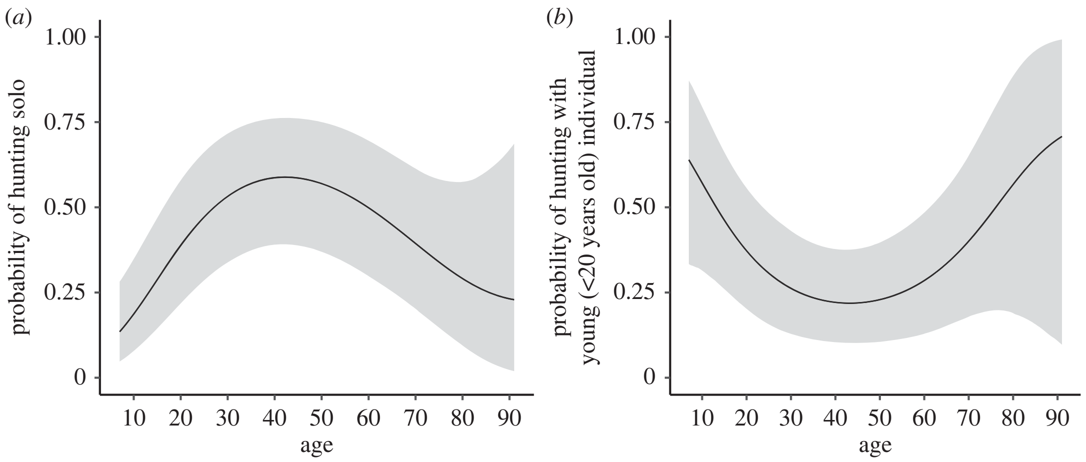

Figure 6. Hunting group composition. The probability of hunting solo (*a*) or having a young (less than 20 years old) companion on a cooperative hunt (*b*) across the life course. Lines and shaded regions represent predicted means and 95% quantile intervals based on multilevel models (see electronic supplementary material for details).

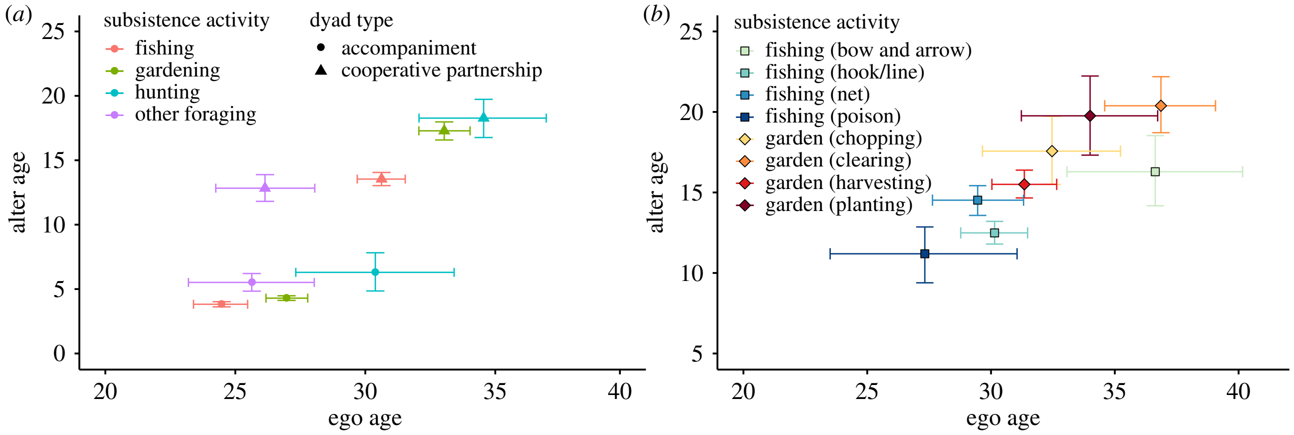

Figure 7. Ages of Tsimane teachers (ego) and students (alter) for (*a*) four major activity categories, and (*b*) sub-categories of fishing and horticulture. 'accompaniment' refers to cases where assistants were present but did not directly contribute to production. $N = 3016$ forager–assistant dyads and 3115 cooperative partnership dyads from Tsimane time allocation data. Points and error bars represent means and bootstrapped 95% confidence intervals, respectively. Subsistence activities vary in participation by sex: teacher % male: fishing = 49% in dyads with accompaniment/59% in dyads with cooperative partners, gardening = 38%/55%, hunting = 52%/81%, other foraging = 52%/60%; assistant % male: fishing = 52%/61%, gardening = 47%/43%, hunting = 37%/71%, other foraging = 44%/56%). (Online version in colour.)

(c) Human hunting and age of teaching

A second empirical test concerns the age at which teaching occurs (e.g. teacher onset) for a high-skill activity such as hunting. Our model suggests that the optimal arrangement for teaching includes relatively young peers and older teachers, with a less optimal outcome for teachers near the age of peak production (figure 4). We would thus expect most teaching arrangements to evince a bimodal age pattern.

The data in [5] provide detailed information on the size and composition of hunting parties that can be used to test this proposition.

Using the subset of data from all societies in which cooperative hunting was documented, we modelled the probability of a hunter foraging solo as a function of age, as well as the probability of a hunter foraging in a group with an individual less than 20 years old, conditional on participating in a group hunt (see electronic supplementary material, §S3 for further details). Consistent with predictions, hunters of peak production ages (e.g. 30–45 years) were the most likely to hunt solo and least likely to hunt with younger apprentices (figure 6). Participants younger than age 20 were also most likely to be found in a hunting group consisting of either relatively old or young hunters, but not with individuals of peak ages (figure 6).

(d) Ages of teacher–student dyads among Tsimane Amerindians

Higher-skill subsistence activities are expected to benefit more from pedagogy, and pupil age should be older for difficult tasks requiring some threshold level of competence. Older student age may be particularly important for sensitive activities like hunting where a novice could get lost, inadvertently scare away prey or reduce the travel speed of foraging parties during pursuit. Teachers are also expected to be older in order to have well-developed skills, but teaching age must also be balanced to spare costs during highly productive years. To test these predictions in a broad range of subsistence activities, we explored age combinations of producer–assistant (teacher–pupil) dyads among Tsimane forager–horticulturalists using a large sample of behavioural scan observations (see electronic supplementary material, §S4 for details) [49]. In increasing order of difficulty (confirmed by ages of peak productive efficiency, informant reports and prior literature), we examined: fishing ($n = 771$ dyads), slash-and-burn farming ($n = 1211$ dyads), fruit and honey gathering ($n = 147$ dyads) and hunting ($n = 104$ dyads). Consistent with predictions, we found that teachers and pupils were both older for more skill-intensive activities (figure 7*a*). We also observed more producer–assistant dyads for the lower-skill activities, suggesting that it is more feasible for assistants to be present.

In a second analysis, we compared age combinations of cooperative dyads in which both individuals were primary producers (as opposed to forager–*assistant* dyads above; see electronic supplementary material). Consistent with our findings on producer–assistant dyads, hunting, followed by horticulture, involved older ego/alter combinations than any other work activities (figure 7*a*). Fishing and fruit/honey gathering, involved similar age combinations (figure 7*a*). Despite having similar mean participant ages, the distribution of ego–alter age combinations is quite different between hunting and horticulture, with a much higher participation in cooperative farming activities by young (less than 15 years old) individuals (electronic supplementary material, figure S7). These results demonstrate that potential opportunities for transmission of high-skill activities are more likely to occur at older ages, and with older-aged role models.

We additionally compared age combinations of cooperative dyads for sub-categories of fishing and horticulture that require different levels of skill and strength for engagement (figure 7*b*). Types of fishing can be ranked in increasing skill requirements: poison fishing (low-skill/low-strength), net fishing (low-skill/low-strength), hook-and-line fishing (medium-skill/low-strength), bow fishing (high-skill/high-strength). Consistent with our prediction, ages are higher in teacher–student dyads the greater the skill required (figure 7*b*). For example, cooperative poison fishing shows mean teacher–dyad ages of 27 and 11 years, respectively, whereas bow hunting shows ages of 37 and 16 years, respectively. For horticulture, planting and harvesting are low-skill/low-strength, effectively clearing underbrush with a machete can be low-skill/medium-strength, and chopping trees is usually a medium-skill/high-strength activity. In partial agreement with our prediction, harvesting shows lowest teacher–student ages, then chopping, planting and clearing in increasing order (figure 7*b*).

5. Discussion

We highlight the value of pedagogy for improving skills acquisition in complex feeding ecologies. Teaching is not expected when proficiency is attained quickly and easily by juveniles, consistent with its reported absence in most species. In a complex ecology, teaching leads to faster mastery of valuable skills that would otherwise be difficult to observe or attain by trial-and-error learning. Our modelling approach illustrates how lifetime food production gains attained from earlier skill mastery compensate for potential production costs borne by teachers. The balance between teacher costs and pupil benefits in different contexts is critical for any evolutionary model of teaching, and requires consideration of not only the evolution of species-specific cognitive abilities, but also the socio-ecological determinants of production, population structure and life history. Though limited in scope, our preliminary analysis of the evidence for costly teaching in subsistence populations supports our theoretical predictions for a two-stage teaching strategy with peer-tutoring among youth, elder instruction of young producers and production prioritized over teaching in peak-producing adults.

Though formal instruction may be rare in subsistence societies, several recent studies find that hunter–gatherers convey information in ways that improve skills and task performance [33,50,51]. Such pedagogy is not just helpful, but is arguably necessary, given the cumulative nature of complex skills in human populations, where proficiency may be difficult to achieve from observation alone. Teaching as a costly trait can invade a non-teaching population where knowledgeable teachers are readily available, relatedness is high between teachers and pupils, opportunity costs to teachers are low and individual learning through direct experience, imitation, or other means does not result in high-fidelity transmission [9]. These combined conditions might suggest why costly teaching may be limited in most species.

While teaching may be viewed as evidence of higher cognitive ability, available comparative evidence suggests that reliance on teaching may not track intelligence and brain size [23,43]. Our closest primate relatives, chimpanzees, learn socially and can imitate others, but have only rarely been observed to teach in the wild [52]. Unlike humans, weaned chimpanzees quickly learn to feed themselves and do not generate large surpluses in adulthood [2]. Comparable to our model results for the low-skill/low-strength condition, this would favour mainly peer tutoring if its costs are low. Indeed, teaching may only be beneficial and frequent in settings where complex skills require multi-step, cumulative knowledge, consistent with the recent finding that chimpanzees are more likely to share tools and teach skills for more complex tasks [53]. Complex behaviours that no individual could acquire on their own, nor through simple imitation, describe many aspects of human subsistence, technology and culture [54]. The capacity to express approval or disapproval can help correct errors that may arise from imitation—a vital component of human teaching that is missing in chimpanzees [55].

To what extent is direct or indirect teaching costly? The actual costs of teaching have not been studied systematically to our knowledge. We tried to indirectly assess costs in one domain (hunting), and found that peak productive age hunters were least likely to go hunting with younger companions (figure 6), and hunting returns were reduced by the inclusion of younger companions in foraging parties (figure 5). These findings support our theoretical model and suggest that foragers are sensitive to the costs/benefits of teaching in the behavioural process of cooperative group formation. We would expect that peak productive age hunters are even more wary of hunting with younger companions during periods of resource scarcity.

In a related analysis of hunting assistants, however, we found that hunting production did not vary among hunters with versus without young assistants present (figure 5). We speculate that no cost was detected for assistants because hunters may be effective at providing pedagogy at low cost: (1) apprentices only accompany hunters when skilled enough to walk quietly, (2) hunters can transmit knowledge during transit, (3) apprentices can still contribute physical labour (e.g. flushing monkeys so that the hunter can get a clear shot), (4) apprentices can carry supplies and game in ways that help reduce transport costs, and (5) apprentices can also help to spot game. Unlike young hunters in cooperative foraging groups, assistants that are not actively participating in pursuit upon encounter could follow hunters at a safe distance, learning by passive observation at a stage in which the assistant is agile and strong enough to not be a significant burden. Indeed, these scenarios accord with our personal observations in several hunter–gatherer and forager–horticulturalist societies.

Examining a broad range of subsistence activities, we found partial support among Tsimane that observed ages of teachers and students reflect activity skill and strength requirements, as predicted by our model. Lower-skill activities like fruit gathering showed lower teacher–pupil ages than hunting, and less difficult types of fishing showed younger pupil and teacher ages. That being said, our observational data reveal a broad range of participant ages for most activities. Given the spot observational nature of the Tsimane data, it is hard to interpret how much pedagogy is occurring and at what cost. Nonetheless, the broad age ranges of potential teachers are consistent with ample opportunities for multi-stage pedagogy.

(a) Pedagogy across the human life course

Studies of Western children show that demonstration, guidance, and other forms of teaching occur as young as 3 years old; contingent teaching, where actions are adjusted based on inferences about the pupil's knowledge state, is reported by age 7 [30]. A normative developmental trajectory of teaching behaviour leads some to argue that teaching itself is a 'natural' cognitive ability [30]. Our modelling exercise predicts pedagogy by both older peers, who are in large supply and possess enough skill, and by older adults, whose lifetime of cumulative skills and lower opportunity costs makes them qualified and eligible teachers. Consistent with these expectations, peak-age foragers participated less in cooperative hunting with young individuals than younger or older hunters (figure 6), and studies of pedagogy in hunter–gatherers suggest a wide age range of instructors (reviewed in [33,50]), consistent with multi-stage teaching over the life course. Many studies also emphasize the close biological kinship between teachers and students [56–59], consistent with the fitness interdependence that mitigates teacher cost and enhances pupil benefits.

For many work activities, vertical transmission is common in infancy and early childhood, and often involves parents with their same-sex children [40,56] across a broad age range of parental teachers. By middle childhood, children often learn from other children (horizontal transmission), from siblings and through mixed-age play groups. Play has long been considered a low-risk means of fostering skill development and socialization [60], and hunter–gatherer parents usually do not expect their children to work intensively to meet their needs. For example, Aka forager parents believe that children cannot learn if they do not play [50]. Recent ethnographic study shows substantial child-to-child pedagogy in middle childhood among Aka and Hadza foragers, with instruction or learning occurring six to eight times per hour [58].

Tolerance for close association among group members engaged in subsistence activities throughout the day also provides rich opportunities for observation, imitation, demonstration and guidance, i.e. 'learning by observing' and 'by doing' [61]. By adolescence, sources of learning tend to shift from peers to parents or grandparents, especially for more complex skills [45,58]; for rarer skills, teaching might be given by other local adult experts (e.g. apprenticeship via 'oblique transmission') [10,40]. For example, older adults were the most commonly named teachers for a wide range of tasks in Fijian horticulturalists, with oblique transmission reported to be most common for high-skill domains, like weaving and farming, and at later pupil ages [57]. Consistent with our modelling approach, direct (i.e. more costly) teaching is documented among subsistence populations mostly for complex skills, such as hunting, tool manufacture, weaving and ritual. These activities are difficult to learn and show greater opportunity for pupil benefits. Indeed, among Tsimane, potential teacher–student dyads for high-skill activities generally involve older teachers and students (figure 7). While basic proficiency in many tasks might coincide with physical maturity in late adolescence and early adulthood (and after some horizontal transmission), recognized expertise in hunting and other complex domains is greatest for middle- to late-middle-aged adults, owing to the combination of high skill requirements, cumulative experience and greater pedagogical efficacy [1].

(b) Pedagogy beyond subsistence

Teaching in humans is pervasive and generalized to many domains. This may be due in part to the utility of language, a rich repertoire of pedagogical cues, and mental state attribution—allowing teachers to adjust their behaviour strategically based on awareness of pupils' knowledge and performance [29,62]. Functional definitions of teaching, such as those introduced by Caro & Hauser [22], help facilitate cross-species comparisons, but by ignoring cognitive mechanisms, they may obscure important aspects of intentional teaching in humans [63]. Though outside the scope of the paper, pedagogy in non-industrialized populations extends beyond subsistence, being applied to learning group-wide social norms, mythology, ritual and kinship [38,56,59,64]. Here we have focused primarily on food production, both in terms of relevant information transfer, and in terms of the currency maximized over the life course. However, production can be conceptualized more generally as any fitness-related, transferable resource—food being a good, but certainly not the only, example. Cultural production in the form of stories and songs that help convey moral norms can be fitness-enhancing if they help facilitate in-group cooperation [65,66]. Ethnobotanical knowledge can help reduce illness and improve health. Social capital can be liquidated to help improve access to resources and buffer risks. A pedagogical pupil boost that improves group coordination and norm adherence could improve fitness in myriad ways, including improved partner choice, risk buffering, coalitionary support and group augmentation.

(c) Limitations

Our modelling framework and preliminary evidence help characterize the role of pedagogy across the human life course. Limitations include: no explicit modelling of how skills might interact and scaffold to shape the production function, nor explicit consideration of skills related to technology manufacture, skill obsolescence in a changing environment, nor time trade-offs associated with teaching. Our approach is also based on a static single life course maximization, and we (conservatively) assume that production is possible without any pedagogy. Addressing each of these invites inquiries is beyond the scope of the current paper. For example, the skills of older adults may be less relevant in a rapidly changing environment, which would put a premium on more individual learning and peer-tutoring to keep skills up-to-date. Similarly, if production curves were more muted in the absence of pedagogy, as has been proposed in models of cumulative culture (e.g. [9]), then pupil boosts would be higher than what we consider here, making our boundary estimates conservative.

We also lack empirical data to investigate the potential cost of teaching for non-hunting subsistence activities. The human ecological niche comprises many complex, high-skill activities, and so evaluation of teaching costs beyond hunting requires new cross-cultural data collection and/or compilation [64]. Honey collecting, for example, in some societies requires a nested series of skills, learned at different ages, with direct instruction focused on the more complex elements in late adolescence and early adulthood [45]. Although other subsistence activities may include costs of teaching, costs may be substantially lower for gathering activities targeting sedentary prey or plants.

Finally, information transfer is relevant to subsistence well beyond skills acquisition. Older adults in foraging societies also serve as repositories of historical knowledge about the locations and seasonal patterns of key food and water sources, and thus their presence can bolster productivity of many group members by directing camp movements or reducing the search time of foraging parties. By considering only pedagogical aspects of information transfer, our modelling exercise therefore omits other important features that make information a fitness-relevant currency for postreproductive adults.

(d) Concluding remarks

We return to our initial question about the role of pedagogy in shaping life histories. In a skills-intensive ecology, older adults carry a lifetime of experience and knowledge, and as argued here, lower opportunity costs to teaching. Though pedagogy spans the life course, our analyses support a pedagogical niche for older adults embedded in multigenerational sharing networks. Slow juvenile physical growth is accompanied by a long pre-adult period combining individual and social learning of the wide range of skills composing human subsistence and social life. By transferring food and providing childcare, grandparents increase kin fitness in ways that can select for survival into postreproductive ages. Here we add informational transfers as an additional currency [1]. Future work should estimate the indirect fitness effects of pedagogy and establish the extent to which informational transfers can compensate for declining production transfers. Pedagogy is aided by an already extended lifespan characterized by intergenerational resource transfers, but also can increase the force of selection at later ages, thereby lowering mortality and increasing lifespan. It is possible and likely that there are positive feedback ratchets. Indeed, vertical and oblique transmission across multiple generations introduces more opportunities for efficient learning and coordinated, cooperative production than the standard two-generation pedagogy.

Despite great interest in the role of human foraging strategies in models of life-history evolution, surprisingly little is known about how human foragers learn hunting and gathering skills, much less social skills, childcare or other activities. In many cases, ages of recognized experts well exceed the ages of peak physical condition [3,4]. Based on our modelling framework, we expect pedagogy to be a general feature of cooperative species with complex feeding ecologies, intergenerational transfers and long lifespan, as has been demonstrated for killer whales (*Orcinus orca*) [67] and African elephants (*Loxodonta africana*) [68].

Data accessibility. Data and code to recreate both model and empirical results are available as supplemental files on the Open Science Framework (https://osf.io/38624/).

Authors' contributions. M.D.G. conceived the study, worked on the model and wrote the paper. R.J.D. designed the model, generated model analyses, compiled and analysed the non-human data, contributed text and revised the paper. T.S.K. analysed human data, contributed text and revised the paper. All authors contributed ideas and gave final approval for publication.

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