



Research



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Variation in the timing of developmental milestones in *Gorilla* does not support the ecological risk aversion hypothesis

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Species comparisons of developmental milestones (behavioural and physical markers of neurodevelopment) allow empirical testing of hypotheses of how distinctive life-history characteristics may have evolved. Here, we analysed developmental milestone emergence in *Gorilla* using data from six mountain gorilla groups and one western gorilla group, collected from 1998 to 2023. The study included 36 mountain gorillas and 7 western gorillas, tracking 28 developmental milestones. Bayesian mixed-effects models (which allowed us to measure and account for the uncertainty from the small sample size in western gorillas) compared milestone timing between species. We then compared developmental milestone emergence in *Gorilla* to available data on western chimpanzees using visual inspection of species averages. In line with the expectations of the 'life-history brain development' and 'delayed benefits' hypotheses, we observed that developmental milestones emerged gradually across ontogeny. However, we found limited species differences among *Gorilla*, and the differences between chimpanzees and gorillas did not conform to the 'ecological risk aversion' hypothesis. Ecological risk aversion may predict growth rates, but it is not a consistent predictor of developmental milestone emergence. Instead, the interplay between ecology, social opportunity and social constraints may be more promising predictors of the development of behavioural and cognitive milestones.

1. Introduction

Two key characteristics of mammalian life history are postnatal parental (principally maternal) care and a protracted immature phase relative to the whole lifespan [1,2]. In primates, and especially apes, these mammalian characteristics are particularly exaggerated [3]. For example, age at first reproduction for female orangutans and elephants is around 15 years [4,5], despite the substantial body size differences. Theoretical modelling suggests that primate life history, and particularly the long delay prior to first reproduction in apes, can be selected for (i) when survival and fertility are size dependent and growth takes time and (ii) when a protracted period of development allows for social learning and skills acquisition across a range of changeable socioecological conditions [6]. Indeed, the ‘life-history brain development’ hypothesis proposes that the evolution of primate life history has been driven by selection for relatively large brains and cognitive development [7–9]. In addition, the ‘delayed benefits’ hypothesis states that protracted development arises from the time needed to develop key adult motor and social skills [10]. In addition, the ‘ecological risk aversion’ hypothesis states that slow growth and protracted development have been selected for in primates to offset a key mortality risk for immatures: having a slower growth, and thus a slower metabolism, reduces feeding competition and starvation risks when living alongside large, energy-demanding adults; however, this slower development also necessitates living in larger groups to offset predation risks, in turn increasing competition [11]. Testing such hypotheses regarding the evolution of life histories requires tracking both brain *and* behaviour development across a range of primate species [9,12–14]. However, tracking the ontogeny of behaviour requires extensive observational effort, especially in long-lived species with protracted developmental phases, which may make this aspect of development potentially more time consuming and less well explored than some neuroanatomical approaches (reviewed in [15]).

Developmental milestones are behavioural and physical skills which are considered markers of neurodevelopment [16]. For nearly a century [17], developmental milestones have been used as a method of tracking typical and atypical development in human infants [16,18,19]. More recently, the framework has been adopted in non-human animal research [20,21], including in non-human primates [12,22,23]. Among non-human primates, developmental milestones have often been characterized in preferred animal models for neuroscience studies so that the emergence of these behavioural traits can be directly linked to neuroanatomical development. For example, in rhesus macaques (*Macaca mulatta*) and common marmosets (*Callithrix jacchus*), individuals with artificially generated adverse early life events (e.g. social deprivation or pharmacologically induced physiological stress) show slower social and motor skill development, as well as altered neuroanatomy (e.g. reduced hippocampal volume), compared to non-manipulated age peers [23,24]. Developmental milestones have also been well studied in chimpanzees (*Pan troglodytes*), where the focus has been more ultimate, using comparisons with human developmental milestones either to understand the evolution of ape life history or to understand the evolution of specific behaviours [12,25–27]. For example, Bründl *et al.* [12] found that, whether taking absolute ages or adjusting them for overall lifespan or age at first reproduction, chimpanzees and humans show remarkably similarly ages of emergence for key motor (e.g. tool use; chimpanzee mean = 40 days old; human mean = 48 days old) and social skills (e.g. attentive looks; chimpanzee mean = 3 days old; human mean = 2 days old). Furthermore, and in support of both the life-history brain development and delayed benefits hypotheses, the more complex the milestone (e.g. tool use), the later it emerged in chimpanzees, as also found in humans. In addition, Heintz *et al.* [26] showed that immature chimpanzees that played more frequently tended to have earlier emerging motor skill milestones, again supporting the delayed benefits hypothesis. Lastly, Lee *et al.* [27] compared developmental milestone emergence in chimpanzees and bonobos (*Pan paniscus*). Bonobos are thought to occupy a less resource competitive environment and, thus, based on the ecological risk aversion hypothesis, were expected to develop more quickly than chimpanzees, yet there were few meaningful differences observed in the study.

Many ape studies have explored rates of development for specific behavioural traits (e.g. tool use in chimpanzees [28], foraging skills in orangutans [*Pongo pygmaeus wurmbii* and *Pongo abelii*] [29] and locomotion in *Gorilla* [30]), but few have explored multiple traits simultaneously using the developmental milestone framework. This presents a significant knowledge gap as testing hypotheses about the evolutionary forces shaping life histories requires comparable data across a range of species with different patterns of maturation and facing different ecological pressures. Unlike exploring the development of behavioural traits in isolation, or specific groups of behaviours (e.g. foraging skills or spatial independence), the developmental milestone framework allows us to examine the sequences and

transitions within a species' developmental [12]. As such, we can directly compare and contrast when certain phases of development (e.g. physical or social) become prioritized within each species, and if differences are found, relate these to socioecological settings that may have driven selection for certain life-history strategies.

Although all apes have long developmental phases relative to their lifespan, we do not yet know whether all apes follow the patterns of milestone maturation observed in chimpanzees and humans. In our study, we address this by mapping developmental milestones in the two species of gorillas, western gorillas (*Gorilla gorilla gorilla*) and mountain gorillas (*Gorilla beringei beringei*). Recent genomic analyses suggest these species split around 150–180 000 years ago [31]. Today, they occupy vastly different ecological habitats [32,33]. Approximately 15% of the Bwindi mountain gorilla diet typically consists of fruit [34], whereas in western gorillas, this rises to 30% [32]. A higher reliance on fruit in western gorillas compared to the more herbaceous diet of the mountain gorillas leads to longer daily travel distances and less social cohesiveness [33,35,36]. Another key ecological difference is the absence of non-human predators in the mountain gorilla range (although they were present historically [37]), whereas leopard attacks have been observed in western gorillas [38,39].

Ecological differences, particularly the species-level variation in frugivory and overall differences in food availability, are probable explanations for the different life-history strategies of mountain and western gorillas [40]. Female western gorillas have a later mean age of dispersal from their natal groups (8.6 versus 7.9 years of age), later first reproduction (12 versus 10 years) and longer mean interbirth intervals (5.5 versus 5 years) than Bwindi mountain gorillas [40]. The overall lower food availability and greater seasonality in food resources in western compared to mountain gorillas should have selected for a slower life-history strategy based on the predictions of the ecological risk aversion hypothesis. Indeed, evidence from adults supports this pattern: male western gorillas reach adulthood (silverback) at later ages than mountain gorillas, while female western gorillas have later ages at first birth compared to mountain gorillas [33,40,41].

In our study, we used the developmental milestone framework to test general hypotheses about the evolution of primate life histories using both a between- and within-species approach in *Gorilla*. First, if the life-history brain development and delayed benefits hypotheses are a universal explanation for the long developmental stages in primates, and especially apes, we should expect both gorilla species to show a gradual emergence of developmental milestones across ontogeny, with more complex milestones emerging later [12]. Second, if ecological risk aversion also contributes to the selection of certain life-history patterns, we should expect immature western gorillas (experiencing more seasonal and overall lower food availability) to show a slower emergence of milestones compared to immature mountain gorillas [11]. In addition, relative to both species of gorillas, chimpanzees typically show a greater dependence on fruit in their diet and thus are expected to experience greater ecological variation and a higher degree of feeding competition [42]. Therefore, ecological risk aversion should result in faster emerging developmental milestones in gorillas compared to slower developing, longer-lived chimpanzees. Alternatively, as chimpanzees also learn highly complex skills in the form of tool use, which are apparently absent in *Gorilla*, the life-history brain development and delayed benefits hypotheses would also suggest slower development in chimpanzees. If ecological risk aversion is the main driver of any species differences seen between chimpanzees and gorillas, we should see the clearest differences in emergence in behaviours related to foraging skill or foraging competition, with these occurring later in chimpanzees. In addition, if the delayed benefits hypothesis is the main driver, the clearest differences should be in either complex social or technical skills, such as grooming or tool use, emerging much later in chimpanzees. This highlights the benefit of the developmental milestone framework in dissecting life-history theories by having multiple behavioural traits and sequences of emergence to compare between species.

Lastly, we examine sex differences in developmental milestone emergence within mountain gorillas (we had an insufficient sample size to do the same with western gorillas). Here, previous studies of growth rates in *Gorilla* suggest that in both species, females undergo earlier growth spurts than males [43] and they reach reproductive maturity earlier than males. Slower male maturation potentially supports a within-species effect of the ecological risk aversion and delayed benefits hypotheses as males need to reach a larger body size overall and need longer to acquire the physical and social skills to achieve dominance within their social groups. However, there is some evidence that immature mountain gorilla males form affiliative ties to adult males earlier, more strongly and more consistently across ontogeny than immature females [44]. Through these adult male ties, younger males may gain access to social learning opportunities related to dominance and reproductive dynamics [44]. Therefore, based on the

ecological risk aversion hypothesis, we expected later maturation for physical developmental milestones in males relative to females. Based on the delayed benefits hypothesis, for social milestones, we expected males to become spatially independent earlier than females to gain social learning opportunities but that these opportunities then led to maturing later when it came to prosocial milestones (e.g. grooming).

Using a unique dataset spanning 25 years of observation of mountain gorillas and 8 years of observation of western gorillas, we test these assumptions and thus provide further vital assessment of hypotheses related to the evolution of primate life history.

2. Material and methods

2.1. Study site and subjects

Data were collected on six habituated mountain gorilla groups in Bwindi Impenetrable National Park, Uganda from 1998 to 2023. Data were collected on one habituated western gorilla group in Loango National Park, Gabon from 2014 to 2023. Several researchers (see 'Acknowledgements') collected the data; they were trained according to the same protocol and supervised on a routine basis by M.M.R. to ensure uniformity and consistency. Specific data for this study were extracted from a long-term behavioural database. Gorillas from birth to 13 years and of known age (less than ± 15 days) were included in the study, totalling 36 individuals from Bwindi and 7 individuals from Loango (supplementary material, fig. S1 illustrating the ages when each individual first and last appears in the used dataset).

2.2. Data collection

For the mountain gorilla data collection, gorillas were observed for approximately 4 h per day in Bwindi, according to guidelines set by Uganda Wildlife Authority. Focal samples were collected [45] lasting between 5 and 60 min, with the goal of 5 h of focal time per individual per month. Focal periods were ended when individuals were out of view for more than 60 s. Focal subjects were chosen pseudorandomly based on who was in view, with an emphasis on securing equal focal time for every individual each month. The maximum of 60 min ensured focal samples from multiple individuals were recorded each day. Ad libitum data were also recorded on all individuals in view, when possible, with particular emphasis on rare behaviours (displacements, drinking water, aggression, mating and carrying immatures). Scan sampling occurred concurrently with focal sampling at fixed intervals (pre-May 2015: every 5 min; post-May 2015: every 10 min). During the time point for each scan, observers recorded the activity of every individual in view (being carried, being nursed, feeding, fruit feeding, playing, locomotion and resting), their height off the ground and their proximity to the focal individuals when focal sampling was occurring.

For the western gorilla data collection, an identical protocol to that in Bwindi was conducted (although with a slightly different ethogram to reflect species differences in western versus mountain gorillas), in compliance with the regulations of the Agence Nationale des Parcs Nationaux and the Centre National de la Recherche Scientifique et Technique of Gabon.

2.3. Developmental milestones

Table 1 lists definitions for all developmental milestones and how their timing of emergence was extracted from the behavioural dataset. Each individual milestone was placed into a broader milestone category, which consisted of five mutually exclusive categories: 'carrying', 'proximity', 'social-affiliative', 'social-agonistic' and 'non-social physicality'.

Milestones in the social-affiliative, social-agonistic and non-social physicality categories were based on first emergence in the focal and ad libitum datasets. As each individual could not be continuously observed across every day of development, the age of emergence was not recorded until the behaviour was observed at least twice within 90 days. This allowed us to ensure that these behaviours had become part of an individual's behavioural repertoire. For certain milestones that occurred relatively rarely, particularly at first emergence (e.g. 'sociosexual behaviour'), the age of emergence was recorded as the first occurrence.

Milestones in the carrying category were based on being carried dorsally by the mother as a proportion of total times the mother was recorded carrying the infant in any manner (see table 1 for description

Table 1. Mountain and western gorilla developmental milestone categories, definitions and calculations.

milestones	definition and calculation	sample size (individuals with milestone data; F/M)		mean age $\pm$ s.d.		complexity	modelled in <i>Gorilla</i> comparisons
		mountain	western	mountain	western		
<i>carrying</i>							
dorsal carry 20%	to calculate the proportion of time dorsally carried, we divided the number of times an individual was carried dorsally by the total number of times carried generally (i.e. including ventral carries) within each month of observation. The age of emergence was calculated as the first month in which at least 20% of carries were dorsal, with only months in which 10 carries were observed included.	8/11	2/3	0.59 $\pm$ 0.19	0.32 $\pm$ 0.14	1	no
dorsal carry 50%	as above but with a 50% threshold for dorsal carrying	8/11	2/3	0.75 $\pm$ 0.21	0.39 $\pm$ 0.12	1	yes
dorsal carry 80%	as above but with an 80% threshold for dorsal carrying	7/12	2/2	1.03 $\pm$ 0.40	1.18 $\pm$ 0.20	1	no
dorsal carry 90%	as above but with a 90% threshold for dorsal carrying	6/10	2/2	1.23 $\pm$ 0.45	1.58 $\pm$ 0.41	1	no
dorsal carry 95%	as above but with a 95% threshold for dorsal carrying	6/10	2/2	1.51 $\pm$ 0.60	2.12 $\pm$ 0.58	1	no
<i>proximity</i>							
no contact with mother 50%	the age of the offspring in the first month when they were not in physical contact with their mother in at least 50% of the combined mother and offspring proximity scans within a month. Only months where at least 20 scans (combined between mother and individual) were recorded were included in this calculation.	3/6	1/2	1.25 $\pm$ 0.45	1.10 $\pm$ 0.22	0	no
no contact with mother 70%	as above, but with a 70% threshold for scans where the mother and offspring were not in physical contact	3/6	1/2	1.29 $\pm$ 0.46	1.14 $\pm$ 0.23	0	no

(Continued.)

Table 1. (Continued.)

milestones	definition and calculation	sample size (individuals with milestone data; F/M)				mean age $\pm$ s.d.		complexity	modelled in <i>Gorilla</i> comparisons
		mountain	western	mountain	western	mountain	western		
2 m spatial independence from mother 50%	the age of the offspring in the first month when they were a minimum of 2 m away from their mother in at least 50% of the combined mother and offspring proximity scans within a month. Only months where at least 20 scans (combined between mother and individual) were recorded were included in this calculation.	8/10	1/2	2.24 $\pm$ 0.61	2.27 $\pm$ 0.63	0	yes		
2 m spatial independence from mother 70%	as above, but with a 70% threshold for scans where the mother and offspring were not within 2m of each other	9/8	1/2	3.71 $\pm$ 1.23	2.27 $\pm$ 0.63	0	no		
5 m spatial independence from mother 10%	the age of the offspring in the first month when they were a minimum of 5m away from their mother in at least 10% of the combined mother and offspring proximity scans within a month. Only months where at least 20 scans (combined between mother and individual) were recorded were included in this calculation.	7/10	1/2	1.95 $\pm$ 0.61	1.62 $\pm$ 0.54	0	no		
5 m spatial independence from mother 20%	as above, but with a 20% threshold for scans where the mother and offspring were not within 5m of each other	7/10	1/2	2.67 $\pm$ 1.04	2.05 $\pm$ 0.59	0	no		
5 m spatial independence from mother 50%	as above, but with a 50% threshold for scans where the mother and offspring were not within 5m of each other.	6/9	1/2	5.29 $\pm$ 1.56	4.11 $\pm$ 1.04	0	no		
10 m spatial independence from mother 5%	the age of the offspring in the first month when they were a minimum of 10m away from their mother in at least 5% of the combined mother and offspring proximity scans within a month. Only months where at least 20 scans (combined between mother and individual) were recorded were included in this calculation.	8/9	0/1	2.69 $\pm$ 0.77	4.27	0	no		

(Continued.)

Table 1. (Continued.)

milestones	definition and calculation	sample size (individuals with milestone data; F/M)		mean age $\pm$ s.d.		complexity	modelled in <i>Gorilla</i> comparisons
		mountain	western	mountain	western		
10 m spatial independence from mother 10%	as above, but with a 10% threshold for scans where the mother and offspring were not within 10m of each other	8/12	0/1	3.64 $\pm$ 0.88	4.27	0	no
non-social physicality milestones							
climb tree using mouth ^{ab}	age at which an individual was first observed 'biting' (using either teeth or mouth) into tree while climbing	8/9	0/0	1.95 $\pm$ 0.53	N/A	1	no
build nest	age at which an individual was first observed bending branches and vegetation, placing it underneath them to make a nest	6/10	2/3	1.22 $\pm$ 0.44	1.68 $\pm$ 0.36	1	yes
drum object ^{ab}	age at which an individual was first observed using its hands or feet to drum an object	7/9	0/0	1.44 $\pm$ 0.42	N/A	1	no
drum individual ^{ab}	age at which an individual was first observed using its hands or feet to drum on another individual	6/11	0/0	1.47 $\pm$ 0.64	N/A	2	no
solo play ^{ab}	age at which an individual was first observed swinging from branches, slapping vegetation and rolling on the ground when no other individuals are around or do not appear to express interest in playing jointly	6/7	2/3	0.76 $\pm$ 0.39	0.39 $\pm$ 0.06	1	yes
chest beat ^b	age at which an individual was first observed beating its own chest with its hands	10/16	2/3	1.31 $\pm$ 0.57	1.03 $\pm$ 0.48	1	yes
pull vegetation ^{ab}	age at which an individual was first observed grabbing a branch or plant and then running, pulling the vegetation along with him/her	7/10	0/0	3.66 $\pm$ 0.91	N/A	1	no

(Continued.)

Table 1. (Continued.)

milestones	definition and calculation	sample size (individuals with milestone data; F/M)		mean age $\pm$ s.d.		complexity	modelled in <i>Gorilla</i> comparisons
		mountain	western	mountain	western		
social-affiliative							
mother grooming ^b	age at which an individual first runs his/her hands/fingers through the hair of their mother	12/8	1/2	2.50 $\pm$ 0.78	2.78 $\pm$ 0.34	2	yes
social grooming ^b	age at which an individual first runs his/her hands/fingers through the hair of a partner that is not its mother	12/11	1/2	2.56 $\pm$ 0.87	3.23 $\pm$ 0.55	2	yes
social play ^b	age at which an individual first wrestles, tickles, chases, hits etc. in a non-aggressive manner and individual that is not its mother	6/6	2/3	0.43 $\pm$ 0.10	0.32 $\pm$ 0.10	2	yes
sociosexual behaviour	age at which an individual first imitates copulation with another individual	9/11	2/3	3.16 $\pm$ 0.93	N/A	2	yes
solicit play ^{ab}	age at which an individual first attempts to seek social play with another individual	5/10	0/0	1.85 $\pm$ 0.80	N/A	2	no
social-agonistic milestones							
give supplant ^b	age at which an individual first gives approaches another and causes him/her to move away	6/3	0/1	6.40 $\pm$ 2.68	6.65	2	no
mild aggression ^b	age at which an individual mildly aggresses another individual (mild aggressions include pig grunts (aggressive vocalization) and charges (short, fast, aggressive and non-contact movement towards another individual))	10/12	2/4	1.61 $\pm$ 0.73	1.57 $\pm$ 0.94	2	yes

^aMilestones were only recorded or observed in mountain gorillas and not in western gorillas.
^bThe behaviour had to occur at least twice within 90 days for the first age to be taken as the age of emergence.

of carrying methods) within a month of observation (at the levels of 50%, 80%, 90% and 95% dorsal carries). Months with fewer than 10 total recorded carries were excluded, to ensure that a small number of carries did not have large effects on monthly proportions. Milestones in the proximity category (those which measure proportion of time spent at different distances from the mother) were based on the number of scans in which mother and infant were a minimum distance away, based on proximity categories (not in physical contact: <2, >2 to <5, >5 to <10 m) as a proportion of total proximity scans of the mother and infant within a month of observation. Months in which there were fewer than 20 scans with both the mother and infant present were excluded.

For each milestone, individuals were only included in the analysis if they met the following criteria: (i) they were born after the behaviour was introduced to the ethogram; (ii) their age of attainment of the milestone did not occur within four months of the resumption of data collection after the COVID-19 pandemic (paused between March and November 2020 for mountain gorilla data collection; there was no interruption in data collection for the western gorillas); and (iii) their age of first appearance in the behavioural data was less than 0.8 times the youngest age that any individual was observed to hit the milestone (calculated independently for each milestone), to reduce uncertainty that the milestone may have occurred during the pause in data collection. We chose 0.8 times the youngest age because it allows a more proportional inclusion given the different milestones have such different ages. For example, using a fixed age range, e.g. six months, would have given negative ages for early emerging milestones.

To examine whether the ‘complexity’ of a developmental milestone was related to the timing of its emergence, we ranked the complexity based on the number of behavioural components and social partners required for the behaviour to be expressed (*sensu* [12,46]):

- the behaviour could be observed without active effort from the individual *per se*, e.g. no contact or spatial independence from the mother;
- the behaviour required combining multiple motor skills but without involving another social partner, e.g. solitary play; and
- the behaviour involves both motor and social skills and a social partner.

2.4. Data preparation and statistical analysis

Data preparation, modelling and visualization of results were performed in R 3.6.3 [47] using the RStudio interface [48]. We used a combination of base R functions, the *tidyverse* [49] suite of packages and *palet-ter* [50] to generate figures. For statistical modelling, we used a Bayesian approach with models fitted and estimated using Hamiltonian Monte Carlo methods and Stan software [51] with the *brms* package [52].

Prior to model fitting, variance inflation factors (VIFs) were generated using the ‘VIF’ function of the *car* package [53]. There were no issues with collinearity among the variables in the final models presented (max VIF = 1.23).

For our analyses, we standardized fixed-effect variables as z-scores. We used weakly regularizing priors for fixed effects (i.e. normal (0,1)), a weakly regularizing exponential prior ($\lambda = 1$) for the random intercepts and a weakly regularizing student-t prior (df = 3, scale parameter = 2.5) for the residual standard deviation.

For modelling, we specified three chains of 5000 iterations, half of which were devoted to the warm-up. Sampling diagnostics (Rhat < 1.01) and trace plots confirmed chain convergence; effective sample sizes confirmed no issues with autocorrelation of sampling. We used the ‘pp_check’ function of *brms* to perform posterior predictive checks (supplementary material, figs. S2–S25). To check the sensitivity of all our models to prior specification, we ran additional analyses wherein we fitted the models again with either uniform priors or strongly regularizing priors on the fixed effects. All priors included in this study are listed in table S26 in the supplementary material. Figures S27–S50 in the supplementary material illustrate comparisons of model coefficients when different priors were specified: all fixed-effect model coefficients were generally robust to different prior specifications. This use of a Bayesian approach and checking results using multiple priors allows us to account for and illustrate the uncertainty that a small sample size of individuals and data points engenders [54].

To report and interpret the strength and uncertainty of associations tested, we present model coefficient estimates (β), their 90% credible intervals (CI) and the proportion of the posterior distribution in support of the direction of coefficient ($p+$ or $p-$) [55].

2.4.1. Models 1–20: species differences in the timing of developmental milestones among gorillas

The western gorilla group has been followed for a shorter period than the mountain gorilla groups, meaning that many milestones for the western gorillas have a very small sample size. Therefore, for our statistical rather than descriptive comparisons, we chose to model a subset of milestones. Within the milestone categories relating to carrying or proximity, as many of these milestones were similar to one another but at different distance thresholds, we chose to model the latest occurring milestone with the best representation of individuals and sexes within each species. This meant fitting models with the ages for ‘dorsal carry 50%’ and ‘2m spatial independence from mother 50%’ as the response. For the remaining milestone categories (non-social physicality, social-affiliative and social-agonistic), we modelled any milestone where we had data on more than one individual from the western gorilla dataset. This meant fitting models with ages for ‘build nest’, ‘solo play’, ‘chest beat’, ‘mother grooming’, ‘social grooming’, ‘social play’, ‘sociosexual behaviour’ and ‘mild aggression’ as the response. The milestones chosen for inclusion are indicated in the ‘modelled in *Gorilla* comparisons’ column in table 1.

For models 1–10, our response was the age at which a milestone was observed, and our main predictor was the species category (two levels: mountain and western gorillas). Owing to the low sample size within western gorillas, for this set of analyses, we did not include sex as a predictor variable. As the timing of certain milestone may rely on group-level factors such as resource competition or the availability of social partners, we included the group size at birth as a control variable in this model. We included group size at birth, rather than at the time of the milestone as females may have transferred to new groups during the development of their offspring. Group size at birth reflects initial social exposure and opportunity and can be measured more consistently. These models using absolute ages were fitted with a Gaussian error distribution.

For each of these milestones, we fitted an additional model (models 11–20) to test species differences in which the response was age adjusted to be a proportion of age at maturation in each species and sex (i.e. when the milestone emerged relative to overall developmental period). For female gorillas, we considered average age at maturation to be the average age at first reproduction: 10.5 years for mountain gorillas and 12.2 years for western gorillas [40]. For male gorillas, we considered average age at maturation to be the average age at physical maturity: 15 years for mountain gorillas and 18 years for western gorillas [41]. As adjusted age is a proportion, these models were fitted with a beta error distribution and a logit link function.

2.4.2. Models 21–24: sex differences in developmental milestones in mountain gorillas

As we had a limited sample size among western gorillas, we ran separate models to examine sex differences in the emergence of developmental milestone among mountain gorillas only ($n = 28$ milestones). In this set of models, we included all milestones in a single model: the response variable was again the age at the emergence of a developmental milestone (either absolute age (models 21 and 23) or relative age adjusted for sexual maturation (model 22 and 24)), and our main predictor variables were the interactions between the sex of the individual and the milestone category (five levels: carrying, proximity, non-social physicality, social-affiliative and social-agonistic) and the interaction between the sex of the individual and the milestone complexity (three levels: 0, 1 and 2). However, there were issues with collinearity when including both milestone category and complexity; therefore, we ran separate models, including either milestone complexity (models 21–22) or milestone category (models 23–24). We once again included group size at birth as a control variable. As we had multiple milestones from individuals and multiple individuals generating milestones for a given level of complexity or category, we included random intercepts for individual and milestone identity, with random slopes for group size within each of these random effects [56]. The absolute ages in this dataset were right skewed, so we used a lognormal error distribution for these models (models 22 and 24); the models using adjusted age were again fitted using a beta error distribution.

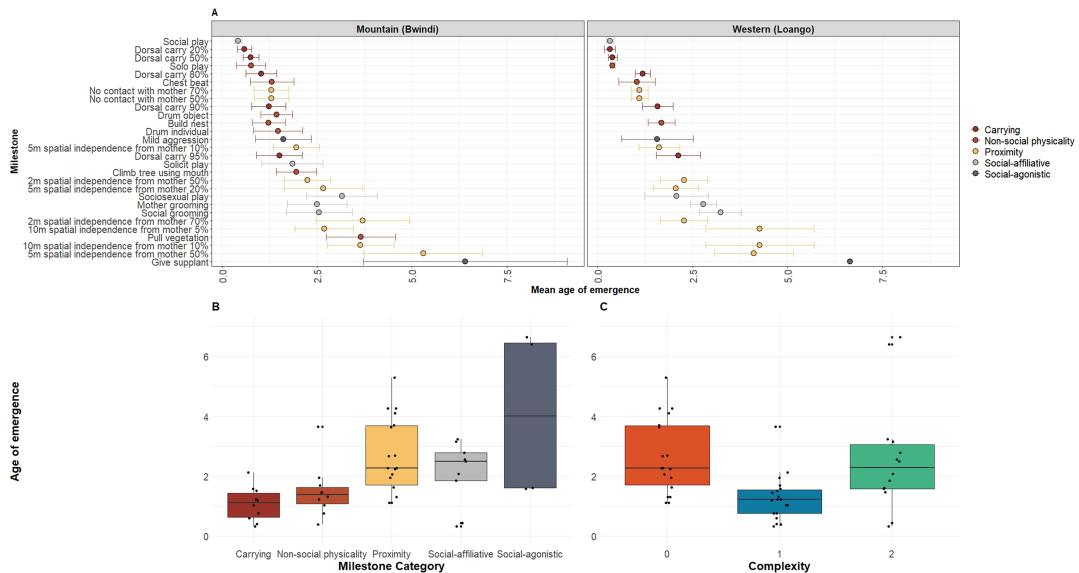


Figure 1. Emergence of development milestones in mountain ($n = 36$ gorillas; $n = 28$ milestones) and western gorillas ($n = 7$ gorillas; $n = 23$ milestones). In (A) points represent the mean absolute age of emergence for a milestone within each species; the error bars represent the standard deviation, with each point and error bar coloured according to the broader category within which the milestone falls; (B and C) each box plot illustrates the mean absolute age (and 25% quartiles) of emergence for each milestone category and level of complexity, respectively, using data from both species; in both the points represent means for each milestone.

2.4.3. Species differences in developmental milestones between gorillas and chimpanzees

Lastly, we present the means and standard deviations of the age of emergence of developmental milestones that are directly relatable to those in chimpanzees. We descriptively compare the ages of emergence in chimpanzees and gorillas by drawing upon published data [12].

3. Results

In line with the expectations of the life-history brain development and delayed benefits hypotheses, we observed that developmental milestones emerged gradually across gorilla ontogeny (figure 1A). There was a lot of variation in individual milestone emergence within each broad milestone category (figure 1B) and based on estimated milestone complexity (figure 1C): although social milestones appeared to emerge later across both species, some of the motor skills behaviours (complexity level 1) emerged very early in ontogeny and ahead of some of the spatial independence milestones (complexity level 0).

3.1. Species differences among Gorilla

Tables 2 and 3 list the results of our *Gorilla* species comparison models using absolute ages and ages relative to sexual maturation, respectively. Using either age measure, western gorillas had earlier occurring milestones compared to mountain gorillas for the ‘dorsal carry 50%’ (absolute age model: $p = 0.998$; relative age model: $p = 0.996$), ‘solitary play’ (absolute age model: $p = 0.958$; relative age model: $p = 0.974$), ‘social play’ (absolute age model: $p = 0.945$; relative age model: $p = 0.997$) and ‘sociosexual play’ (absolute age model: $p = 0.982$; relative age model: $p = 0.994$) milestones. When considering relative ages only, we also found that the milestone ‘chest beat’ occurred earlier in the western gorillas compared to the mountain gorillas ($p = 0.979$). The only milestone that occurred earlier in mountain gorillas was ‘build nest’ and only when considering absolute ages ($p = 0.962$). For three milestones (‘2m spatial independence 50%’, ‘mother grooming’ and ‘mild aggression’), there were no clear species differences when considering either absolute or relative ages.

Overall, our *Gorilla* species comparison suggested earlier occurring milestones in western rather than mountain gorillas (figure 2). Group size did not show consistent associations with the timing of milestone emergence across all models (tables 2 and 3).

Table 2. Models 1–10 results testing species differences in the absolute age of emergence of developmental milestones in wild gorillas.

model/milestone	predictor	estimate	est. error	Q5	Q95
(1) 2m spatial independence (50%)	intercept	2.278	0.161	2.018	2.540
	group size	−0.070	0.159	−0.333	0.192
	species (mountain)	−0.180	0.404	−0.849	0.486
(2) dorsal carry (50%)	intercept	0.745	0.049	0.667	0.827
	group size	0.039	0.047	−0.038	0.117
	species (mountain)	−0.321	0.111	−0.505	−0.139
(3) build nest	intercept	1.233	0.115	1.049	1.422
	group size	−0.022	0.105	−0.195	0.147
	species (mountain)	0.422	0.237	0.034	0.809
(4) solitary play	intercept	0.763	0.1180	0.583	0.939
	group size	−0.022	0.105	−0.192	0.150
	species (mountain)	−0.378	0.218	−0.726	−0.023
(5) chest beat	intercept	1.326	0.116	1.131	1.520
	group size	−0.141	0.112	−0.321	0.043
	species (mountain)	−0.352	0.288	−0.821	0.126
(6) mother grooming	intercept	2.501	0.179	2.210	2.786
	group size	−0.004	0.172	−0.289	0.289
	species (mountain)	0.229	0.448	−0.517	0.967
(7) social grooming	intercept	2.576	0.184	2.278	2.884
	group size	0.202	0.174	−0.083	0.485
	species (mountain)	0.492	0.485	−0.306	1.288
(8) social play	intercept	0.428	0.033	0.374	0.483
	group size	−0.001	0.031	−0.052	0.049
	species (mountain)	−0.104	0.066	−0.212	0.004

(Continued.)

Table 2. (Continued.)

model/milestone	predictor	estimate	est. error	Q5	Q95
(9) sociosexual play	intercept	3.141	0.216	2.776	3.494
	group size	−0.173	0.206	−0.515	0.170
	species (mountain)	−0.993	0.467	−1.743	−0.213
(10) mild aggression	intercept	1.620	0.180	1.327	1.908
	group size	−0.035	0.171	−0.314	0.246
	species (mountain)	−0.064	0.381	−0.698	0.553

Note: Variables in bold had more than 90% of the posterior distribution supporting the direction of effect. For categorical variables, the reference category is given in parentheses.

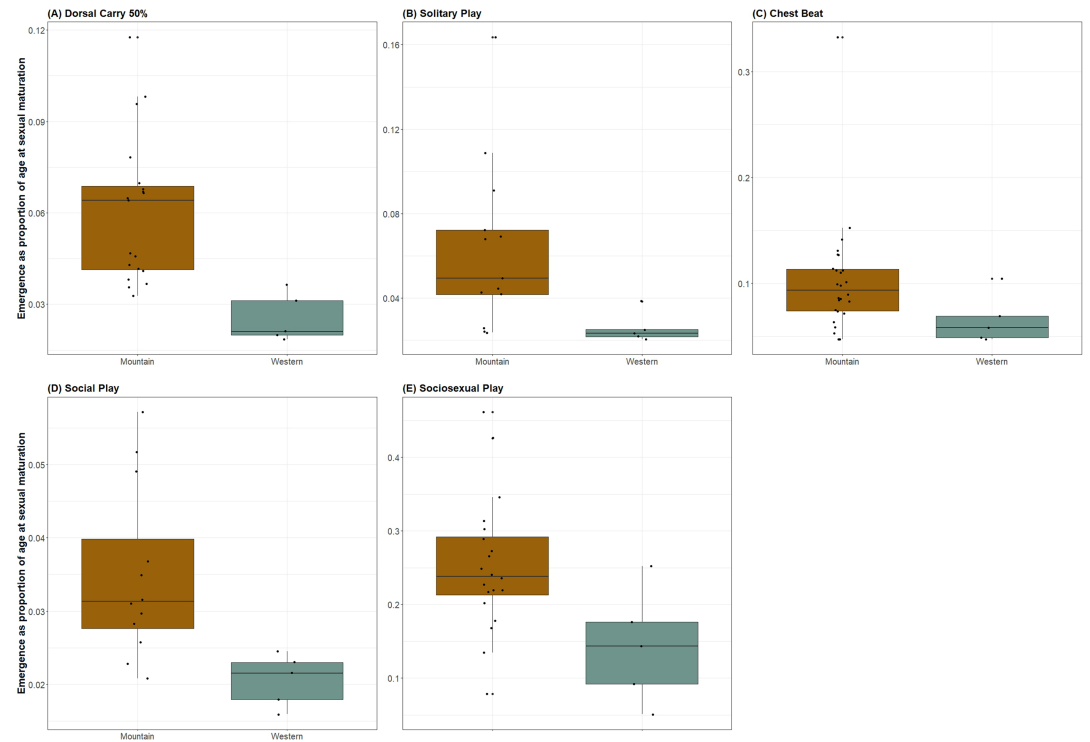


Figure 2. Emergence of developmental milestones where species differences were observed between mountain and western gorillas. In all plots (A–E), the box plots illustrate the mean relative age (and 25% quartiles) of emergence for each milestone with the points representing the relative age, that is, as a proportion of age at maturation, for an individual gorilla.

3.2. Sex differences in developmental milestones in mountain gorillas

Our data for models 21–24 included 473 ages of emergence for 28 milestones from 36 mountain gorillas.

In model 21 (table 4), among mountain gorillas and considering the absolute age of milestone emergence, males tended to have earlier emerging milestones, although this general sex difference was associated with a high degree of uncertainty ($p = 0.851$). Sex differences were clearest among milestones with complexity level 2 ($p = 0.979$; note: the positive estimate here is due to the use of the lognormal error distribution and the negative estimate for complexity level 1). Although there was a high degree of

Table 3. Models 11–20 results testing species differences in the relative age of emergence (i.e. as a proportion of age at maturation) of developmental milestones in wild gorillas.

model/milestone	predictor	estimate	est. error	Q5	Q95
(11) 2m spatial independence (50%)	intercept	−1.507	0.102	−1.675	−1.349
	group size	−0.047	0.106	−0.221	0.124
	species (mountain)	−0.362	0.294	−0.863	0.108
(12) dorsal carry (50%)	intercept	−2.762	0.099	−2.920	−2.599
	group size	0.064	0.100	−0.098	0.230
	species (mountain)	−0.703	0.271	−1.176	−0.277
(13) build nest	intercept	−2.260	0.109	−2.436	−2.080
	group size	−0.031	0.099	−0.195	0.130
	species (mountain)	0.162	0.214	−0.202	0.504
(14) solitary play	intercept	−2.701	0.166	−2.980	−2.425
	group size	−0.100	0.177	−0.384	0.200
	species (mountain)	−0.701	0.361	−1.292	−0.109
(15) chest beat	intercept	−2.152	0.094	−2.303	−1.992
	group size	−0.118	0.095	−0.276	0.040
	species (mountain)	−0.505	0.266	−0.956	−0.085
(16) mother grooming	intercept	−1.359	0.092	−1.510	−1.211
	group size	−0.005	0.084	−0.141	0.133
	species (mountain)	−0.146	0.255	−0.573	0.257
(17) social grooming	intercept	−1.365	0.075	−1.489	−1.243
	group size	0.104	0.073	−0.015	0.226
	species (mountain)	−0.012	0.220	−0.379	0.330
(18) social play	intercept	−3.316	0.116	−3.507	−3.125
	group size	−0.001	0.117	−0.191	0.191
	species (mountain)	−0.458	0.245	−0.875	−0.063

(Continued.)

Table 3. (Continued.)

model/milestone	predictor	estimate	est. error	Q5	Q95
(19) sociosexual play	intercept	−1.082	0.115	−1.269	−0.891
	group size	−0.037	0.113	−0.230	0.148
	species (mountain)	−0.710	0.303	−1.214	−0.224
(20) mild aggression	intercept	−1.927	0.112	−2.109	−1.736
	group size	−0.013	0.105	−0.187	0.160
	species (mountain)	−0.302	0.263	−0.751	0.119

Note: Variables in bold had more than 90% of the posterior distribution supporting the direction of effect. For categorical variables, the reference category is given in parentheses.

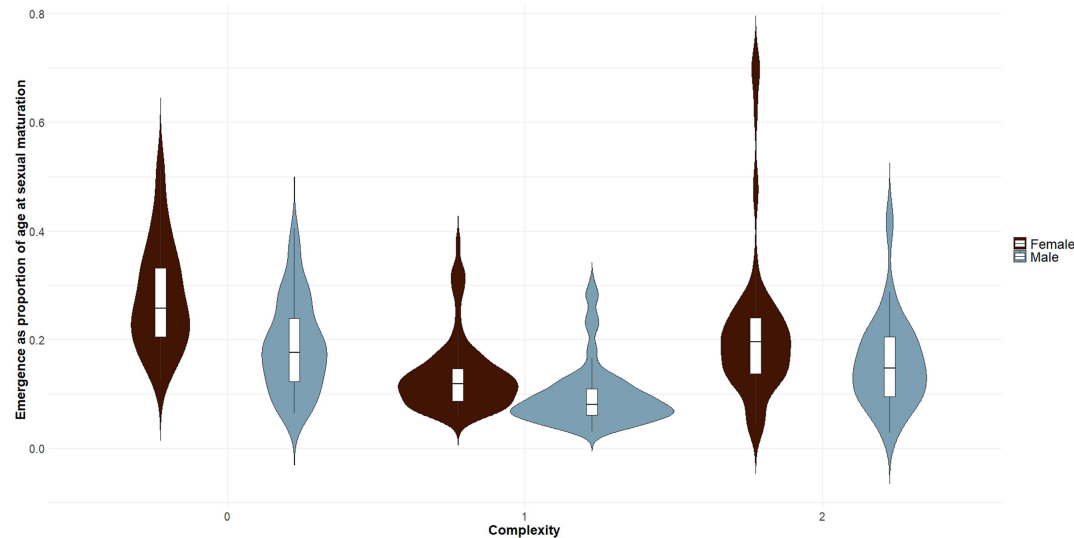


Figure 3. Sex differences in the emergence of development milestones in mountain gorillas as a proportion of sexual maturation when considering milestone complexity. Violin plots represent kernel probability density of fitted values in the posterior; the box plots illustrate the mean (horizontal line), and 50% (box) and 75% (vertical line) quartiles ranges of these values.

certainty of this association, the effect size appeared small, with males predicted to reach any milestone in this complexity category approximately 1 month (0.09 years) earlier than females.

In model 22 (table 4), among mountain gorillas and considering ages relative to sexual maturation, milestones at complexity level 1 ($p = 0.995$) and level 2 ($p = 0.910$) both emerged earlier than those at complexity level 0, with males having earlier occurring milestones than females across all categories (complexity level 1: $p = 0.917$; complexity level 2: $p = 0.996$; figure 3).

In model 23 (table 5), among mountain gorillas and considering the absolute age of milestone emergence, there was an uncertain association between sex and milestone emergence, with males having earlier occurring milestones compared to females ($p = 0.850$). However, for both the social-affiliative ($p = 0.948$) and social-agonistic ($p = 0.982$) categories, males had later occurring milestones (figure 4). For both sexes, the carrying milestones occurred earlier than the milestones in other categories (table 5, figure 4).

Table 4. Models 21–22 results testing whether complexity or sex differences were associated with the age of emergence of developmental milestones in wild mountain gorillas.

model	predictor	estimate	est. error	Q5	Q95
(21) sex differences (absolute ages) and complexity	intercept	1.014	0.194	0.704	1.340
	group size	−0.006	0.047	−0.083	0.071
	sex (female)	−0.103	0.099	−0.264	0.064
	complexity level (0)				
	complexity level 1	−0.643	0.247	−1.056	−0.230
	complexity level 2	−0.310	0.270	−0.756	0.127
	sex (female):complexity level (0)				
	sex male:complexity level 1	0.001	0.064	−0.106	0.106
	sex male:complexity level 2	0.136	0.069	0.023	0.250
(22) sex differences (relative ages) and complexity	intercept	−1.064	0.219	−1.426	−0.719
	group size	−0.004	0.064	−0.110	0.098
	sex (female)	−0.567	0.117	−0.761	−0.380
	complexity level (0)				
	complexity level 1	−0.748	0.267	−1.184	−0.309
	complexity level 2	−0.359	0.275	−0.813	0.084
	sex (female):complexity level (0)				
	sex male:complexity level 1	0.119	0.085	−0.023	0.259
	sex male:complexity level 2	0.231	0.089	0.084	0.382

Note: Variables in bold had more than 90% of the posterior distribution supporting the direction of effect. For categorical variables, the reference category is given in parentheses.

In model 24 (table 5), among mountain gorillas and considering ages relative to sexual maturation, males generally had earlier occurring milestones compared to females ($p = 0.998$); however, this model did not find clear sex differences within the different milestone categories.

3.3. Species differences between gorillas and chimpanzees

Table 6 and figure 5 show the means and standard deviations for the ages at which comparable developmental milestones emerge in 19 wild western chimpanzees (*P. troglodytes verus*; taken from Bründl *et al.* [12]) and the two species of gorilla in our study. In table 6, these ages are listed as absolute ages (in years); in figure 4, we plot both (a) absolute ages (in days) and (b) ages as a proportion of developmental period within each species (averaged across the sexes). For earlier occurring milestones (i.e. solo play,

Table 5. Models 23 and 24 results testing whether milestone category or sex differences were associated with the age of emergence of developmental milestones in wild mountain gorillas.

model	predictor	estimate	est. error	Q5	Q95
(23) sex differences (absolute ages) and milestone category	intercept	0.160	0.238	−0.222	0.559
	group size	−0.004	0.049	−0.083	0.075
	sex (female)	−0.109	0.105	−0.281	0.060
	category (carrying)				
	non-social physicality	0.418	0.313	−0.104	0.936
	proximity	0.850	0.286	0.371	1.297
	social-affiliative	0.421	0.326	−0.113	0.947
	social-agonistic	0.787	0.410	0.097	1.451
	sex (female):category (carrying)				
	sex male:non-social physicality	−0.002	0.080	−0.136	0.125
	sex male:proximity	0.004	0.079	−0.127	0.132
	sex male:social-affiliative	0.145	0.088	−0.001	0.287
	sex male:social-agonistic	0.258	0.123	0.057	0.463
(24) sex differences (relative ages) and milestone category	intercept	−2.065	0.267	−2.489	−1.625
	group size	−0.006	0.066	−0.116	0.100
	sex (female)	−0.451	0.142	−0.685	−0.220
	category (carrying)				
	non-social physicality	0.488	0.324	−0.064	1.008
	proximity	1.006	0.308	0.489	1.492
	social-affiliative	0.620	0.347	0.028	1.173
	social-agonistic	0.663	0.443	−0.089	1.374
	sex (female):category (carrying)				
	sex male:non-social physicality	−0.010	0.125	−0.215	0.196
	sex male:proximity	−0.120	0.115	−0.307	0.065
	sex male:social-affiliative	0.111	0.128	−0.102	0.327
	sex male:social-agonistic	0.218	0.174	−0.069	0.504

Note: Variables in bold had more than 90% of the posterior distribution supporting the direction of effect. For categorical variables, the reference category is given in parentheses.

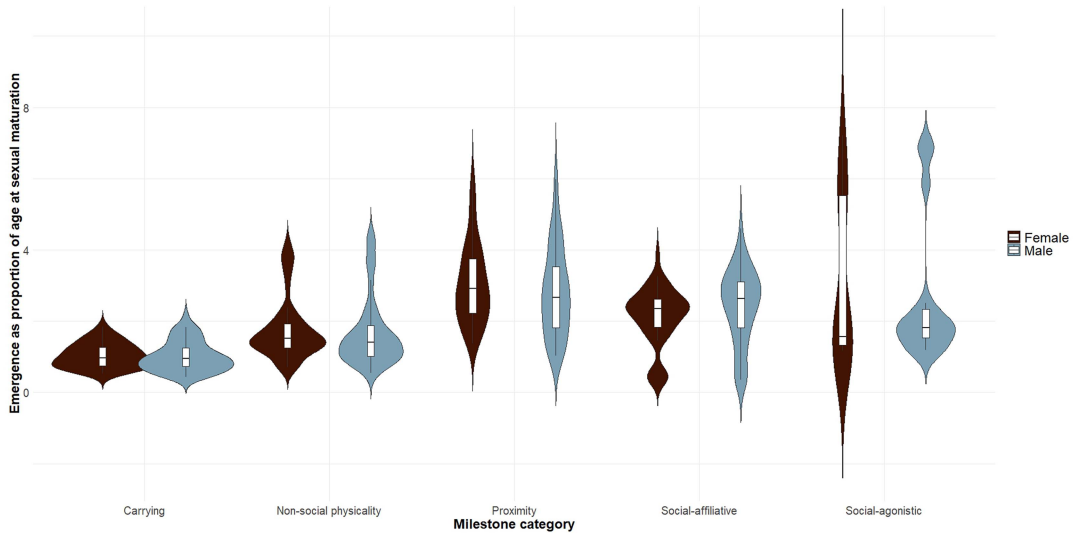


Figure 4. Sex differences in the emergence of development milestones in mountain gorillas using different milestone categories. Violin plots represent kernel probability density of fitted values in the posterior; the box plots illustrate the mean (horizontal line), and 50% (box) and 75% (vertical line) quartiles ranges of these values.

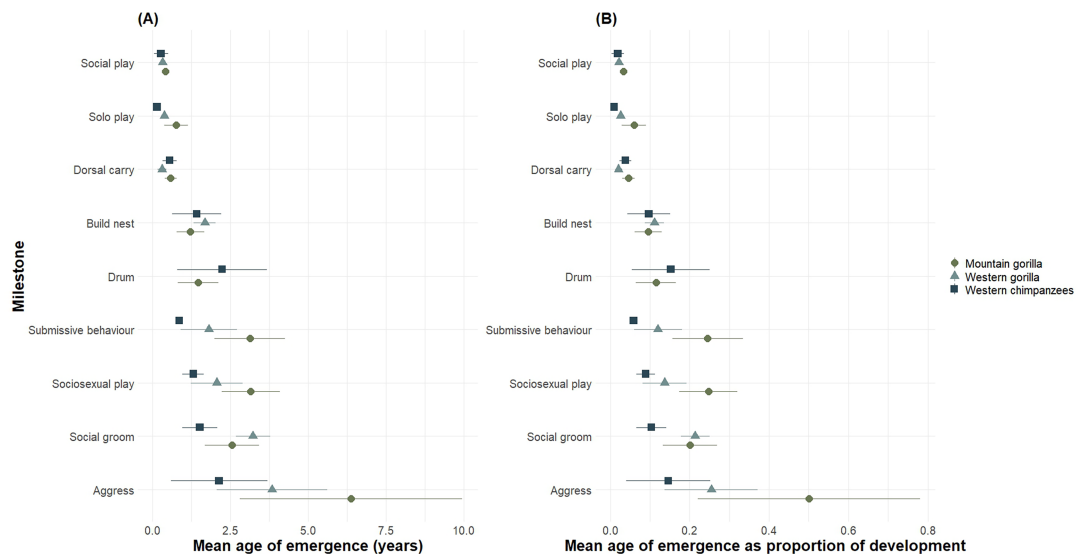


Figure 5. Comparison of emergence of development milestones in western chimpanzees, mountain and western gorillas as (A) absolute ages in days and (B) a proportion of total developmental period for the species (averaged across the sexes). Points represent the mean age of emergence for a milestone within each species; the error bars represent the standard deviation. Each point is coloured and shaped to represent species.

social play, dorsal carry and build nest), there were few clear differences between western chimpanzees and either species of gorilla. For the later occurring and social milestones (i.e. submissive behaviour, sociosexual play, social grooming and aggressive behaviour), these tended to emerge earlier in western chimpanzees compared to either species of gorilla.

4. Discussion

Using a unique long-term dataset, which includes data from one population of each of the two gorilla species, our study tests several prominent hypotheses related to the evolution of primate life history using a developmental milestones framework. Although we had a small sample size of individuals among western gorillas, our Bayesian statistical approach allowed us to model species differences while

Table 6. Descriptive statistics for age of emergence of comparable milestones for western chimpanzees and two species of gorilla.

developmental milestone	western chimpanzees			mountain gorillas			western gorillas		
	<i>N</i>	mean	s.d.	<i>N</i>	mean	s.d.	<i>N</i>	mean	s.d.
solo play	17	0.15	0.12	13	0.76	0.39	5	0.39	0.06
social play	17	0.28	0.23	12	0.43	0.10	5	0.32	0.10
dorsal carry ^a	16	0.56	0.22	19	0.59	0.19	5	0.32	0.14
sociosexual play	7	1.31	0.34	20	3.16	0.93	5	2.07	0.84
build nest	14	1.43	0.79	16	1.22	0.44	5	1.68	0.36
social groom	13	1.52	0.56	23	2.56	0.87	3	3.23	0.55
aggress	8	2.14	1.55	22	1.61	0.73	6	1.57	0.94
drum	6	2.24	1.44	17	1.47	0.64	NA	NA	NA

Note: We present the means and standard deviations in age (in years) of emergence, as well as the number of individuals that contributed to these values in each species. Western chimpanzee values are taken from Bründl *et al.* [12]; this paper includes operational definitions for these milestones in western chimpanzees.

^a For *Gorilla* species, the measure refers to age at first month in which 20% of all carries were dorsal rather than ventral, rather than the first single observation of dorsal carrying, as in the chimpanzee data.

incorporating the uncertainty that a small sample size engenders. Furthermore, our sample size overall compares favourably with other non-human ape studies in this field [12], meaning we can draw some cautious but important conclusions about species differences within *Gorilla* and among hominids in general.

In support of the life-history brain development [7–9] and delayed benefits [10] hypotheses, developmental milestones emerged gradually across ontogeny, with more complex milestones (i.e. social interactions with multiple actions or behaviours comprising the milestone [12]) generally emerging later in development in both species of *Gorilla*. However, contrary to this pattern, certain milestones related to spatial independence from the mother occurred relatively late in development in both species, despite us considering these milestones to be low in complexity. Our measure of complexity related to the number of behavioural components and social partners required for the milestone to be expressed. However, many of the milestones that we have defined as ‘low’ in complexity relate to spatial independence, which, while not requiring multiple behaviours or any social partners, still require physical and cognitive maturation to minimize any potential risks from predators or conspecifics when exploring away from their mothers.

Defining and measuring complexity is contentious [46,57]; therefore, including the broader milestone categories (carrying, non-social physicality, proximity, social-affiliative and social-agonistic) allowed for a clearer exploration of species and sex differences in our study. However, despite previous studies recording differences between mountain and western gorillas in the timing of developmental and reproductive life-history events [40,58], we found limited evidence for species differences in the timing of developmental milestones, with only half of the milestones tested showing clear species differences. Lastly, when comparing both gorilla species to western chimpanzees, overall, there was no clear pattern regarding which genus had the slower or faster emerging milestones. However, for later emerging, social milestones, it seems that western chimpanzees had earlier emergence than either species of gorilla, contradicting our predictions related to the delayed benefits hypothesis [10]. Below, we explore potential explanations for our findings in relation to both the delayed benefits and ecological risk aversion hypotheses. However, overall, our results, and previous studies of gorillas [33,40,58,59], suggest that there is a complex mosaic of life history and developmental metrics, and that factors such as maternal energetics, physical environment and social settings may complicate the slow/fast dichotomy present in life-history literature when applied to developmental milestones.

4.1. Explaining sex differences and similarities in milestone timing in mountain gorillas

Owing to constraints of sample size, we were only able to conduct a meaningful analysis of sex differences in developmental milestone emergence in mountain gorillas. In keeping with the predictions of the ecological risk aversion hypothesis, studies of growth rates in *Gorilla* suggest that in both species, females undergo earlier growth spurts than males [43] and they reach reproductive maturity earlier than males. However, in our study, mountain gorillas of both sexes had similar timings for physical milestones. There were sex differences when we examined social milestones: females had earlier emerging social-affiliative and agonistic behaviours when using absolute age, but this difference was less obvious when controlling for age at maturation. Compared to young mountain gorilla females, young males build stronger ties with adult males, presumably for increased social learning opportunities to cope with highly competitive social environments in adulthood [44]. In addition, studies of adult mountain gorillas suggest a selection pressure for females to be more gregarious than males in order to reduce infanticide risk [60,61]. Young male Bwindi mountain gorillas show clear differences in how they allocate time to affiliative behaviours: males play more than females, particularly between the ages of 2 and 6 years [62], while females spend more affiliative social time in grooming [62]. As play is thought to be an integral part of both social and physical development [63], and males face a more physically competitive adult environment compared to females, male mountain gorillas may delay certain social milestones until they are physically more well developed to integrate in social networks and compete in dominance hierarchies. In this light, our findings are largely in keeping with the delayed benefits hypothesis. Furthermore, females typically disperse to new groups as subadults [40], which may require them to develop agonistic behaviours at an earlier age than males. Another possibility is that increased socialization inherently leads to more agonism at younger ages [64], but this requires a more detailed analysis of the social dynamics of immature gorillas, especially among the less well-studied western species. For example, future research might want to focus more on changes in rates of interactions, rather than just the onset or first emergence of a given behaviour.

4.2. Explaining species differences and similarities in milestone timing in wild apes

Drawing upon the ecological risk aversion hypothesis [11], we predicted that western gorillas would have slower development than mountain gorillas to offset the mortality risks of living in a more resource-variable ecological environment. Previous studies have found support for this hypothesis as wild western gorillas achieve major life-history events, including weaning and age of first reproduction at a later age than mountain gorillas [40], both indicative of a slower life history. Furthermore, western gorillas raised in captivity (with higher food availability, less energy expenditure and veterinary care) had shorter interbirth intervals and earlier age of first parturition than wild western gorillas [40] suggesting plasticity plays a role in the timing of life-history events owing to environmental conditions. However, in our study, the only clear differences were that western gorillas had *earlier* rather than later occurring milestones when compared to mountain gorillas, and the milestones with species differences came from a range of categories and levels of complexity (i.e. observed species differences found were not purely related to physical or social maturation). The western gorilla sample size was very small, and across all milestones, there was considerable individual variation in the emergence of individual milestones. Therefore, we cannot entirely eliminate the possibility that the species differences observed were driven by our sample being dominated by some relatively rapidly developing western gorillas. However, this seems unlikely, and there are plausible alternative or non-mutually exclusive explanations to ecological risk aversion. For example, despite having more fruit in their diet, the smaller group sizes of western gorillas may offset 'ecological risks' (i.e. competition) for this species compared to mountain gorillas. Alternatively, or perhaps concurrently, more fruit in the diet of western gorillas may mean more spatial clumping of individuals around some resources, with such spatial tolerance either requiring or leading to more social affiliation even among immatures [65]. Differences in the physical environment, particularly the extremely dense understory vegetation for mountain gorillas compared to western gorillas, may also restrict their ability to exhibit particular locomotory behaviours linked to individual and social milestones at a young age (e.g. less than 2 years). Although group size at birth was rarely a significant factor in our models, future studies should examine in more detail how social factors like the number of age-peers young gorillas have available as social partners, adult sex ratios (to account for levels of competition) and more fine-grained measures of social cohesion (e.g. using social network metrics) or

tolerance (e.g. including maternal rank as a predictor) influence the timing of social versus physical developmental milestones in *Gorilla*.

Physical milestones emerged at similar ages in each gorilla species, and this held even when running models when adjusting milestone ages by the average of first reproduction in each species. The exceptions to this were in the transition to dorsal carrying making up 50% of all carrying events, where again, western gorillas showed faster maturation than mountain gorillas, and nest building, where western gorillas had slower maturation than mountain gorillas when considering absolute ages only. One possible explanation here is the difference in the terrain each species occupies and their relative arboreality. Western gorillas are more arboreal and regularly move across swampy areas. Both in trees and when traversing swamps, it is presumably far easier to move with dorsal rather than ventrally placed infants. It may also explain why nest building, which occurs on the ground, emerges later in this species: the terrain may be more variable and slightly longer learning is required when it comes to building a nest. This result is more in keeping with the delayed benefits hypothesis; however, it was only clearly observed when comparing the absolute ages of each species.

As described above, physical growth, nutritional and reproductive maturation typically occur later in western compared to mountain gorillas [33,40,58]. The seasonality of the western gorilla food availability [32,66] could generate energetic constraints that delay physical, nutritional and reproductive maturation, but not the development of the cognition and coordination skills required for the physical (and social) milestones in our study. Indeed, taken in combination with many social-affiliative milestones occurring earlier in western gorillas (when controlling for age of first reproduction), our study suggests cognitive development is not well predicted by a single hypothesis within life-history theory, and that the development of each milestone probably involves multiple trade-offs across ontogeny.

Our comparison of both species of *Gorilla* with western chimpanzees also generated results neither clearly in alignment with the expectations of the ecological risk aversion nor delayed benefits hypotheses. Chimpanzees were expected to have slower emerging milestones owing to occupying highly seasonal and resource variable environments and later age of attaining life-history traits, especially compared to mountain gorillas. Instead, most physical milestones occurred at similar ages; in addition, social-affiliative milestones (notably grooming and play) occurred earlier in chimpanzees compared to both species of *Gorilla*. Furthermore, aggressive behaviours emerged later in chimpanzees compared to *Gorilla*. Following the line of argument above, a greater reliance on fruit, and thus clumped food resources, may select for fast-developing affiliative skills to mediate social tolerance [67,68]. In addition, aggression towards immatures is not uncommon in chimpanzees [69]; therefore, young chimpanzees may be less likely to risk any agonistic behaviour in case of more severe retaliation from conspecifics. Alternatively, this finding of later emerging aggressive milestones in chimpanzees could suggest some support for both the ecological risk aversion and delayed benefits hypotheses, with chimpanzees avoiding competitive encounters until much later in their development when both physically able to compete (ecological risk aversion) and cognitively developed (delayed benefits) enough to do so strategically. Importantly, comparisons of proximity patterns during development between western chimpanzees and both species of gorilla were not possible. More data on how individuals in each of these species gradually explore more of their social environment would be useful for understanding more fully the species differences identified.

We only have comparable developmental milestone data from western chimpanzees; eastern chimpanzees (*P. troglodytes schweinfurthii*) tend to have higher levels of feeding competition and intragroup aggression [69]. Expanding comparisons across multiple species and populations of apes is clearly required to understand potential drivers of differences and similarities in developmental patterns in apes. Previous comparisons of developmental patterns in apes have also failed to find robust support for the ecological risk aversion hypothesis [27]. Bonobos are much more frugivorous than mountain gorillas, but they also experience low seasonality and an abundance of terrestrial herbaceous vegetation, providing a reliable fallback food supply [70]. However, although bonobos physically mature faster than chimpanzees [71], the timing of behavioural and social maturation is largely similar in bonobos and chimpanzees [27].

5. Conclusion

Overall, species comparisons of development among chimpanzees, bonobos and both species of gorillas suggest that neither the ecological risk aversion nor delayed benefits hypotheses are entirely consistent with patterns of developmental milestone emergence. Instead, our results suggest more work needs to

be conducted to assess the interplay between ecology, social opportunity, social constraints and the development of behavioural and cognitive milestones in wild apes. In wild chimpanzees and Assamese macaques, immatures that spend more time socializing tend to have earlier emerging physical and locomotor milestones [26,63]. However, interspecific and intraspecific comparisons in how social opportunity and resource availability influence development are currently lacking and would clearly benefit our understanding of the evolution of developmental strategies among long-lived primates.

The developmental milestone framework places a large emphasis on using milestones to track neurobiological and cognitive maturation [16]. However, body growth and brain growth during development may occur at different paces [72]. In addition, in species like apes, social learning is a key aspect of cognitive development and maturation [73]. Therefore, predictions from life-history theory related to ecology, i.e. the ecological risk aversion hypothesis [11], may be well suited to predicting growth rates and timing of reproductive maturation, but a poorer predictor of rates of cognitive development, where social dynamics may be more important. Here, the delayed benefits may be more informative: in our sex comparisons in mountain gorillas and our species comparison between chimpanzees and gorillas, we saw that the more aggressive sex/species had later emerging agonistic milestones, suggestive of the social and physical skills involved in aggression taking longer to mature. This highlights the benefits of the developmental milestone framework: studying the timing and sequence of multiple trait emergences across ontogeny in one study, rather than focusing on individual behaviours, helps in determining where and when life-history selection has favoured physical or cognitive development.

Our study adds to a growing body of literature using the developmental milestone framework and shows the benefit of long-term field studies of long-lived species. Although direct comparisons of milestones are challenging, even among closely related species such as apes, our study and others show that it is a useful method for testing key and long-standing evolutionary hypotheses.

Ethics. All work was conducted under research permits and with ethical approval from Uganda Wildlife Authority, Uganda National Council for Science and Technology, Agence Nationale des Parcs Nationaux and the Centre National de la Recherche Scientifique et Technique of Gabon.

Data accessibility. Data and relevant code for this research work are stored in GitHub (https://github.com/ptkaczynski/gorilla_developmental_milestones) and have been archived within the Zenodo repository [74].

Supplementary material is available online [75].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. P.J.T.: data curation, formal analysis, investigation, methodology, validation, visualization, writing—original draft, writing—review and editing; J.R.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, writing—original draft, writing—review and editing; M.M.R.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, writing—original draft, writing—review and editing.

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