Introduction

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Introduction to special issue: 'Life history and learning: how childhood, caregiving and old age shape cognition and culture in humans and other animals'

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This special issue focuses on the relationship between life history and learning, especially during human evolution. 'Life history' refers to the developmental programme of an organism, including its period of immaturity, reproductive rate and timing, caregiving investment and longevity. Across many species an extended childhood and high caregiving investment appear to be correlated with particular kinds of plasticity and learning. Human life history is particularly distinctive; humans evolved an exceptionally long childhood and old age, and an unusually high level of caregiving investment, at the same time that they evolved distinctive capacities for cognition and culture. The contributors explore the relations between life history, plasticity and learning across a wide range of methods and populations, including theoretical and empirical work in biology, anthropology and developmental psychology.

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

In evolutionary biology, 'life history' refers to the developmental programme of an organism, including its period of immaturity, reproductive rate and timing, caregiving investment and longevity [1,2]. Life history has played an important role in evolutionary theory going back at least to Macarthur and Wilson's distinction between 'r' and 'k' species [3]. It is especially relevant to human evolution. Human life history is distinctive, it is very different from the life history of even closely related species [4]. In a remarkably short time, humans evolved an exceptionally long childhood and old age, and an unusually high level of caregiving investment, with a wide range of caregivers, including pair-bonded fathers [5], unrelated alloparents [6] and post-menopausal grandmothers [7] . This stands in contrast to our closest primate relatives. There is even fossil evidence for changes in life history during hominin evolution [8,9].

Yet, until recently, few psychologists talked about 'life history'. Evolutionary approaches to psychology typically focused on the adaptive advantages of features of adult human minds. They talked about adult cognition, communication, culture and cooperation and emphasized adult activities such as hunting, warfare and building [10]. The distinctively long human childhood received less attention and was even treated as epiphenomenal, a side-effect of narrow pelvises and large brains, rather than a phenomenon with potential adaptive significance itself (see [11]). A few psychologists pointed, in a general way, to the fact that a long childhood allows a long period of learning [12–14].

But, beyond this, there were few attempts to connect human life history to formal theories and empirical studies of learning and plasticity across species.

More recently, though, developments in biology, anthropology and psychology, many pioneered by the authors in this special issue, have radically changed this situation. Advances in all these areas raise the exciting prospect of a new interdisciplinary research area combining developmental psychology, evolutionary biology and anthropology, and employing a wide range of methods, from experiments in biology, neuroscience and psychology to computational modelling, naturalistic observation and behavioural ecology.

All these separate areas of research progress weave together in the papers in this issue. The papers are organized methodologically, beginning with broad theoretical discussions [15–17], moving to studies of birds [18,19] and primates [20,21], looking at human evolutionary history as reflected in anthropology and archaeology [22–26] and finally, focusing on studies of humans in modern societies [27–29]. But much of the interest of this special issue comes in the cross-cutting themes across these different methodologies and populations. We emphasize three such themes in this introduction—the very general relation between plasticity, early life environments and later development; a more specific relation between an early period of protected immaturity and capacities for learning and exploration; and, finally, an even more specific relation between life history and the distinctive human social phenomena of culture and cooperation.

2. Plasticity, early life environments and development

One set of papers look at how events early in development can distinctively shape later outcomes. This is the area where 'life history' terminology has been applied most extensively in developmental psychology. However, Nettle & Frankenhuis [15] argue that these applications of life history in psychology are often not straightforward extensions of life-history research in evolutionary biology. The core research programme in evolutionary biology uses formal modelling to predict how natural selection should shape the mean value of life-history traits (such as growth, maturation and senescence) in a species, depending on ecological and demographic conditions. The core research programme in psychology that has invoked the concept of 'life history', by contrast, uses verbal (non-formal) theory to predict the development of individual differences in traits, including traits like impulsivity and aggression, and argues that these traits may result from adaptive developmental plasticity in response to childhood experience. This application of life-history theory to individual differences is a topic of current theoretical and empirical debate [30,31]. This paper emphasizes that we need formal theory to explore how natural selection might favour developmental mechanisms that produce different life-history strategies given different early experiences. Furthermore, we need to test these models in diverse human populations, preferably in combination with measures of social and environmental statistics [32].

Snell-Rood & Snell-Rood [16] ask why experiences of social support early in life influence the development of much later cognitive abilities. In particular, they wonder why, across mammals, early cues of social support (such as licking, touching or attention) appear to stimulate later learning, exploration and brain development. They argue that learning is both costly and risky—it requires energetically expensive neural systems and exposes exploratory animals to greater predation risk. Their 'developmental support hypothesis' says that young mammals should invest in learning, and bear its associated costs, to the extent that they receive sufficient nutritional and protective support from their parents. Without such support, juveniles have fewer resources and are exposed to greater risk. In that case, it might be adaptive to develop a phenotype that learns and explores less, but is also less costly and risky, and improves the chance of survival in difficult conditions. This hypothesis also suggests intriguing directions for future research. For example, we could measure how much early cues of social support actually predict real parental support later in life. Similarly, researchers could test the adaptive value of investing time and energy in neural systems and exploratory behaviours in stressful versus supportive environments.

Rojas-Ferrer & Morand-Ferron [19] report empirical studies that examine how experiences early in life shape later cognitive abilities in another cognitively sophisticated class of animals, birds. Specifically, these authors investigate how early opportunities for learning affect choice accuracy and decision-making speed in captive juvenile zebra finches (*Taenopygia guttata*). Their research shows that information in the early developmental environment may shape the ability to learn and make accurate decisions several weeks later. Moreover, when information in the early developmental environment is very complex, this might reduce learning, potentially because this makes it harder to discern the statistical structure of the environment. These findings suggest that animals are not only plastic due to learning, but also exhibit phenotypic plasticity in their learning abilities themselves. They may develop the highest learning ability if the early environment presents a moderate amount of information; not too little or too much. These findings raise such interesting questions as: does the information structure of developmental conditions enhance specific types of learning abilities or all types of learning abilities? How should we expect phenotypic plasticity in learning abilities to covary with phenotypic plasticity in life-history strategies? Is this covariance similar or different for individual and social learning?

3. Extended childhood as a period of active exploration and learning

A second theme of the papers in this issue is that specialized learning abilities may be manifested in an early protected development period. There are distinctive cognitive, motivational and affective features of young animals that allow particularly powerful and active learning, and distinctive aspects of parental care that enable this learning. It could be that an extended childhood only involves an essentially passive period of plasticity in which early environmental inputs can shape later development. But these papers suggest that early learning is more active and more developmentally distinctive.

Although there have recently been striking advances in the comparative study of cognition, there is still a dearth of developmental studies of other species—the studies that are the foundation of human developmental psychology. Uomini *et al.* [18] provide two case studies of cognitive development in corvids, a family of birds well known for their sophisticated cognitive skills, which can rival those of primates. Both Siberian

jays and New Caledonian crows have an extended juvenile period in which young animals live with and are cared for by parents. Uomini *et al.* [18] show that these corvids' cognitive abilities depend on this protected period and extended parenting. Although these birds do not engage in the kinds of sophisticated cultural and social learning we see in humans, parents nevertheless provide a tolerant environment that allows the young to develop distinctive cognitive skills. Moreover, the young New Caledonian crows are able to engage in extensive active exploration and trial and error learning during this period, even with little immediate benefit or reward.

Perry [20] reviews a unique dataset of extensive longitudinal observations of a community of white-faced capuchins, with an emphasis on the development of foraging skills. The researchers found that younger capuchins are more active, curious and inventive. They more often seek social information by watching other foragers (especially older foragers) and they are more creative, and playful, and less neophobic. While adults more often stick with old solutions, younger individuals often incorporate recently acquired experience (both social and asocial) into their foraging techniques. Again, although these animals do not show sophisticated cultural transmission, they do engage in extensive social learning, and the distinctive characteristics of both the young and the old contribute to this learning.

Turning to humans Morgan *et al.* [27] describe a new method which combines ideas from classical agent-based-evolutionary modelling and human experiments. Human participants, recruited through the internet, serve the same function as simulated agents in classic evolutionary modelling. Using this method, the authors demonstrate that learning and memory emerge in tandem in development. Intriguingly, they also find that over many generations of the simulation the equivalent of childhood emerges. Agents develop an early period in which there is more exploration and learning, followed by a later period in which they rely more on what they have already learned. This life-history development, however, depends on the variability of the environment.

Pelz & Kidd [28] explore the development of play. Younger animals of many kinds, including humans, appear to engage in more play than older animals. Play, by definition, also requires a transfer of resources from more obviously productive activities to apparently unproductive play, and so is also related to parental investment [33]. However, spontaneous free exploratory play, and changes in that play, are difficult to study systematically and quantitatively. Pelz & Kidd [28] report a new technique for studying play across development by giving children from 2 to 12 years old an interactive touch-screen game and automatically recording their behaviour as they spontaneously play with the toy. They find, contrary to other expectations from the literature, that younger children play less with the toy and produce a less varied set of responses than older children. This suggests that exploration changes in more qualitative and complex ways than a simple linear decline with age.

Finally, Gopnik [29] argues that the development of childhood, in general, across many animals, can be understood in terms of a resolution of explore–exploit dilemmas. Researchers in computer science and neuroscience point to a fundamental tension between exploration and exploitation—the ability to search through a wide space of possible hypotheses, actions or problem solutions, and the ability to use those hypotheses, actions and solutions to bring about desirable and useful outcomes. These two types of cognition require very different, and in some ways opposing, characteristics. Exploration may benefit from variability, impulsivity and intrinsically driven curiosity and neophilia, for example, whereas exploitation requires focused capacities for executive function and long-term planning. Resolving the tension between exploration and exploitation is extremely challenging computationally, and a common solution is to begin with exploration and later move to exploitation. The requirements of the two types of cognition appear to map well on to characteristic features of children and juveniles and adults respectively. Gopnik [29] also outlines empirical research from her lab and others which shows that children may actually outperform adults on tasks that require exploration. Moreover, parental investment provides the conditions that make exploration possible.

4. Human life history and the evolution of cooperation and culture

Human cultural organization differs from the social organization of other primates in two key dimensions: (i) synchronically, humans are much more motivated and skilful at collaboration and other forms of cooperation; and (ii) diachronically, humans share knowledge and information within and between generations in ways that lead to the accumulation of cultural artefacts, skills and knowledge. Several papers in this special issue focus on the possibility that changes in human life history—when compared with nonhuman primate life histories—played a key role in the emergence of humans' unique forms of cooperation and cultural transmission and learning.

Deffner & McElreath [17] present a new formal model that explores the evolution of social learning in a population characterized by age structure and population regulation. These features, which are pervasive in nature, have been omitted in nearly all models of social learning to date. Their model specifically explores the extent to which reliance on social (versus individual) learning should evolve as a function of vital rates (births and deaths in different age classes) and population density (i.e. more conspecifics increases competition) in a fluctuating environment. Their results show that organisms that have 'fast' life histories (high mortality, high fertility) often evolve greater reliance on social learning than organisms that have 'slow' life histories (low mortality, low fertility). This finding is surprising, because many primates, and humans in particular, have slow life histories yet are prodigious social learners. This model thus reveals gaps in our knowledge and highlights the need for future theory and data on the evolution of social learning in populations characterized by age structure and population regulation.

Gurven *et al.* [26] examine the conditions in which pedagogy might evolve. Pedagogy involves teaching by a more skilled individual that improves the ability of a less skilled individual, potentially at a cost to the teacher's own productivity, and plays a central role in culture. The authors present a new formal model that explores the conditions that favour teaching, and the optimal ages of teaching and learning. In many conditions, the model favours a two-stage teaching strategy that includes peer-tutoring among youth, elder instruction of young producers, and peak-productive adults producing rather than teaching. Gurven *et al.* [26] document support for these predictions in empirical analyses of hunting, a high-skill activity for which extensive cross-cultural data

exists, in a recently published dataset that includes more than 23 000 records of 1800 individuals from 40 locations. They also show that ages of teachers and students reflect skills and strength requirements as predicted by their model for a variety of subsistence tasks, including fishing and fruit gathering, using rich observational data from their long-term study of Tsimane forager-horticulturalists. This suggests that both older age and childhood play an essential role in cultural learning.

Richerson & Boyd [25] note the classic signatures of human life history within the primate clade—i.e. their relatively long lives and their special forms and amounts of dependence on others in the group for normal development—and argue that these have led to much larger brain growth unfolding at a slower pace, as the individual interacts with its physical and social environment. They argue that this larger brain growth—which enables so many of humans' unique behavioural and cognitive capabilities—was manifest as more and better cultural learning, and emphasize the role of humans' larger and more complex social networks, both for creating and for transmitting cultural knowledge, especially to children. Without these larger social networks, children's big brains and long lifespans would not lead to humans' distinctive forms of cultural skills and knowledge.

Sterelny [24] focuses on a very specific puzzle in human technological evolution. In the archaeological record, there seems to be a long period of technological stasis associated mainly with *Homo erectus* in the period from 1.7 to 0.8 Ma. It does not seem to be due to ecological or economic factors. He thus considers whether, as some theorists argue, it is due to intrinsically inferior social learning capacities of hominins during this million-year period. While not rejecting this hypothesis totally, he finds it insufficient. He argues that social and life history factors were more likely the decisive ones. When compared with *Homo sapiens, Homo erectus* had much more ape-like patterns of ontogenetic growth and lived in smaller groups. These factors would constitute severe constraints on the ability of developing *Homo erectus* children to assimilate, innovate and transmit cultural skills and knowledge, including in the technological sphere. After 0.8 Ma, humans began living in much larger and more complex social groups, including nested structures of bands within communities and so forth. This, in combination with slower life histories of children, rendered technological stasis a thing of the past.

Hrdy & Burkart [22], Hawkes [23] and Tomasello [21] focus less on cultural learning and transmission, and more on humans' unique skills of collaboration and communication (which, in important ways, underlie and/or facilitate the unique aspects of human cultural learning and transmission, e.g. cooperative information transfer or teaching based on human cooperative communication). Hrdy & Burkart argue that the crucial factor leading to humans' greatly extended ontogenies was the help that male and female allomothers provided to biological mothers in raising their offspring. This help in rearing youngsters—which is decidedly not present in humans' closest primate relatives—enabled mothers to enhance their fitness by having more offspring at more closely spaced intervals. In the current paper, Hrdy & Burkart stress the flipside of this pattern of cooperative breeding and childcare, namely, the new socioecological challenges that it presented for developing children. With more adults to relate to and solicit care from, along with more 'competitor' siblings and other children at similar ages, there was social selection on children who could more effectively ingratiate themselves with adults. Young human children who could best read the minds of adults and communicate with them more effectively formed stronger relationships with them, to their advantage. This pattern of interaction in which children learn to share attention with others then transformed human social interactions and cultural learning across the board.

Hawkes [23] takes this same general perspective on things, but emphasizes that another unique characteristic of human life history is increased postmenopausal longevity. Grandmothers, in particular, have a fitness interest in their children's offspring, and this frees up the mother to engage in all kinds of foraging and other activities while the infant is relatively young, such that weaning ages are younger in humans than in their nearest primate relatives. She conjectures that the evolutionary foundation of uniquely human social cognition and cultural learning was early hominins' exploitation of savanna plant foods that gave cooperatively foraging adults economic benefits. These were foods that were effective in provisioning youngsters and that grandmothers could obtain in sufficient quantities independently, so mothers spent less time on offspring, enabling them to have more babies at shorter intervals, even though these babies developed more slowly. Their dependence on others led babies to prioritize sensitivity to others' intentions, and to begin to focus on not only social learning but also on reputation and reputation management. Again, changes in the socioecology of human ontogeny were the main selective factors for the special skills of shared intentionality and cooperative communication characteristic of the human species.

Tomasello [21] proposes a hybrid hypothesis that synthesizes his previous evolutionary speculations about uniquely human cognition and sociality with those of Hrdy & Burkart and Hawkes [22,23]. He notes that children's unique skills of joint attention, collaboration and cooperative communication emerge in nascent form before the child's second birthday. This is at least a decade before they will be needed in the kinds of collaborative activities, such as collaborative foraging, that he initially hypothesized as the selective context for these skills. In this paper, he also notes that in the early ontogeny of these skills, they are practiced almost exclusively with adults, and not with peers. This early emergence and confinement to adults provide support for Hrdy & Burkart's hypothesis. But Tomasello stresses that the essence of all of these skills, as instances of shared intentionality, is that participants align their psychological states (emotions, attention, attitudes, knowledge) with one another, and much research in social psychology suggests that aligning psychological states leads to feelings of social closeness. The proposal is then that the first step in the process was that adults felt socially closer to those with whom they shared psychological states, and then infants evolved to exploit this adult tendency. The result is that humans at all ages after infancy cooperate, communicate and socially learn from others in their group in all of the unique ways that characterize human culture.

5. Conclusion

These essays raise new questions that are as exciting as they are challenging. How and why might learning and plasticity have co-evolved with life history? How do evolution, development and learning work together to adapt organisms to local environments? How might human capacities for learning, innovation, cooperation and culture, in particular, be related to the evolution of our extended childhood and longer lifespan? The theoretical

and empirical papers in this issue contribute to answering these important questions, and also raise fruitful and intriguing possibilities for further interdisciplinary collaboration and research.

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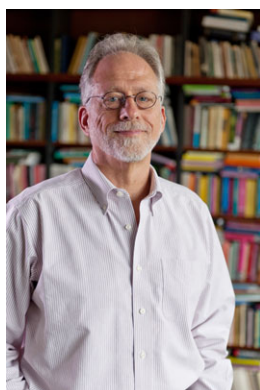
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