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The promise of great apes as model organisms for understanding the downstream consequences of early life experiences

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ABSTRACT

Early life experiences have a significant influence on adult health and aging processes in humans. Despite widespread interest in the evolutionary roots of this phenomenon, very little research on this topic has been conducted in humans' closest living relatives, the great apes. The longitudinal data sets that are now available on wild and captive great ape populations hold great promise to clarify the nature, evolutionary function, and mechanisms underlying these connections in species which share key human life history characteristics. Here, we explain features of great ape life history and socioecologies that make them of particular interest for this topic, as well as those that may limit their utility as comparative models; outline the ways in which available data are complementary to and extend the kinds of data that are available for humans; and review what is currently known about the connections among early life experiences, social behavior, and adult physiology and biological fitness in our closest living relatives. We conclude by highlighting key next steps for this emerging area of research.

1. Introduction

One major branch of research in the study of health and aging focuses on the long-term effects of early life experiences (Bateson et al., 2004; Gluckman et al., 2005). Events and circumstances during development—which we will define broadly as any point between conception and puberty—are known to be linked to a long list of common causes of adult morbidity and mortality, including metabolic disorders, cardiovascular disease, strokes, cancer, psychiatric disorders, kidney disease, and cognitive decline (Gluckman and Hanson, 2004; Forman et al., 2005; Nilsson et al., 2008; Muhlhausler and Smith, 2009; Bentall et al., 2012; Murphy et al., 2017). They also predict a variety of outcomes associated with reduced adult quality of life, including increased risk of health-reducing behaviors (e.g. smoking, excessive alcohol use), poor social functioning, unstable social relationships, and dysregulation of the hypothalamic-pituitary-adrenal (HPA) axis (Bunea et al., 2017; Duffy et al., 2018; Levis et al., 2021). The list of adult health and wellness outcomes that are believed to have developmental origins is long and varied (Newnham and Ross, 2009; Johnson and Schoeni, 2011).

Given the awareness of the importance of developmental experiences to long term health and social functioning, there is considerable interest in the biological and evolutionary origins of these effects (Gluckman et al., 2010). Experimental research on model animal species has demonstrated that exposure to early life stressors, starting during or even prior to birth (e.g. Schmidt, 2010, Yehuda and Lehrner, 2018, Alhassen et al., 2021), replicates many of these same outcomes, highlighting the likelihood of deep phylogenetic roots. At the same time, there is considerable variation in the type and magnitude of such effects across species. As one example, the intergenerational impacts of maternal dietary restriction during pregnancy on offspring growth rate and long-term health has been shown to vary across species based upon body size (Kuzawa and Thayer, 2011). This work underscores the considerable species differences in maternal buffering of the impacts of early stressors that vary in relation to factors like the ratio of offspring or litter size to maternal body size. Thus, work to date on early life effects has pointed to the universality of such effects in mammals and other

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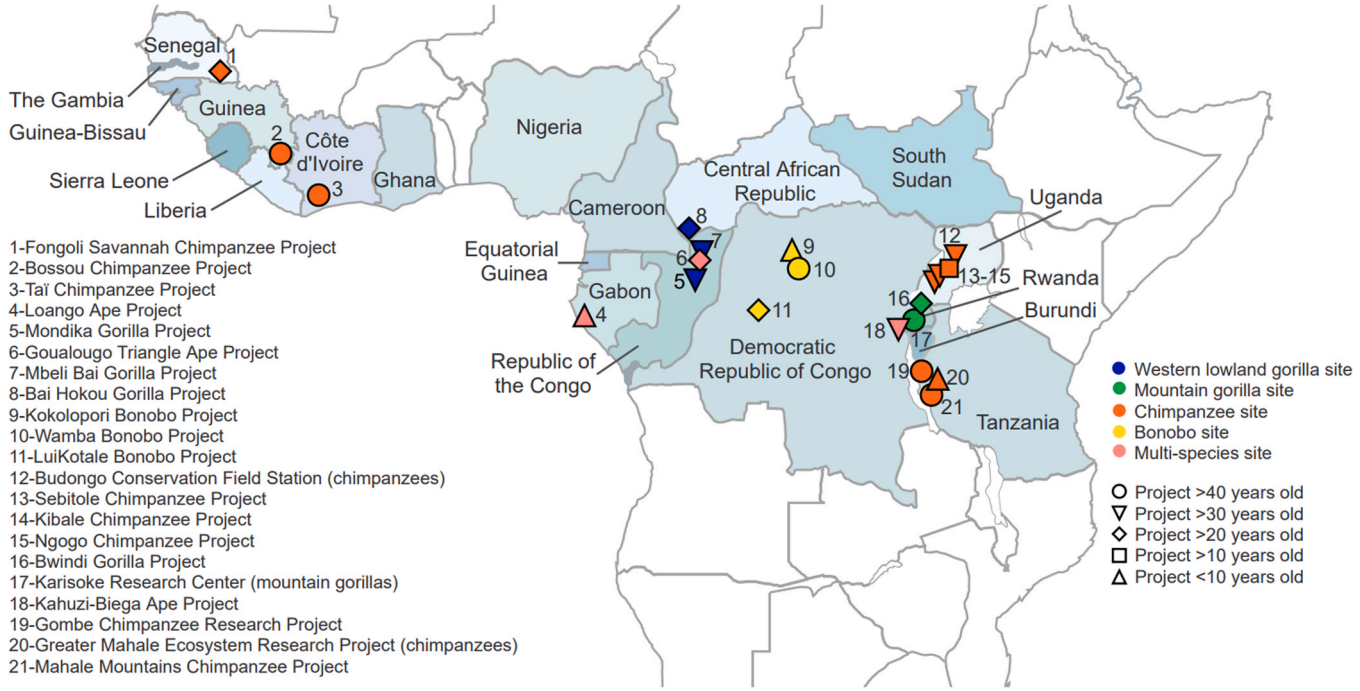

Fig. 1. Map of field sites collecting demographic, behavioral, and/or biomarker data on wild African great apes. Countries with names listed are those that contain known living non-human great ape populations. Geographic locations of projects are approximate. As of 2023, data are not being collected at Bossou (site 2; Koops, pers. comm.). To the best of our knowledge, there is also currently no data collection occurring at Kahuzi-Biega (site 18).

vertebrates, but also their tendency to vary in impact in relation to key features of a species' life history.

In light of this variability, it is notable that one taxonomic group that has remained conspicuously underrepresented in the early life effects literature is our closest living relatives, the non-human great apes. The four species that collectively make up the genera *Pan* and *Gorilla*[1] share many important characteristics with humans (above and beyond genetic similarity) that are of potential importance for understanding early life effects, including their evolution, function, and long-term impacts. Not only do they share our large bodies, long lifespans, and high levels of parental investment in singleton offspring, but the African great apes are also highly social and share humans' predominantly female-biased dispersal (a dispersal pattern that is uncommon in primates more generally; Lee and Strier, 2015, Emery Thompson and Sabbi, 2019). Furthermore, apes kept in captivity demonstrate changes in many of the same biomarkers associated with 'diseases of affluence' (e.g., cardiovascular disease, metabolic syndrome) as humans, suggesting overlap in the pathways through which environments influence their health and aging processes (Nunamaker et al., 2012; Cabana et al., 2018; Murphy et al., 2018; Cole et al., 2020).

Their notable similarities to humans are also the features that have most likely kept them largely absent from the early life effects literature. As is also true for our own species, studying animals with lifespans of 50 + years presents significant logistical and financial challenges (Holliday, 1996; Wood et al., 2017). There are serious ethical concerns surrounding invasive research on endangered and cognitively sophisticated species, which all great apes are (IUCN, 2022). This often precludes the use of invasively obtained biomarkers (e.g. serum or whole blood) that are heavily used in human health research. In some cases, it is possible to capitalize on biomarker sample collection during veterinary procedures that occur for management reasons in both captive and wild populations (Hyeroba et al., 2011; Robbins et al., 2011; Murphy et al., 2018; Cole et al., 2020), but samples collected in this manner represent a small and potentially biased sample.

Despite these challenges, however, there are two reasons that apes' exclusion from early life effects research is coming to an end. One is sample size: the rapidly accumulating number of years of research at multiple long-term wild great ape field sites (Watts, 2012; Robbins et al., 2016; Thompson et al., 2020; Fig. 1), along with impressive data on multi-generational captive populations, means that research no longer has to be limited to the kind of case study reports that has typically characterized much of the great ape health literature (e.g. Boesch, 2008, Masi, Chauffour et al., 2012). Second, the growing availability of affordable non-invasive biomarker measurement options (e.g. Higham et al., 2015, Behringer and Deschner, 2017, Emery Thompson, 2017, Higham et al., 2020, Negrey et al., 2022), along with improving laboratory resources in some great ape range countries, mean that there are now more opportunities to examine the ways in which early life experiences are connected to adult health and aging in our closest living relatives.

In this review, we summarize the features of great ape ecology, life history and sociality that are relevant to understanding the downstream effects of early life experiences and discuss the ways in which research on non-human great apes may contribute to a better understanding of early life effects in humans. We conclude by outlining what is currently known about early life experiences and their relationship to adult behavior, physiology, and fitness (i.e., reproduction) in non-human great apes. Our goal is to help stimulate further comparative early life effects research on our closest living relatives by highlighting current gaps in the literature, including areas in which the study of great apes seems particularly likely to make substantive contributions. To set the stage, we first provide a brief overview of the life histories and social systems of great apes, which illustrates both their broad similarities to humans and the opportunities that they provide for examining diverse early life contexts as influences on long-term outcomes.

[1] The third ape genus, *Pongo* (orangutans), also shares our large bodies and extended lifespans, but are semi-solitary and thus less likely than *Gorilla* and *Pan* to be useful models for understanding the interplay between social dimensions of early life effects. Given that this special issue focuses on the social dimensions of health and aging, we primarily focus on the African great apes in this review.

Table 1
Socioecological characteristics of the African great apes.

Species	Habitat type	Diet	Social group configuration	Social cohesion	Dispersal regime
Mountain gorillas (*Gorilla beringei*)	Lowland and montane rainforests	Herbivorous	Varied	High (except solitary males)	Mixed
Western lowland gorillas (*Gorilla gorilla*)	Lowland rainforests	Frugivorous/herbivorous	Single-male, multi-female	High	Mixed
Chimpanzees (*Pan troglodytes*)	Lowland forests, savannahs	Opportunistic omnivory (more frugivorous than *P. paniscus*)	Multi-male, multi-female	Medium (fission-fusion)	Female-biased
Bonobos (*Pan paniscus*)	Lowland rainforest	Opportunistic omnivory (more herbivorous than *P. troglodytes*)	Multi-male, multi-female	Medium (fission-fusion)	Female-biased

Table 2
Life history characteristics of the African great apes.

Species	Size (kg)[1]	Age[2] at first & last reproduction	Interbirth interval[3]	Generation times[4]	Lifespan[5]	Lifespan (captivity)[6]
Mountains gorillas						
♂	162.5	8.6 - 30.9		20.4	Median = 23 Max = 37	N/A (none in captivity)
♀	97.5	7.3 ($\bar{x}$ = 9.9) - 38.0	4.3 ± 1.0	18.2	Median = 33 Max = 43	N/A (none in captivity)
Western gorillas						
♂	170.4	ND[2a]		ND	ND	Max = ~61.0
♀	71.5	$\bar{x}$ = 12.2	5.2 ± 0.8	ND	ND	Max = 60.1 $\bar{x}$ = 26.2 ± 10.2
Combined ♂/♀						
Chimpanzees						
♂	40.9	9.3 - 50.2		24.1	Median = 11	Max = ~63.0
♀	33.4	11.7 ($\bar{x}$ = 13.6) - 45.4	4.9 ± 0.9	25.2	Median = 16 Max = 41[5a]	Max = 57.4
Combined ♂/♀						$\bar{x}$ = 25.2 ± 10.6
Bonobos						
♂	45.0	ND		ND	ND	Max = ~42.0
♀	33.2	$\bar{x}$ = 14.2	4.7 ± 0.6	ND	Max = 40	Max = 52.2
Combined ♂/♀						$\bar{x}$ = 23.5 ± 9.8
Humans						
♂	59.7	16.0 - 45.0		31.2		N/A
♀	54.6	15.9 ($\bar{x}$ = 18.6) - 36.0	3.2 ± 0.8	26.5		N/A
Combined ♂/♀					Median = ~35 Max = 100+	N/A

Abbreviations: ND=no data

[1]All non-human species weights taken from (Smith and Jungers, 1997). Human data are from (Ruff, 1994) and are within-sex averages from 25 and 31 different human populations around the world for females and males, respectively. Inter-population variation in humans is considerable (range for females = 38.2 – 80.5; range for males = 43.4 – 76.1). In general, humans that live in colder areas are larger than humans that lives in warmer areas.

[2]Age ranges provide the youngest and oldest known ages at which non-human great apes have reproduced; for humans, it is reproductive lifespan representative of hunter-gatherer groups (which are typically natural fertility populations). For females, average age at first birth is provided when available. Similar numbers are unavailable for males due to the difficulty of establishing paternity in most wild ape populations. References: mountain gorillas (Langergraber et al., 2012; Galbany et al., 2017); western lowland gorillas (Robbins et al., 2022); chimpanzees (Langergraber et al., 2012; Walker et al., 2018 (mean for females averaged from Walker and colleagues' Table 1)); bonobos (Ishizuka et al., 2020); humans (Marlowe, 2005; Kramer et al., 2017). Values for human female age at last reproduction, and human male ages at first and last reproduction, are those used by Kramer and colleagues for beginning/end of reproductive lifespan in models of partner scarcity in hunter-gatherers.

[2a]Male western lowland gorillas in captivity have sired infants as early as age 6 (Emery Thompson and Sabbi, 2019).

[3]References: mountain gorillas (Robbins et al., 2006, Robbins et al., 2009; values averaged across the Virunga population (4.0 yrs) and Bwindi population (4.7 yrs)); western lowland gorillas (Stoinski, Perdue et al., 2013); chimpanzees (Lemoine et al., 2020); bonobos (Hashimoto et al., 2022; value from post-2002 data collection only); humans (Marlowe, 2005).

[4]Data for humans are averages of the values provided for 157 hunter-gatherer societies and 360 country-level societies (Langergraber et al., 2012). We were unable to find published data on generation times in wild bonobos or western lowland gorillas.

[5]Medians for gorillas and chimpanzees reflect the age at which 50% of individuals are dead. Max ages are for individuals where age was certain rather than estimated. References: mountain gorillas (Bronikowski et al., 2011; Lowenstine et al., 2016); chimpanzees (Bronikowski et al., 2011); bonobos (Lowenstine et al., 2016); humans (Gurven and Kaplan, 2007). Human data are aggregated from multiple hunter-gatherer and pre-industrial societies. Average modal age at death was 70, but we report median to facilitate comparison with available non-human data. We were unable to find lifespan estimates for wild western lowland gorillas.

[5a]Estimated ages suggest chimpanzees can live considerably longer (60 + years; e.g. Wood et al., 2017)

[6]Reference: (Harwell and Knott, 2020). Approximate max captive lifespan values for male western lowland gorillas, chimpanzees, and bonobos were taken from news reports of the deaths of geriatric animals living in American Zoological Association accredited zoos, when the institution was confident of the animal's birthdate +/- one year.

2. Great ape life history and socioecology

2.1. Background

The genera *Pan* and *Gorilla* are humans' closest living relatives, sharing 99% and 98% of our DNA, respectively (Waterson et al., 2005). While divergence time estimates can be controversial (Glazko and Nei, 2003), molecular clock data suggest that the gorilla lineage split from the lineage that led to *Pan* and *Homo* between 9 and 12 million years ago, while the *Pan* lineage split from the *Homo* lineage between 7 and 9 million years ago (Moorjani et al., 2016). Though *Pan* is more closely related to *Homo* than it is to genus *Gorilla*, in ~30% of the genome, *Gorilla* is more genetically similar to *Pan* and to *Homo* than those two genera are to each other (Scally et al., 2012, reviewed in Groves, 2018). Fully annotated, high-quality reference genomes for the great apes are a relatively recent phenomenon (Gordon et al., 2016; Mao et al., 2021), and thus functional differences—including differences that may underlie intra or inter-species health and longevity outcomes—are still poorly understood. Thanks to the increasingly accessible cost of sequencing and the ever-growing integration of genetic and epigenetic data into behavioral and health analyses in humans (D'Urso et al., 2021; Ryan et al., 2022; Lea et al., 2023), we are hopeful that the next decade will provide opportunities to expand such analyses to research involving great apes.

2.2. Ecology

Pan and *Gorilla* are made up of four species that collectively occupy habitats as different as high-elevation montane rainforests and semi-arid tropical savannah (Doran and McNeilage, 1998; Caldecott and Kapos, 2005; Wessling et al., 2018) (Table 1). Gorillas are almost exclusively vegetarian (other than occasional instances of ant-eating) and thus have digestive systems adapted to consuming large amounts of fibrous, relatively low-quality food, while chimpanzees and bonobos (*Pan*) are opportunistic omnivores who take advantage of a wide range of plant, and to a lesser extent animal, foods (Morgan, 2017) (Table 1).

While there is considerable inter-population variation, *Pan* on average likely experiences greater swings in food and water availability and has a diet that more closely resemble those of recent human ancestors, than *Gorilla* does (Andrews and Johnson, 2020). This plus the more specialized digestive systems of gorillas likely makes *Pan* a more human-relevant model for research on the long-term effects of early life nutrition or caloric restriction than gorillas are likely to be. That said, the lower food-related resource competition that gorillas experience may mean that they provide 'purer' tests of hypotheses about the effects of sociality on health and aging. In species in which close social partners may also represent the biggest competitors for food simply by virtue of their close spatial proximity, this can make it difficult to disentangle social and ecological effects (e.g., Lea and Rosebaum, 2020). For example, if lower-ranking animals routinely struggle to obtain as many calories as higher-ranking animals do, it is difficult to determine whether observed effects are due to their low rank *per se*, or to the energetic deficits their low rank imposes. It is easier to discern social effects if lower-ranking animals have access to similar ecological resources as higher-ranking animals do.

While orangutans are not a primary focus of this review because they are semi-solitary, food availability/resource competition is a specific area in which the only Asian great ape species deserves particular mention. Orangutans routinely experience ecological boom-bust cycles due to masting events (Knott, 1999; Harrison, Morrogh-Bernard et al., 2010), wherein large numbers of trees produce an extreme amount of fruit in one year, but then will produce none in one or more subsequent years. This means there are likely substantially more monitored orangutans who experienced extended famine-like conditions during development than monitored individuals of either African ape genus. However, the implications of this for research on the long-term effects of nutritional stress are ambiguous. Orangutans have specialized physiological adaptations to deal with famine (Wich, Utami-Atmoko et al., 2006; Harrison, Morrogh-Bernard et al., 2010), which on one hand may limit the applicability of lessons learned to other species. On the other hand, research on orangutan physiology and behavior could provide important information about tradeoffs that bodies make to protect large brains or other key organs during times of starvation (Kane, Susanto et al., 2020), including the long-term health and reproductive consequences of such tradeoffs.

2.3. Life history

In captivity and in certain wild populations, African great apes' lifespans can approach those of modern human hunter-gatherer populations (Wood et al., 2017), even if they do not routinely live beyond 40 years of age (Bronikowski et al., 2011; Che-Castaldo et al., 2021) (Table 2). While great apes do not have a formally defined childhood stage, like humans they experience a considerable lag between weaning and sexual maturity (approximately 5–8 years, with considerable inter-population and inter-individual variation; Breuer et al., 2009, Walker et al., 2018). While there is debate over the specifics of human generation times, great apes fall in the plausible range typically cited in human studies (sex averaged for gorillas 19.3 years; chimpanzees 24.6 years; humans 26.9 years: Langergraber et al., 2012, Wang et al., 2021), though their age at first reproduction is younger, and they reproduce more slowly, than humans (Table 2). Female great apes invest heavily in raising singleton (or rarely, twin) infants, but receive far less assistance from other group members than many human mothers do (Hrdy, 2009; Hrdy and Burkart, 2022). While female great apes do not routinely outlive their reproductive years (Emery Thompson et al., 2007), there is evidence from both captive and wild apes that females can have post reproductive lifespans of > 25% of their total lifespan (Mitani et al. pers. comm; Atsalis and Margulis, 2006).

These life history similarities mean that great apes are particularly useful models for understanding the effects of early life experiences on reproductive outcomes (e.g., ages at reproductive commencement or senescence, reproductive pacing, total fertility) and longevity (Table 2). As noted earlier, the effects of some early life experiences may be body size-dependent (Kuzawa and Thayer, 2011), and body size is inextricably linked to a host of other life history traits, including lifespan and reproductive strategies (Stearns, 1983). Great apes' relatively human-like body size (apart from male gorillas, who typically weigh close to 400 pounds; Table 2) and life history scheduling means that the trade-offs and constraints they experience may be more similar to those of humans than the animal models in which early life effects have typically been studied.

Dispersal regimes—i.e., the patterns that govern which individuals leave their natal groups, and when in their lives this occurs—are another life history feature which African great apes share with humans. They are members of a relatively small subset of primates, including humans, in which female dispersal is routine; in most primates, it is males who leave their natal group at sexual maturity (Yamagiwa et al., 2014). As well as affecting key long-term social partner (including kin) availability (Grebe et al., 2022), this may be particularly important as a sex-specific constraint on intergenerational biological signaling of long-term, future socio-environmental realities across generations (Kuzawa and Eisenberg, 2014; Toepfer et al., 2017). Due to the difficulty of tracking the dispersing sex over time in wild animals, there is currently very limited information about the long-term impacts of early life circumstances for male non-human primates. Human research suggests that some early life effects may be sex-specific (Rincel et al., 2019; Bath, 2020; Kuzawa et al., 2020; Wells et al., 2022), highlighting the need for additional information about males. The ability to follow males across the lifespan (or in the case of mountain gorillas, both sexes, as their dispersal is not sex-biased) is a potential strength of research on great apes.

2.4. Sociality

Great ape social organization is variable. Both species of *Pan,* chimpanzees and bonobos, live exclusively in multi-male, multi-female groups. In western lowland gorillas (*G. gorilla*) nearly all groups are composed of a single male, one or more females, and their offspring, while in mountain gorillas (*G. beringei*), group structure is highly variable. They can occur in all-male, multi-male multi-female, and single-male multi-female groups, and some males spend many years or even their entire adult lives as solitary individuals (Robbins and Robbins, 2018). In addition to these differences in social organization, the two genera have considerable differences in intra-group dynamics. Chimpanzee and bonobo groups have a fission-fusion system. This means that all group members are rarely or never in the same location, and the size and sex composition of smaller 'parties' changes frequently (Furuichi 2009). In contrast, gorilla groups are quite cohesive; while sub-grouping can occur in larger groups, it is usually only for short periods of time (Doran and McNeilage, 1998).

The functional consequence of this natural variability (in gorillas from group to group, and in *Pan* between parties) is that there are opportunities to answer questions about how group demographics, partner availability, and network position are related to health and aging outcomes across the lifespan. For example, two young chimpanzees who grow up in the same group may have very different social experiences, depending on the choices their mothers (and eventually, they themselves) make about which parties to spend time in. Similarly, a young gorilla that grows up in a group that consists solely of its mother and father has a very different social history than one surrounded by a wide variety of adult kin and non-kin, along with many unrelated age-mates. This flexibility is shared by humans, who also exhibit extensive across- and within-population diversity in social organization (Kaplan et al., 2009).

Another important social dimension of within-group heterogeneity is dominance hierarchies. While males' dominance hierarchies are typically more overt, and thus easier to quantify, dominance rank is an important predictor of health and proxies of Darwinian fitness outcomes (e.g. lifetime reproductive success) for both sexes, in both *Pan* and in *Gorilla* (Mitani, 2009; Vigilant et al., 2015; Wright et al., 2020). While rank is not 'inherited' in great ape species as it is in (e.g.) baboons, maternal rank can nonetheless have important ramifications for offspring. For example, Markham and colleagues found that while nursing, low-ranking female chimpanzees' fecal glucocorticoid levels were significantly more sensitive to social context (in particular, party size and sex ratio) than those of high-ranking females, an effect which was independent of nutritional stress. They posited that psychosocial stressors may keep low-ranking females from making decisions that are optimal from the point of view of offspring socialization and/or food resource availability (Markham et al., 2014). More generally, higher-ranking females typically have access to higher-quality habitat than lower-ranking females do, which presumably translates to benefits to offspring (e.g., more or higher-quality milk before weaning, and access to better quality food after).

3. Complementarity of human and great ape research

Data on humans and other apes have different strengths and weaknesses. Human-focused early life effects research is often biomarker heavy and avails of questionnaires and recall for most behavioral data, social and otherwise. These types of data have costs and benefits. Biomarkers are very helpful for understanding physiological processes that are associated with various health and longevity outcomes, but may not provide critical event or input-specific information when multiple inputs converge on the same physiological pathways. For example, cortisol is a commonly-used biomarker of HPA axis function, but interpretation of inter and intra-individual differences are complex given the number of bodily processes the HPA axis is involved in (Spencer and Deak, 2017). Interviews can be very helpful for understanding the social or psychological pathways by which early experiences lead to various outcomes, but they may also generate data that are subject to recall bias, deception (intentional or otherwise), and the subjective nature of reported experiences (Bell et al., 2019). Time, cost, and ethical constraints mean that studies which contain detailed, direct longitudinal behavioral data on humans are relatively rare.

Conversely, direct collection of detailed longitudinal behavioral data is precisely the area in which research on wild animals, including great apes, excels. Because animals cannot be questioned about their behavior and social lives, researchers have devoted untold hours to directly documenting myriad aspects of the animals' lives. At long-term field sites, researchers routinely collect behavioral data across the course of individually identified animal's lives. This includes direct observations of who they spend time with; who they affiliate with, mate with, and aggress towards; and the way they are parented and how they in turn behave as parents.

While great ape data sets will always suffer from small sample sizes relative to most human research, the depth of the data available about individual subjects is often orders of magnitude greater, as is the breadth of data on the specifics of social behaviors. For example, it is a rare human study that records exactly who touches a subject and in what context over the course of even a single 12-hour day, but this is precisely the data that many long-term great ape research projects repeatedly collect over the course of animals' lifespans. However, these detailed behavioral data sets often lack complementary health data, particularly biomarker data, due to the difficulty of and ethical constraints on collecting (e.g.) blood, and even simpler, less invasive metrics such as body weight or heart rate.

In light of the nature of data gathered on apes, these species provide particularly strong opportunities to explore hypotheses linking early life social experiences to later outcomes. For example, great ape data contain extensive direct information on who interacts with whom and how, allowing for (among other things) fine-grained analysis of individual-level positions in social networks (Rosenbaum et al., 2016; Feldblum et al., 2018; Morrison et al., 2020; Thompson González, Machanda et al., 2021). Social networks and social support–or lack thereof–are believed to be important contributors to health outcomes in humans, in part via their ability to encourage resilience to early life adversity (e.g. Sippel et al., 2015, Racine et al., 2018). Such data from our own species are usually coarse at best, and thus limit our ability to determine specifically what feature(s) matter. At field sites where animals are tracked as they move from group to group, the same individual can be observed in two entirely different social networks, permitting the type of within-subject comparison that is virtually never possible in humans. Such scenarios could be especially useful when attempting to unravel the relative contributions of past (developmental) versus current (adult) environments to observed outcomes. Furthermore, the extensive data available on the specifics of their social behavior could provide important clues about which particular features of relationships matter. Do greater amounts of social touching and affiliative contact predict better health – or in pregnant females, improved survival or long-term health in their offspring after birth? Is it worse for an individual's health to be largely ignored by group members, or to receive aggression from group members? Questions like these are answerable using great ape data. Answers could provide important insights into how such processes work in species which are phylogenetically close to *Homo sapiens*, and potentially provide clues about what follow-up work may be particularly fruitful in human subjects.

Great apes are also potentially good candidate subjects for research focused on the 'mismatch' hypothesis, which proposes that health issues in adulthood are a result of dissimilar developmental and adult environments. There is considerable debate over the applicability of this hypothesis to organisms with slow life histories (Kuzawa, 2005; Wells, 2012; Nettle et al., 2013), but it is impossible to test without subjects that live in both matched (i.e., some feature(s) of their developmental

and adult environments are the same) and mismatched (developmental and adult environments are different) conditions (Malani et al., 2023). Great apes offer opportunities to examine the effects of match/mismatch on a number of socioecological parameters (e.g., group size, rainfall, food availability), while retaining the life history features—long lifespans, slow reproduction, big brains—that are especially relevant to humans. It is also potentially feasible to test the evolutionary version of the mismatch hypothesis, which proposes that poor health is the result of a mismatch between historical environments during a species' evolutionary history and the current environment(s) species inhabit (Hoogland and Ploeger, 2022). This could be done using data from animals residing in zoos and sanctuaries, or potentially from wild animals that are residing in particularly marginal or degraded habitats that are unlikely to be representative of what the species historically experienced.

Historically, a primary difficulty of conducting tests of the mismatch hypothesis with great apes has been a lack of data on health outcomes, which are often challenging to measure in wild primates. However, many physiological parameters that are measured invasively in humans have non-invasive proxies that allow an expanding suite of biological endpoints to be linked to early experiences in primate field studies. Fecal and urinary glucocorticoids—a measure of HPA axis function—are routinely obtained at many long-term great ape sites. There is considerable human research suggesting that HPA axis 'programming' may play an important role in adult health and aging (Miller et al., 2009; Nusslock and Miller, 2016), and elevated fecal glucocorticoid concentrations have been linked to both early life adversity and elevated adult mortality risk in baboons (Rosenbaum et al., 2020; Campos et al., 2021). Urine samples can provide information about suPAR, neopterin, leucocytes, and IL-6:IL-10 ratios to gain insight into chronic and acute inflammatory processes (Higham, Stahl-Hennig et al., 2020). DNA damage and lipid damage can be measured using fecal or urinary 8-OHdG and urinary F-isoprostane assays, respectively (Thompson González et al., 2020; Negrey et al., 2021). With a few notable exceptions, these parameters are quite understudied in great apes, highlighting the many opportunities for research that integrates the detailed behavioral data available on great apes with novel physiological measures (Urlacher et al., 2022).

4. Limitations of great ape research

While great ape-focused research holds promise, it is also important to acknowledge its limitations. One of the biggest is the constraints on sample collection for biomarker analysis. Most biomarker research will inevitably be limited to things that can be measured in feces or urine, narrowing the range of parameters that can be studied. Logistical constraints also mean that even some things that can be measured in these matricies cannot be measured in ways that are directly comparable to human research. For example, it is most likely infeasible to study cortisol or testosterone awakening responses (Engert et al., 2011; Kuzawa et al., 2016) using urine due to the difficulty of getting sufficient sampling density, or of doing a full 24-hour urine collection cycle (though note that methodological innovations can sometimes overcome these difficulties: e.g., muscle mass has been measured in wild chimpanzees via urinary creatinine, something that typically requires 24-hour urine collection in humans (Emery Thompson et al., 2012)). While there are a wide range of potential non-invasive biomarkers available, careful biochemical and biological validation work has yet to be conducted for many of them, a process that can be expensive and time-consuming.

In addition, given great apes' slow life histories and the difficulties of studying them, sample sizes are small and will inevitably remain so. Small sample sizes exacerbate the variety of analysis challenges that early life effects research already faces. For example, it can be especially difficult to distinguish prenatal and postnatal effects, or the effects of rearing environments from those of genetics, under naturalistic conditions. One the primary advantages of most animal models—the ability to do carefully controlled experimental work—is largely absent in great apes. This means it will be especially important to rely on clearly defined theory, place particular weight on results associated with early life events or experiences that are unlikely to suffer from endogeneity problems (e.g. droughts, predator attacks, human-caused events), and capitalize on the strengths of the within-subjects, social groups, and/or family comparisons that longitudinal data can facilitate (Malani et al., 2023).

Data on wild great apes may also suffer from selection bias problems that are difficult to address. Data collection is limited to specific groups of animals that are habituated to human presence. These groups and their experiences may not be representative of great apes more generally; for example, since many predators fear humans, human presence may reduce predation pressure, an important cause of mortality wild primates (LaBarge et al., 2020). Given the concerns about their conservation status, in some cases they receive veterinary care for specific illnesses or injuries, meaning that longevity and health outcomes may not always represent what would happen to a given animal absent human intervention (though note that most such interventions are also treating human-caused problems (Robbins et al., 2011, Emery Thompson et al., 2020)). It is also possible that their habitats may not be representative, since humans are inevitably more likely to habituate animals who live in closer proximity to infrastructure such as roads, towns, and airstrips than a typical gorilla or chimpanzee does.

5. The current state of early life effects research in non-human great apes

In the final section of this review, we provide an overview of what is currently known about early life effects in great apes in three areas: behavior, physiology, and fitness proxies (i.e., lifespan and reproduction). While we have chosen to particularly highlight the possibilities of long-term field sites above, this section, by necessity, primarily contains results obtained from captive animals living in zoos, sanctuaries, and research facilities. This reflects the dearth of information currently available for wild great apes. The results available for captive great apes can, along with the human literature, help inform and guide future research priorities.

5.1. Behavior

Most research on the connection between early life experiences and adult behavior in great apes has been conducted in captive chimpanzees. One recent study found that chimpanzees reared without conspecifics spent less time grooming with others as adults, though interestingly, their grooming behavior was indistinguishable from that of captive (adult) chimpanzees who were wild-caught (Crailsheim et al., 2020). Another reported that stereotypic behavior (e.g. pacing, hair plucking) was more common among adult chimps whose attachment to their primary human caregiver at age 1 was characterized as disorganized (i.e., they responded to being reunited with their caretaker with abnormal behaviors such as freezing or clutching other objects, rather than approaching and seeking contact) (Clay et al., 2015). Ex-laboratory chimps who had been subjected to solitary confinement were less social and had more non-social behavioral idiosyncrasies once confinement ended, if their confinement started at a younger age (Kalcher et al., 2008). Animals that experienced early maternal deprivation, irrespective of whether they subsequently spent their lives in a lab or a zoo, were less well integrated into grooming networks as adults compared to chimpanzees raised by their mothers in zoos (Kalcher-Sommersguter et al., 2015). In a sanctuary setting, orphaned juveniles played more than mother-reared juveniles, though their social play was also more likely to elicit aggression from others, suggesting social deficiencies (van Leeuwen et al., 2014). Similarly, captive chimpanzees who spent less time with conspecifics early in their lives were rated as less extroverted by their human caregivers (Freeman et al., 2016).

Overall, the literature suggests that early social deprivation or trauma in chimpanzees can have lasting impacts on adult social relationships and increase the tendency to engage in 'abnormal', asocial behaviors (Bloomsmith et al., 2006; Lopresti-Goodman et al., 2013; Freeman and Ross, 2014; Ortín et al., 2019). However, given the many idiosyncrasies of captive environments and the sheer range of captive circumstances studies like the ones cited above represent—from captive-born animals housed in American Zoological Association-approved zoos with extensive enrichment and expert caretakers, to bushmeat-trade orphans raised in extreme social and physical deprivation—it is difficult to know how generalizable the findings are, what particular aspects of the environment cause the observed effects, and what mechanistic pathways they might operate through.

Currently, little information is available on the behavioral consequences of early life adversity in wild great apes. A recent study of mountain gorillas found that animals who lose their mothers strengthen their social bonds with other group members—particularly age-mates and dominant males—immediately after the maternal loss, but it is unclear how long these effects are sustained, or how they ultimately might manifest in altered adult behavior (Morrison et al., 2021). A small study of recently-orphaned wild chimpanzee siblings suggests that post-maternal loss bond strengthening also occurs in chimps (Reddy and Mitani, 2019). Finally, there is evidence that differences in aggression patterns in chimpanzees may be related to exposure to aggression during development (Sabbi et al., 2021). As for the maternal loss study in gorillas, however, it is currently unclear what either of these findings in chimpanzees mean for social behavior across the lifespan.

5.2. Physiology

Information on the physical/physiological effects of early life adversity among great apes is even sparser than information on behavior. A recent study of chimps housed at the MD Anderson Cancer Center found that varying CpG methylation levels at specific dopamine receptor D2 gene sites were associated with changes in extraverted personality characteristics in nursery-reared (as opposed to mother-reared) chimpanzees (Staes et al., 2022).

Other studies using MRI data (collected while animals were anesthetized for routine veterinary procedures) have found differences in brain structures in chimpanzees raised by mothers versus those raised in nurseries. One found that machine learning (ML) could discriminate between the brains of the two groups with almost 70% accuracy, based primarily on differences in the superior middle parietal lobe (Bennett et al., 2021). Intriguingly, when ML mis-classified nursery-reared chimps as mother-reared, it was disproportionately likely to do so with chimpanzees who had undergone social stimulation interventions early in life. Similarly, a study of chimpanzees raised at three research facilities found that an early-life intervention that aimed to provide the animals with species-typical socioemotional rearing prevented changes in brain development (in particular, lower structural covariation and gray matter volume) associated with standard nursery rearing (Bard and Hopkins, 2018).

We were only able to identify a single study that examined long-term changes in physiology in response to early life adversity in wild great apes. Girard-Buttoz and colleagues found differences in the diurnal urinary cortisol metabolite slopes of immature chimpanzees who lost their mothers; specifically, orphans' cortisol metabolite concentrations rose in the afternoons, while the metabolites of non-orphans fell (Girard-Buttoz et al., 2021). However, by the time animals were adults, there was no difference in the cortisol profiles of animals who did and did not lose their mothers at an early age. This was only assessed in males, since female chimpanzees usually disperse from their natal groups at sexual maturity. Another recent paper highlighted significant population-specific variation in urinary cortisol concentrations across development in both bonobos and chimpanzees, which the authors tentatively attributed to differences in the consistency of social environment, including consistency in maternal behavior (Tkaczynski et al., 2020). However, currently it is unclear what implications these differences might have in adulthood.

Table 3
High-priority questions and considerations for early life effects research in non-human great apes.

Domain	Central question	Constituent parts	Considerations
Definitions	How do we define early life adversity in great apes?	• What constitutes a typical early life environment? • What events or states constitute 'adversity?'	• What is socioecologically relevant for the species? • What definition(s) maximize comparability to other studies, including those on humans?
Outcomes	Do great apes experience long-term health or fitness costs of early adversity?	• Does early adversity negatively affect lifespan? Reproduction? Health? Social standing or functioning?	• Is all-cause mortality a sufficient metric? • What fitness proxies are/are not appropriate measures? • How should health be operationalized?
Mechanisms	What are the pathways linking early life adversity to later outcomes?	• What biomarker profiles are associated with different types of early life adversity, *and* with negative consequences (e.g. shortened lifespan, worse health)? • Are long-term impacts ecology and/or social system -dependent?	• What biomarkers are available (e.g. feasible, validateable, cost-effective)? • What biomarkers best facilitate inter-species and inter-population comparisons? • What socioecological parameters should/could be conceptualized as potential mediators?

5.3. Fitness proxies (i.e., lifespan and reproduction)

Similarly little information is currently available linking early social or other experiences to adult lifespan or reproductive success. Maternal loss before adulthood (age 15–16) was found to predict shorter lifespans among male chimpanzees (Nakamura et al., 2014; Stanton et al., 2020), as did maternal loss before age 10 for female chimps (Stanton, Lonsdorf et al., 2020). In addition, chimpanzees whose mothers weaned them early had diminished growth trajectories relative to peers who weaned later, potentially implying reduced fitness downstream (Emery Thompson et al., 2016). However, wild mountain gorillas who survive more sources of early life adversity, including maternal loss, have similar lifespans to those who face fewer or no sources of adversity (Morrison et al., 2023), nor does maternal loss predict age at first birth or survival of first offspring through infancy (Morrison et al., 2021). As a rule, studies on captive apes are not a useful source of information on fitness proxies. There is substantial human manipulation of their reproduction and they receive extensive veterinary care when living in accredited facilities.

5.4. Summary of current results

There are four primary lessons to be drawn from our review of the current early life effects literature on great apes. First, the number of early life effects studies in non-human apes is so limited that it is difficult to draw meaningful conclusions. Second, what is available has focused heavily on the effects of maternal loss. It contains very little information about the effects of other sources of adversity (alone or in combination

with maternal loss), or of the consequences of early life circumstances that do not fall under the rubric of "adversity." Third, most research is on captive chimpanzees. This almost certainly reflects their greater availability as research subjects—they are both the most numerous great ape and the species most likely to be kept in captivity, due to their history as subjects of biomedical research. However, one of the difficulties with such studies is that their external validity may be limited, as it is unclear if the kinds of adversity they experience in captivity have clear analogues in wild populations. Their experiences in captivity can differ dramatically across institutions and animal care protocols, and different kinds of adversity may be conflated. Fourth, the very small amount of work that does exist on wild great apes suggests there may be resiliency to maternal loss, and that bond-strengthening with other group members could play a role in this resilience. Given the small number of studies available, however, we caution against drawing strong conclusions.

6. Next steps

Our review of the available non-human great ape literature makes it clear that there are a wide variety of under-exploited opportunities to address questions about the early-life origins of adult health in these close human relatives, especially for the significant number of field sites that have longitudinal data on wild animals. Fine-grained demographic, behavioral and biomarker data of the type typically collected at such sites could provide very important insights on the role that early experiences—especially early social experiences—play in life-long outcomes.

There are three fundamental question categories that are useful for structuring future research on early life effects in great apes (Table 3). The first concerns definitions: before we can study this topic, we need to decide what constitutes early life adversity in great apes. This entails describing typical experiences, as well as negative ones, and thinking carefully about how to define early life adversity in a way that is both socioecologically relevant for a given species or population, and to the degree possible, maximizes comparability across studies. While the current focus on understanding the effects of maternal loss is certainly understandable, as this is a highly salient form of adversity in species with such extended, intensive maternal care, young apes may experience a wide range of other early life stressors that could impact developing systems in distinct ways. For instance, wild apes can experience food shortages, droughts, predator attacks, disease outbreaks, accidents, loss of key non-maternal social partners, and social group disruption. Currently, we know remarkably little about if and how such experiences affect what happens across the life course. We also lack a good understanding of how variation in typical experiences (e.g., the structure of the social group they grow up in, or the place that they occupy in a social network) affects long-term outcomes.

The second fundamental category of questions are those focused on consequences of early life experiences (Table 3). Our review of the available literature highlights just how little is currently known about the consequences of early life in humans' closest living relatives. For those who are interested in the evolutionary drivers of early life effects, research will center around the fitness consequences: i.e., what early life experiences mean for reproduction directly, but also what they mean for lifespans, which are often the primary determinant of fitness outcomes in long-lived species (Weibel et al., 2020). However, there are also many reasons to be interested in the repercussions of early life experiences that have little to do with evolutionary dynamics. Health and social consequences are interesting in their own right, especially if one goal of the research is to generate insights that could help improve human health and well-being. Importantly, great apes offer an interesting opportunity to examine the consequences of early life experiences in species which share key features of our life histories, but which do not have the cultural complexity that makes untangling biological effects especially challenging in humans. This is a strength of animal models in general, but great apes are particularly valuable in this regard.

Table 4
Predictions generated by non-mutually exclusive hypotheses about the relationship between early life effects and socioecology in great apes.

Hypothesis	Prediction	Rationale
Early life effects are mediated via social cohesion (shorter-term social support)		
Genus-based prediction	*Pan* < *Gorilla*	*Gorilla* social groups are more cohesive and typically have less short-term social partner variability than *Pan* groups, who employ fission-fusion.
Early life effects are mediated via social stability (long-term social support)		
Sex-based prediction	♀< ♂ (*Pan* ssp.)	Male philopatry in *Pan* facilitates life-long social relationships for males specifically.
Dispersal-based prediction	Dispersers < non-dispersers (*G. beringei*)	Since non-dispersal facilitates life-long social relationships, there should be a disperser/non-disperser difference in mountain gorillas. (In western lowland gorillas (*G. gorilla*), dispersal is 100% in both sexes.)
Early life effects are mediated by dominance hierarchies		
Sex-based prediction	♂ < ♀	Female African great apes have weak, relatively 'flat' dominance hierarchies, while males have very strong, linear ones.
Species-based prediction	*P. troglydytes* < *P. paniscus*	Chimpanzees are more hierarchical than bonobos and more likely to use aggression to establish/maintain hierarchies.
Early life effects are ecologically mediated		
Genus-based prediction	*Pan* < *Gorilla*	If inhabiting a more difficult environment (especially one with less, or less stable, food availability) drives negative effects of early life adversity, then more folivorous gorillas should fare better than more frugivorous chimpanzess and bonobos.
Species-based prediction	*G. gorilla* < *G. beringei*	If inhabiting a more difficult environment drives negative effects of early life adversity, then folivorous mountain gorillas should fare better than the dietarily more varied western lowland gorillas.
Habitat-based prediction	Gradient across *P. troglydytes* habitat	If inhabiting a more difficult environment drives negative effects of early life adversity, there should be inter-site differences across chimpanzee habitats (e.g., the Fongoli chimpanzees (site 1 in Fig. 1) occupy a very challenging hot, dry habitat, while the Ngogo chimpanzees occupy a resource-rich forested habitat (site 14 in Fig. 1).

Finally, once we have a better understanding of the consequences of early life experiences, we can explore the mechanisms that connect experiences to outcomes (Table 3). As an increasing number of non-invasive biomarker assays are developed, this opens up opportunities to link early life experiences to a variety of physiological systems. The explosion of field research on non-invasive cortisol measures over the last 20 years is an example of the utility of sustained sample collection from known individuals. Our hope is that, following careful validations—both biological, to verify that we are capturing something of real-world relevance to the animals, and biochemical, to ensure our assays are working as intended (Higham, 2016)—far more sites will routinely monitor physiological systems that are known or strongly suspected to be affected by early life. These include measures of HPA axis function such as cortisol, but also oxidative stress, immune function, growth, and metabolism (Urlacher et al., 2022).

While 'mechanism' can be narrowly construed as relating specifically to biomarkers, it is also the case that sociality and ecology can be conceptualized as mediators; i.e., these may constitute a pathway via which links between early adversity and adult outcomes flow (e.g. Friedman et al., 2015, Rosenbaum et al., 2020). Great ape-focused

research can diversify the information available on the roles that social organization, dispersal, and ecology play in determining the effects of early life experiences. Gorillas in particular offer a wealth of opportunity in this area, given their extreme social flexibility (Robbins and Robbins, 2018). However, chimpanzees' female-biased dispersal and strong, lasting male-male bonds also present an interesting comparison point for the existing body of work on Old World monkeys, where male dispersal and strong female bonds are the norm (Amici et al., 2019). A recently published paper on humans highlights the potential importance of sex and dispersal regimes for generating unequal outcomes in adulthood (Chen et al., 2023), emphasizing the importance of understanding the role such variables play. To this end, we propose several intra- and inter-specific predictions about the potential role that sociality and ecology may play in early life effects in great apes (Table 4). The state of the literature is such that it is unrealistic to expect that many of these predictions can be tested in the short term, but nonetheless, they provide a framework for thinking about how to capitalize on the diversity of great ape socioecology within the context of socially-focused early life effects research. Information on great apes can help fill important gaps in the comparative literature that are created by focusing on species with particular socioecologies. It is interesting to note that what little evidence exists suggests that gorillas may indeed be more resilient to early life adversity than chimpanzees, as theory predicts they might be (Table 4).

In the predictions column, the left-hand side of the inequality represents the species/sex/individuals which would be expected to be less resilient to early life adversity (i.e., show more or more severe consequences) if the hypothesis in the first column is true. For example, in the second row, female chimpanzees and bonobos might be expected to be more susceptible to negative effects of early life adversity if social stability has protective effects than males are, since the species' female-biased dispersal means that males have longer-term, more stable social relationships than females do.

Our understanding of the biological roots of early life effects benefits greatly from integrating information obtained from a range of species, ecologies, and methodological approaches. While non-human great apes currently remain largely absent from this important body of research, their life history characteristics, complex social dynamics, and close relatedness to humans make them particularly valuable models for understanding how and why early life experiences 'get under the skin' in animals like us. Decades of sustained data collection by many of our esteemed colleagues on both captive and wild ape populations has provided a wealth of potential research opportunities. We look forward to reading and contributing to what promises to be an exciting new avenue of scholarship in the early life effects literature.

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