

Title: Behavioural variation and learning across the lifespan in wild white-faced capuchin monkeys.

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Abstract: Natural selection has evidently mediated many species characteristics relevant to the evolution of learning , including longevity, length of the juvenile period, social organization, timing of cognitive and motor development, and age-related shifts in behavioural propensities such as activity level, flexibility in problem-solving, and motivation to seek new information. Longitudinal studies of wild populations can document such changes in behavioural propensities, providing critical information about the contexts in which learning strategies develop, in environments similar to those in which learning strategies evolved. The Lomas Barbudal Monkey Project provides developmental data for the white-faced capuchin, *Cebus capucinus*, a species that has converged with humans regarding many life history and behavioural characteristics. In this data set, focused primarily on learned aspects of foraging behaviour, younger capuchins are more active overall, more curious and opportunistic, and more prone to inventing new investigative and foraging-related behaviours. Younger individuals more often seek social information by watching other foragers (especially older foragers). Younger individuals are more creative, playful and inventive, and less neophobic, exhibiting a wider range of behaviours when engaged in extractive foraging. Whereas adults more often stick with old solutions, younger individuals often incorporate recently acquired experience (both social and asocial) when foraging.

1. Introduction:

Evolutionary biologists have come to appreciate the role of innovation and social learning in altering selective pressures on both anatomical and behavioural traits [1][2][3][4]. In many taxa, encephalization seems to have co-evolved with cognitive skills such as social learning, ability to innovate new behaviours, and perspective-taking [4]. Behavioural ecologists have begun to explore potential relationships among life history, environmental context and learning [5][6][7]. Various hypotheses [8][9] suggest that mastery of difficult foraging skills is involved in the evolution of large brains and long juvenile periods; empirical tests of these hypotheses have produced mixed results [10][11][12][9]. Behavioural ecologists and developmental psychologists have focused attention on developmental changes in learning strategies [13][14][15], including the questions – raised, but rarely addressed with field data -- of whether and why juveniles of various species show greater exploration, flexibility and creativity in problem-solving.

Optimal learning strategies, particularly those involving social learning, are partly a function of the species-specific constraints posed by life history stage. Traits that have been shaped by selection into functionally integrated packages – e.g. longevity, length of the juvenile

period, timing of cognitive and motor development, timing of reproduction, philopatry, social organization, and levels of social tolerance – affect the sex- and age-related variation in individual attributes such as physical strength, motor skills, cognitive skills, attitudes/personality traits, relative competitive abilities, and access to tolerant models/demonstrators [16]. These age-dependent individual attributes, in turn, are expected to influence the costs and benefits, in each behavioural domain (e.g. foraging), of individually different levels of behavioural propensities relevant to learning, e.g. innovativeness and careful attention to older conspecifics' behaviour. Furthermore, even two individuals of the same age and sex may differ with respect to optimal learning strategies, because they differ in some relevant phenotypic trait (e.g. neophobia) or because of demographic happenstance (e.g. number of peers). Untangling these variables and their relationship to age is an important part of discovering how learning strategies have co-evolved with life history strategies. But we lack quality data, particularly from wild populations, demonstrating these relationships.

Although there are many species for which we have both relative brain size data and data on the timing of life history events [17][18], there are far fewer data sets for which we have nuanced data on the relationship between age/life history stage and (a) behavioural repertoires, (b) innovative propensities, (c) social learning strategies, and (d) the underlying attitudes/personality traits that influence the choice of learning strategies. In this paper, I will begin to address some of these gaps in knowledge, using longitudinal data from a wild population of white-faced capuchins studied from 1990-2019 at Lomas Barbudal Biological Reserve and surrounding public and private lands in Guanacaste, Costa Rica (for more details of the site see [19]). These data were collected in the context of a long-term study of the behavioural biology of white-faced capuchin monkeys, *Cebus capucinus* begun in 1990, though the data presented here were collected during 2001-2019. The subjects were wild animals residing in 11 habituated social groups; more specific details of the data sets for particular analyses are presented in subsequent sections of the manuscript.

These monkeys live in relatively stable, female-bonded groups of 5-40 individuals, characterized by female philopatry and male parallel dispersal, which enable most individuals to form enduring relationships with the kin of at least one sex; descriptions of their natural history, derived primarily from the two main long-term study sites (Lomas Barbudal and Santa Rosa, both in Costa Rica) are reviewed in [20]. Capuchin females give birth to single offspring every second year, nursing their infants until the next one is born. The infants experience particularly intense amounts of alloparental care during the period of 3-6 months of age, and relationships formed then tend to persist much later in life. Capuchins have evolutionarily converged with humans with regard to many traits of interest: large relative brain size and long life span (up to 55 years in captivity) [21], slow development (being completely weaned by age 2, and reaching maturation at 6 years for females and 10 for males) [22], an omnivorous diet relying heavily on extractive foraging [23], frequent alloparenting [20], frequent co-residence with grandparents of both sexes [24], and a propensity to innovate [25] and form social traditions [26].

It is difficult (though not necessarily impossible) to demonstrate exactly what behaviour was learned, and from whom, without experimental manipulation. However, naturalistic studies of wild animals in settings with high ecological validity can illuminate age-related changes in five variables: (a) cognitive and motor abilities; (b) accessibility of knowledgeable

models/demonstrators; (c) general motivational and emotional propensities that may affect learning; (d) rates of attention toward potentially knowledgeable models/demonstrators, and (e) breadth of task-related behavioural repertoires. Here, I focus on the last three of these variables. I will present new analyses of age-related changes in (a) rated personality traits that may affect or express learning styles, and (b) ethologically assessed behaviour consisting of (i) focused attention toward foraging conspecifics, and (ii) number of techniques used in a specific food-processing task. I also review published findings from my research group on age-related changes in performing a different, experimentally induced, food-processing task [27], and in innovation rates [25]. These findings will be discussed in terms of two kinds of trade-offs: (a) asocial vs. social learning [28], and (b) creative vs. tried-and-true solutions to problems (exploration vs. exploitation) [14].

2. How do personality traits/attitudes relevant to learning change with age?

Methods: At the end of their internships (typically a year in duration), each research assistant was asked to rate each monkey from social groups s/he knew well, on a list of 26 behavioural traits, using a 5-point scale. Each trait was defined in terms of two antonymous adjectives. Raters were instructed not to discuss these ratings with other observers, and no one had access to the personality questionnaire until the last month of their internship, so as to reduce temptation to discuss individuals' traits. Each rater was told to create a normal distribution of rating values within each trait (10% 1, 20% 2, 40% 3, 20% 4, 10% 5). Under the assumption that raters' evaluations were biased towards their more recent observations of each individual, the monkey age assigned to each trait-rating-monkey-rater combination was determined by subtracting the monkey's birth date from the last date that the rater spent with that monkey before filling out the personality questionnaire. The list of traits and information about interobserver reliability are found in Manson & Perry [29]. There were 84 raters in total (though two did not rate all traits), and the dates of the ratings spanned April 2002 to September 2018. 439 monkeys were rated, with each monkey being rated by an average of 18.3 observers (ranging from 1 to 66, SD=15.0). With one exception, each observer rated each monkey only once. The monkeys' ages ranged from 1 month to 39 years.

I selected for analysis only those eight traits that seemed relevant to learning: "*active vs. sluggish*" (because greater activity might lead to more trial-and-error learning); "*alert/vigilant vs. inattentive*", "*curious vs. uninterested*", and "*opportunistic vs. narrow-minded/conservative*" (as more alert, opportunistic or curious monkeys might be more prone to discovering useful features of their environments); "*attentive to conspecifics vs. more focused on own actions*" (because more socially attentive monkeys might be more prone to social learning); "*neophobic vs. neophilic*" (as neophobic individuals might be less likely to learn about aspects of their environment that repel them), and "*playful vs. serious*" and "*creative vs. unimaginative*" (as more playful or creative individuals might be more prone to behavioural innovation even in problem-solving situations in which they already have a solution, particularly regarding investigation of their environments or developing new types of social interactions).

The relationship between age and personality traits was tested using a linear mixed model including random effects for monkey, rater, and the effect of age on an individual monkey. The model was fit using the R 3.6.1 lme4 package and the following equation:

$$\text{rating}_{ijk} = b_0 + (b_1 + u_i)\text{age}_{ik} + v_i + w_j + e_{ijk}$$

where i =monkey, j =rater, and k =monkey age at time of rating, b_0 = intercept, b_1 = fixed age slope, u_i = monkey-specific age effect, v_i =monkey-specific intercept, w_j = rater-specific intercept, and e_{ijk} = error.

Results: All of the personality traits tested, with the exception of “attentiveness to conspecifics,” were significantly influenced by age (see SI Tables 1 & 2 for details of the models, both linear and quadratic versions, and Fig. 1 for the slopes. See SI Fig. 1 for quadratic versions of these models, which indicate possible plateaus or reversals in slopes of some traits during middle to late adulthood.). Estimates tend to be less reliable for older monkeys (mid-20’s and 30’s), due to smaller sample sizes. Monkeys became steadily less active as they aged. Monkeys became steadily more alert/vigilant throughout the juvenile phase and early adulthood, declining in alertness during mid-to-late adulthood. Attentiveness to conspecifics was fairly stable, possibly decreasing very slightly in older individuals. Playfulness and curiosity started out high in infancy, declined at least until middle adulthood and possibly plateaued in late adulthood. Neophobia increased throughout the period of immaturity and early adulthood, possibly stabilizing in late adulthood. Opportunism and creativity declined steadily over the lifespan.

Discussion: Younger individuals, compared to older individuals, had higher levels of traits likely to facilitate innovation (creativity, playfulness), trial and error learning more generally (curiosity, opportunism, neophilia, activity), and social learning (curiosity and possibly activity). Surprisingly, attentiveness to conspecifics did not decline with age, but this may be because it was not defined with regard to learning contexts specifically. Alertness/vigilance increased with age, at least until age 20 yrs, (see quadratic model in SI Fig. 1), but it is not clear to what extent raters interpreted this as vigilance towards danger, as distinct from social learning opportunities.

Although we cannot deduce from personality rating data what the animals actually did learn, most of the results are consistent with the idea that younger individuals are more motivated to engage in activities that will result in more learning (both asocial and social), and that they may be more prone to playful, experimental, creative types of problem-solving rather than “low temperature” searches for solutions. Knowledge of the age-related changes in these traits should guide experimental approaches to investigating age-dependent shifts in problem-solving approaches in this species.

3. How do capuchins change with age regarding their motivation to seek information about foraging from conspecifics?

In order to assay changes in motivation to seek information from conspecifics, I investigated the rates of “peering”, i.e. close-range, often intrusive, observation of another individual’s activities. SI Figure 2 shows three juvenile capuchins peering at an adult male who is foraging on insects, while a fourth juvenile watches from a greater distance.

Methods: In order to determine the impact of age on the rates at which monkeys peer at other foraging monkeys, I used a data set comprised of 21,599 hours of focal animal data on 359 monkeys, ranging in age from birth to 39 years of age. Each monkey was observed during an average of 4.9 yrs (range: 1-18), yielding 1766 monkey-years, which comprised the data points. The predictor variable was year of age, the outcome variable was counts of peering, and the exposure was the amount of time that each focal animal was observed during each year of

life. Focal monkey identity was a random effect in the model. Because these were count data, with too high a ratio of variance to mean to use a Poisson model, I ran a negative binomial mixed effects GLM model with monkey identity as a random effect. Linear and cubic models yielded virtually identical results, so here I report the results of a linear model. The analysis was run in Stata 13.1.

Results: During the first year of life, peering rates were around 0.92 times per hour, rapidly declining through the early infant and juvenile phase to plateau at <0.05 times/hr in early adulthood (between 10-16 years of age). Age was a significant predictor of peering rate (coeff -0.250, SE 0.008, $P < 0.001$, 95% CI -0.266 to -0.235). Fig. 2 shows the model predictions. This finding suggests motivation to closely observe conspecifics' behaviour declines with age. This observation contrasts with the finding that attentiveness to conspecifics, as a rated personality trait, was relatively stable across the lifespan. Importantly, the peering data were restricted to foraging contexts, whereas rated attentiveness applied to all contexts. Age-related declines in peering rates have been observed in orangutans [30] and callitrichids [31][32] as well; in both of these taxa it is believed that peering is a mechanism for learning about foraging, and that peering rates decline with increased foraging competence.

4. What is the role of age in individuals' choices about whose foraging to observe?

Methods: During Jan 2002-June 2012 and Jan-Aug 2019, we recorded each instance in which another monkey (the "forager") approached the focal animal to within 5 body lengths (~200 cm) and began foraging; we also recorded whether the focal animal paid visual attention to that forager (i.e. watched it) or ignored it. This protocol enabled us to document monkeys' preferences for observing foragers of varying ages as they themselves age, while correcting for opportunity. These data were analysed in Stata 13.1 using a mixed effects logistic regression model (see SI for data and code) in which the focal monkey's age and the forager's age were the predictors of whether the focal monkey watched the forager, and the identities of the focal monkey and the forager were random effects. The sample size included 72749 observations, i.e. opportunities for a focal monkey to watch another monkey foraging within 5 body lengths; 25794 of these resulted in the focal monkey watching the forager. The sample sizes are small for older monkeys, sometimes dropping below 100 observations per year in years above age 20, so the model was run a second time excluding years above age 20 that might be vulnerable to outliers; results were qualitatively similar (SI Table 3).

Results: With the exception of the first year of life, the average age of foragers whom the focal watched was substantially older than the average age of foragers that the focal monkey ignored, for all ages for which there were adequate sample sizes of observation opportunities (i.e. <21 years) (see SI Fig. 3). Both the ages of the focal and the forager had significant effects ($P < 0.001$) on the odds of the focal monkey watching the foraging monkey (Fig. 3; see SI Table 3 for model details). The younger the focal was, the more likely s/he was to look at the forager, with a 3.4% decrease in the odds of looking at the foraging monkey for each increase of one year in the focal animal's age. The older the forager was, the more likely the focal was to look at the forager, with a 9.1% increase in the odds of being watched by the focal animal for each increase of one year in the forager's age. These results are consistent with predictions that more naïve monkeys will seek information about what to eat and/or how to eat it by watching older, more experienced individuals.

5. Age-related changes in innovation rates.

It has been hypothesized [33] that innovative tendencies have coevolved with life history characteristics as part of an evolved adaptive package designed to cope with environmental change, and that innovation is expected to be most common in large-brained, generalist species that prioritize future reproduction over current reproduction. Given this comparative framework, it is no surprise that the omnivorous capuchins, with their large brains and slow development, are prone to frequent innovation.

Researchers of the Lomas Barbudal capuchin population have been coding all observations of novel behaviours since 2002, with the aim of documenting innovation rates. Analysis of a subset of these data (10 years, 10 social groups, 234 individuals) was conducted, and described in [25]. In this paper, a behaviour was scored as an innovation if (a) it was absent in some social groups studied, i.e. not a behaviour that necessarily emerges in any social group, (b) the behaviour was seen for the first time in that social group during the 35196 hours of data collected during 2007-2011, and (c) the behaviour had also not been seen during the 37514 hours of observations collected in 2002-2006, during the lifetime of the putative innovator, in any social group where the putative innovator was residing. See [25] for details of the data analysis. Whereas older individuals were more prone to invent new forms of social interaction, younger individuals were more prone to invent new foraging, investigative, and self-directed behaviours. This age effect was particularly strong for the investigative category, which included creative object play, innovative ways of locomoting, and creative ways of manipulating other species (e.g. grooming porcupines or flipping over turtles). Most of these investigative innovations seemed playful, exuberant, and rather pointless, in that they did not appear to solve any immediate fitness-relevant problem; however, they probably provided these young monkeys with useful information about the affordances of the manipulated objects and creatures. Fewer than 15% of observed investigative innovations were retained in the innovator's repertoire.

6. Age-related changes in behavioural repertoires:

Methods: To examine the relationship between age and diversity of problem-solving techniques, I re-analysed a portion of a data set originally collected to examine the influence of social learning on the development of food processing techniques for extracting seeds from *Luehea candida* fruits [34]. Given behavioural repertoires that include some rarely observed behaviours, and unequal sampling times that are inadequate to capture every rare behaviour, even two individuals with equivalent actual repertoire sizes will seem to have different repertoire sizes if one is sampled at a higher density than the other. To circumvent this problem, I used a subset of the original data set, in which I selected only the first 10 instances of *Luehea* processing in each year of age, for each monkey-year (i.e. a year of life for a particular monkey), so that each monkey was sampled an equivalent amount of time during each year. Monkey-years with <10 observations were dropped from the sample. The data set presented here includes data collected from "Abby's group" and its fission product "Flakes group" between 2001-2007, and includes data from 37 individuals, each of whom contributed 1-6 years of data, for a total sample of 68 monkey-years.

The ten events of *Luehea* processing within each monkey-year were coded for the presence or absence of (a) 16 types of action applied by a hand or foot to the fruit, (b) 4 types

of extraneous movements by body parts not contacting the fruit, (c) which of the monkey's limbs contacted the fruit during processing, (d) the position of the fruit, (e) the manner in which seeds were delivered to the mouth, and (f) the substrate used to process the fruit. The data set was coded in two ways: a more conservative estimate of behavioural elements that included just the 20 action types, and a more liberal coding that also included the remaining factors (which were possibly affected relatively more by physical constraints, and less by individuals' behavioural choices). The data were also coded regarding the efficacy of the technique. See the SI for further details of the coding, which are presented in the same file with the raw data. Poisson models with cluster-robust standard errors were used to model the relationship between age and number of techniques in the *Luehea*-processing repertoire.

Results: Figure 4 shows a plot of the raw data, for more liberal scorings of number of elements in the behavioural repertoire for capuchins processing *Luehea* fruits; the plot for the more conservative coding is in the SI (Figure 5). Younger animals, in general, have more elements in their behavioural repertoires. SI Table 4 shows the results of the statistical models: in both the liberal and the conservative coding methods, there was a significant age-related decline in number of techniques used. The primary "sensible" techniques, i.e. pounding, scrubbing, or performing a combination "pound-scrub" – all of which yield large numbers of seeds to eat -- are techniques that most, if not all, capuchins discover at some point in their development, though typically a monkey will comfortably settle into the usage of just one these for almost all of its *Luehea* processing once it reaches adulthood [34]. Exploration of other techniques is more common in younger monkeys, though not completely absent in adults. In the supplementary information (SI Figs. 6&7), the diversity of techniques is broken down by "sensible" techniques (those yielding high foraging returns) vs. "silly" techniques (i.e. actions that yield few or no seeds to eat, but may provide the young forager with information about the affordances of the *Luehea* fruit or the payoffs of particular actions); both the numbers of sensible and silly techniques decline significantly with age (see SI Table 4 for model details).

7. Age-related changes in learning strategies

The best field data from wild capuchins indicating age-related changes in learning strategy come from a field experiment at Lomas Barbudal [27] in which *Sterculia apetala* fruits, the most difficult to process item in their diet, were experimentally presented to members of the one group of capuchins that does not have these trees in its home range. This group (N=25 members) included five adults who had grown up in groups that did have *Sterculia* fruits in their ranges, and hence had prior experience, but the other 20 group members had no prior exposure. By controlling access to the fruits, and recording each food processing attempt, it was possible to document the entire learning history of each individual in the experimental group. The data were then analysed using experience-weighted attraction models [27] [35], permitting quantification of the individual evidence for trial-and-error learning and various types of social learning strategies within the same modelling framework. In this experiment, younger individuals were more likely to seek social information (by closely observing older foragers interact with the *Sterculia* fruits). Younger individuals, relative to older individuals, were less canalized in their approach, i.e. more willing to incorporate recent information into their behavioural strategy, suggesting that younger individuals might be more exploratory.

Younger individuals were also more likely to incorporate social information into their future processing attempts. All capuchins were more likely to copy older demonstrators.

8. Conclusions and future directions

The picture that emerges from this set of results is that the capuchin infancy and juvenile period (relative to adulthood) is characterized by higher levels of curiosity, a greater propensity to investigate new objects and invent new behaviours, and a greater tendency to seek social information. Furthermore, younger capuchins more readily incorporate recent experience (both asocial and social) into their problem-solving efforts when engaged in processing *Sterculia* fruits. This combined set of results enhances the plausibility that observed changes in attitudes and behaviours across the life span are part of an adaptive strategy in which younger individuals are more curious, exploratory and flexible in their problem-solving strategies, whereas older individuals, having developed a strategy set that works for them, rarely deviate from these routines. Presumably as a result of these processes, juveniles' behavioural repertoires (at least with regard to the extractive foraging tasks investigated) are more diverse than adults' repertoires. This finding is relevant to another important process, cultural evolution. To understand the role of life history in the population dynamics of innovation and cultural transmission, researchers need a better understanding of the age structure of behavioural practices (i.e. who is innovating, demonstrating, and copying what behaviours).

The demonstrated parallels between capuchin and human cognitive development are unsurprising, given that the two taxa have converged with respect to several relevant life history and ecological variables (encephalization, age at first reproduction, life expectancy, diet breadth, range of foraging techniques, and frequent alloparenting). The comparative method will generate more insights into the relationships between life history and learning when studies similar to this one are carried out on a wider range of taxa, encompassing a greater range of variation in these variables. Extending the approach demonstrated here to species that are less similar to humans will facilitate the examination of both convergent and divergent evolutionary processes. Data sets relevant to such endeavours are beginning to appear (particularly for birds (see for example [33]), but more are needed, particularly in non-avian taxa.

The findings that younger capuchins are less neophobic and more prone to innovation (particularly of the investigative type) are consistent with the predictions of a model developed by Sherratt and Morand-Ferron [13], in which older individuals are less likely to investigate unfamiliar objects. The authors propose that this age-related shift may be an adaptive response because (a) older individuals are more likely to perceive novel objects as being sufficiently rare that the information value gained from investigating them is low, or (b) they have less remaining lifetime to take advantage of any knowledge gained. This same logic might be extended to explain why it is not worthwhile for older individuals to gather social information about new food processing techniques, if they already have a method that yields profitable results. Models such as this one [13] highlight the importance of considering the structure of environmental variability and the quality of cues available to individuals in assessing relevant aspects of their environment, when studying the relationship between learning and life history. Future work in this area should attempt to measure environmental variability and also age- and sex-related variation in the types of asocial and social information available to individuals, e.g.

as a consequence of their different positions in social networks during different life history stages. Such variation is likely to impact not only cultural evolution dynamics, but probably also fitness outcomes that impact the evolution of life history variables and learning processes.

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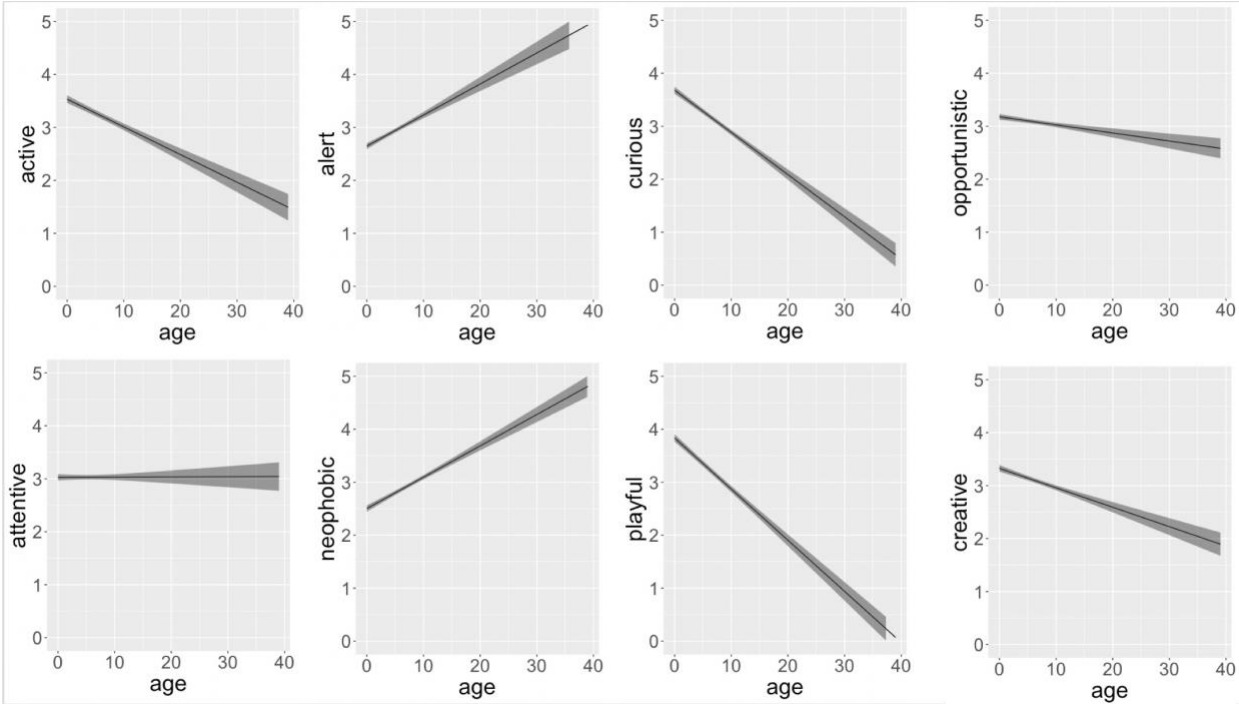
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Ethics: The study was strictly observational, all protocols were approved by UCLA's Animal Care Committee (protocol 2016-022). All necessary permits were obtained from SINAC and MINAE (the Costa Rican government bodies responsible for research on wildlife) and renewed every 6 months over the course of the study; the most recent scientific passport number being #027-2019-ACAT and the most recent permit being Resolución # M-P-SINAC-PNI-ACAT- 020-2019. This research is in compliance with the Animal Behavior Society's Guidelines for the Use of Animals in Research.

Figures:

Fig. 1. Adjusted predictions of means of personality ratings (scale 1 to 5) for each year of life, with 95% confidence intervals. (Linear model: see text and SI for further model details and quadratic versions.)



403 Fig. 2: Adjusted predictions of mean hourly rate of peering at nearby foragers, by focal
404 monkey's year of life, with 95% confidence intervals

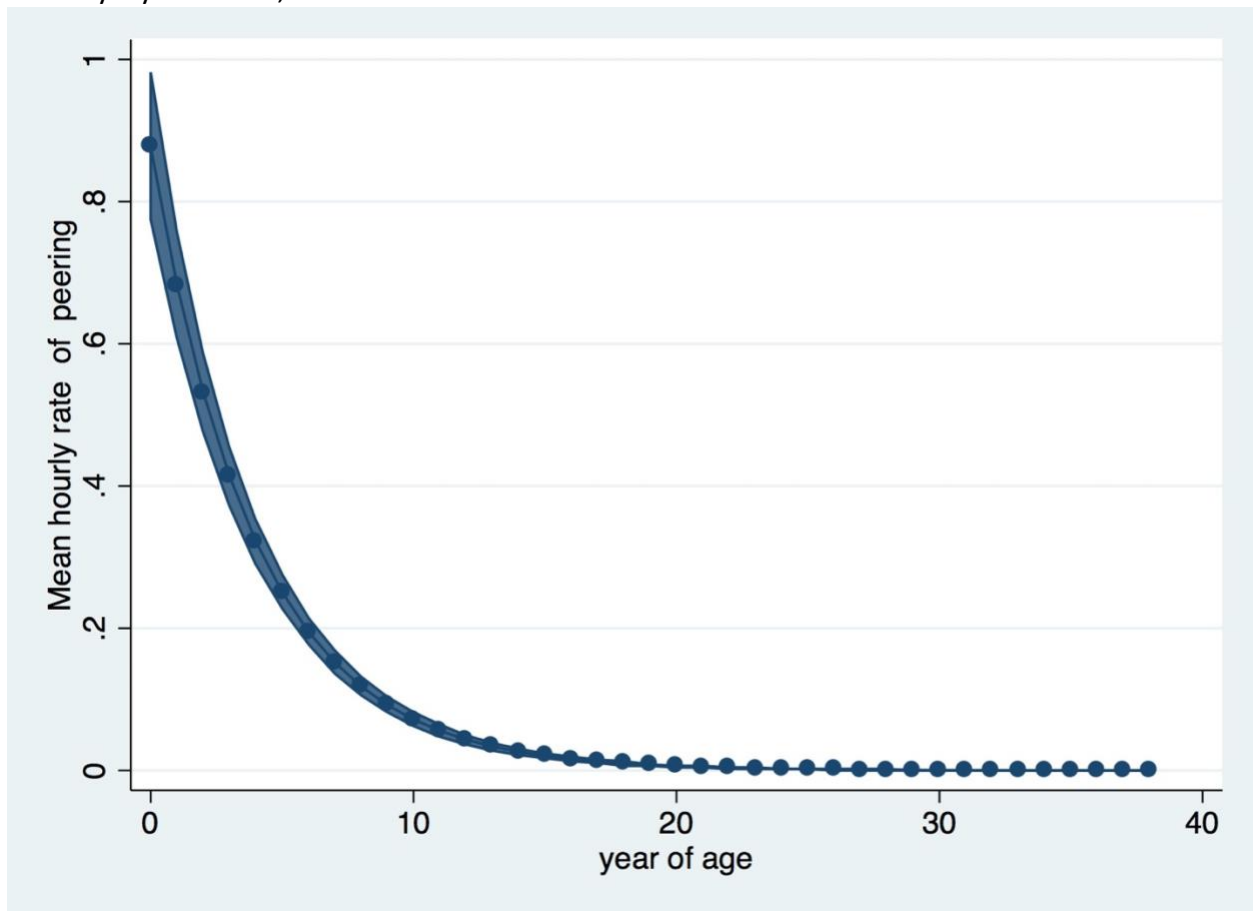
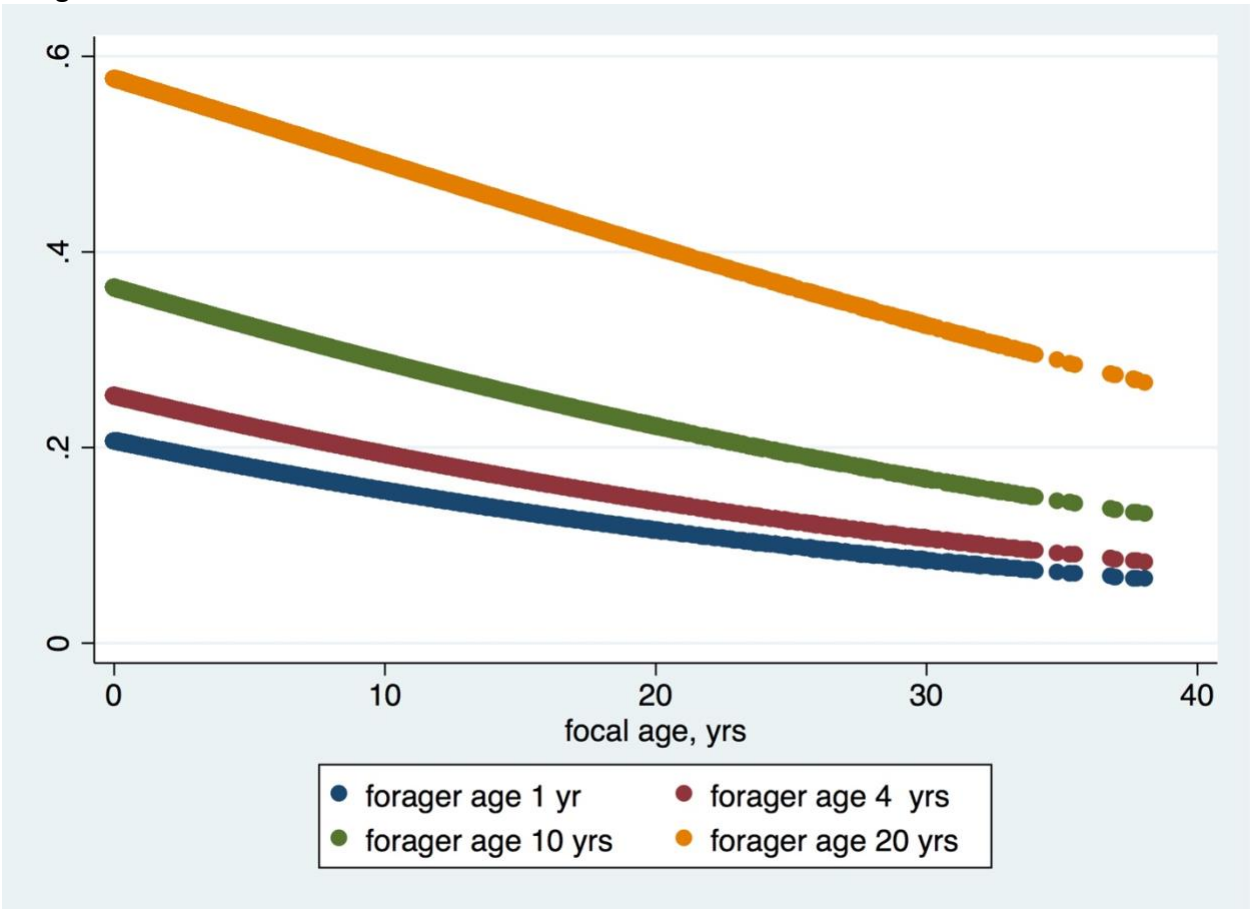


Fig. 3: Model predictions regarding impact of focal age and forager age on the odds of the focal watching the forager. See SI for alternative version of this graph, from the perspective of the forager.



References:

1. Baldwin JM. 1896 A new factor in evolution. *American Naturalist* **30**, 441–451. (doi:10.1086/276408)
2. Wyles JS, Kunkel JG, Wilson AC. 1983 Birds, behavior, and anatomical evolution. *Proceedings of the National Academy of Sciences* **80**, 4394–4397. (doi:10.1073/pnas.80.14.4394)
3. West-Eberhard MJ. 2003 *Developmental plasticity and evolution*. Oxford, UK: Oxford University Press.
4. Laland KN. 2017 *Darwin's Unfinished Symphony: How Culture Made the Human Mind*. Princeton University Press.
5. Kaplan H, Hill K, Lancaster J, Hurtado AM. 2000 A theory of human life history evolution: diet, intelligence, and longevity. *Evolutionary Anthropology* **9**, 156–185. (doi:doi:10.1002/1520-6505(2000)9:4<156::AID-EVAN5>3.0.CO;2-7)
6. Schuppli C, Graber SM, Isler K, van Schaik CP. 2016 Life history, cognition and the evolution of complex foraging niches. *Journal of Human Evolution* **92**, 91–100. (doi:10.1016/j.jhevol.2015.11.007)
7. Fawcett TW, Frankenhuys WE. 2015 Adaptive explanations for sensitive windows in development. *Front Zool* **12**, S3. (doi:10.1186/1742-9994-12-S1-S3)
8. Ross C, Jones KE. 1999 Socioecology and the evolution of primate reproductive rates. In *Comparative Primate Socioecology* (ed PC Lee), pp. 73–110. Cambridge: Cambridge University Press.
9. Eadie E. 2015 Ontogeny of foraging competence in capuchin monkeys (*Cebus capucinus*) for easy versus difficult to acquire fruits: A test of the needing to learn hypothesis. *PLoS One* **10**, e0138001.
10. Blurton Jones N, Marlowe FW. 2002 Selection for delayed maturity: Does it tak 20 years to learn to hunt and gather? *Human Nature* **13**, 199–238. (doi:10.1007/s12110-002-1008-3)
11. Johnson S, Bock J. 2004 Trade-offs in skill acquisition and time allocation among juvenile chacma baboons. *Human Nature* **15**, 45–62. (doi:10.1007/s12110-004-1003-y)
12. Schuppli C, Isler K, van Schaik CP. 2012 How to explain the unusually late age at skill competence among humans. *Journal of Human Evolution* **63**, 843–850. (doi:10.1016/j.jhevol.2012.08.009)
13. Sherratt T, Morand-Ferron J. 2018 The adaptive significance of age-dependent changes in the tendency of individuals to explore. *Animal Behaviour* **138**, 59–67. (doi:https://doi.org/10.1016/j.anbehav.2018.01.025)

- 448 14. Gopnik A, Griffiths TL, Lucas CG. 2015 When younger learners can be better (or at least
449 more open-minded) than older ones. *Current Directions in Psychological Science* **24**, 87–92.
450 (doi:10.1177/0963721414556653)
- 451 15. Gopnik A, O’Grady S, Lucas CG, Griffiths TL, Wente A, Bridgers S, Aboody R, Fung H,
452 Dahl RE. 2017 Changes in cognitive flexibility and hypothesis search across human life
453 history from childhood to adolescence to adulthood. *Proceedings of the National Academy*
454 **114**, 7892–7899. (doi:10.1073/pnas.1700811114)
- 455 16. Russon AE. 2003 Developmental perspectives on great ape traditions. In *The Biology of*
456 *Traditions: Models and Evidence* (eds D Frigaszy, S Perry), pp. 329–64. Cambridge:
457 Cambridge University Press.
- 458 17. Isler K, van Schaik CP. 2012 Allomaternal care, life history and brain size evolution in
459 mammals. *Journal of Human Evolution* **63**, 52–63. (doi:10.1016/j.jhevol.2012.03.009)
- 460 18. Shultz S, Dunbar RIM. 2010 Social bonds in birds are associated with brain size and
461 contingent on the correlated evolution of life-history and increased parental investment:
462 AVIAN BRAIN EVOLUTION. *Biological Journal of the Linnean Society* **100**, 111–123.
463 (doi:10.1111/j.1095-8312.2010.01427.x)
- 464 19. Perry S, Godoy I, Lammers W. 2012 The Lomas Barbudal Monkey Project: Two decades of
465 research on *Cebus capucinus*. In *Long-term Field Studies of Primates* (eds P Kappeler, D
466 Watts), pp. 141–165. New York: Springer.
- 467 20. Perry S. 2012 The behavior of wild white-faced capuchins: Demography, life history, social
468 relationships, and communication. In *Advances in the Study of Behavior*, pp. 135–181.
469 Elsevier. (doi:10.1016/B978-0-12-394288-3.00004-6)
- 470 21. Hakeem A, Sandoval RG, Jones M, Allman J. 1996 Brain and life span in primates. In
471 *Handbook of the Psychology of Aging* (eds JE Birren, KW Schaie), pp. 78–104. San Diego:
472 Academic Press.
- 473 22. Fragaszy DM, Visalberghi E, Fedigan LM. 2004 *The Complete Capuchin: The Biology of the*
474 *Genus Cebus*. Cambridge: Cambridge University Press.
- 475 23. Perry S, Ordoñez Jiménez JC. 2006 The effects of food size, rarity, and processing
476 complexity on white-faced capuchins’ visual attention to foraging conspecifics. In (eds G
477 Hohmann, M Robbins, C Boesch), pp. 203–234. Cambridge: Cambridge University Press.
- 478 24. Godoy I, Vigilant L, Perry SE. 2016 Cues to kinship and close relatedness during infancy in
479 white-faced capuchin monkeys, *Cebus capucinus*. *Animal Behaviour* **116**, 139–151.
480 (doi:10.1016/j.anbehav.2016.03.031)
- 481 25. Perry SE, Barrett BJ, Godoy I. 2017 Older, sociable capuchins (*Cebus capucinus*) invent
482 more social behaviors, but younger monkeys innovate more in other contexts. *Proceedings of*
483 *the National Academy of Science USA* **114**, 7806–7813. (doi:10.1073/pnas.1620739114)

26. Perry S. 2011 Social traditions and social learning in capuchin monkeys (*Cebus*). *Phil. Trans. R. Soc. B* **366**, 988–996. (doi:10.1098/rstb.2010.0317)
27. Barrett BJ, McElreath R, Perry SE. 2017 Payoff-biased social learning underlies the diffusion of novel extractive foraging traditions in a wild primate. *Proceedings of the Royal Academy B* **284**. (doi:10.1098/rspb.2017.0358)
28. Rendell L *et al.* 2010 Why Copy Others? Insights from the Social Learning Strategies Tournament. *Science* **328**, 208–213. (doi:10.1126/science.1184719)
29. Manson JH, Perry S. 2013 Personality structure, sex differences, and temporal change and stability in wild white-faced capuchins, *Cebus capucinus*. *Journal of Comparative Psychology* **127**, 299–311. (doi:10.1037/a0031316)
30. Schuppli C, Meulman EJM, Forss SIF, Aprilinayati F, van Noordwijk MA, van Schaik CP. 2016 Observational social learning and socially induced practice of routine skills in immature wild orang-utans. *Animal Behaviour* **119**, 87–98. (doi:10.1016/j.anbehav.2016.06.014)
31. Schiel N, Huber L. 2006 Social influences on the development of foraging behavior in free-living common marmosets (*Callithrix jacchus*). *Am. J. Primatol.* **68**, 1150–1160. (doi:10.1002/ajp.20284)
32. Dell’Mour V, Range F, Huber L. 2009 Social learning and mother’s behavior in manipulative tasks in infant marmosets. *Am. J. Primatol.* **71**, 503–509. (doi:10.1002/ajp.20682)
33. Sol D, Sayol F, Ducatez S, Lefebvre L. 2016 The life-history basis of behavioural innovations. *Philosophical Transactions of the Royal Society B* **371**. (doi:10.1098/rstb.2015.0187)
34. Perry S. 2009 Conformism in the food processing techniques of white-faced capuchin monkeys (*Cebus capucinus*). *Animal Cognition* **12**, 705–717. (doi:10.1007/s10071-009-0230-3)
35. Camerer C, Hua Ho T. 1999 Experience-weighted Attraction Learning in Normal Form Games. *Econometrica* **67**, 827–874. (doi:10.1111/1468-0262.00054)

**Supplementary materials for “Behavioural variation and learning across the lifespan in wild white-faced capuchin monkeys.”
(Susan Perry)**

Materials are arranged according to the section of the article where they are mentioned in the main text.

Section 2: How do personality traits/attitudes relevant to learning change with age?

Table S1: Model predictions (estimate of fixed effects, with standard errors) for linear mixed effects models in which age predicts values of personality ratings. *** PrChi <0.001. df=1 in all models.

	creative	active	alert	attentive	curious	opportunistic	neophobic	playful
fixed effects (estimate, SE)								
intercept	3.326 ± 0.032	3.533 ± 0.037	2.646 ± 0.029	3.028 ± 0.030	3.681 ± 0.035	3.178 ± 0.030	2.502 ± 0.031	3.836 ± 0.036
age	-0.037 ± 0.003	-0.052 ± 0.004	0.059 ± 0.004	0.0004 ± 0.0041	-0.080 ± 0.003	-0.015 ± 0.003	0.059 ± 0.003	-0.097 ± 0.004
LRT and significance level, fixed effect age	95 ***	107 ***	167 ***	0.0067 P= 0.9	306 ***	24 ***	249 ***	312 ***
Random Effects: SD [correlation]								
Monkey (intercept)	0.439	0.507	0.274	0.368	0.517	0.312	0.423	0.533
monkey-age slope	0.036 [corr. -0.74]	0.040 [corr. -0.64]	0.052 [corr. -0.83]	0.044 [corr.-0.61]	0.042 [corr.-0.82]	0.021 [corr. -0.41]	0.033 [corr. -0.81]	0.041 [corr.-0.69]
rater intercept	6.48E-05	0.128	0.104	3.90E-05	0.072	0.00013	0.0007375	0.104
# ratings	7928	7996	7996	7918	7995	7920	7843	7996
# monkeys	439	439	439	439	439	439	439	439
# raters	83	84	84	83	84	83	82	84

Table S2: Model predictions (estimate of fixed effects, with standard errors) for 8 quadratic mixed effects models in which age predicts values of personality ratings. ** PrChi<0.01, *** PrChi <0.001. df=1 in all models.

	creative	active	alert	attentive	curious	opportunistic	neophobic	playful
fixed effects (estimate, SE)								
intercept	3.357 ± 0.038	3.474 ± 0.043	2.450 ± 0.032	2.976 ± 0.036	3.829 ± 0.039	3.184 ± 0.034	2.358 ± 0.035	3.977 ± 0.039
age	0.046 ± 0.007	-0.035 ± 0.007	0.122 ± 0.007	0.017 ± 0.008	-0.123 ± 0.006	-0.017 ± 0.007	0.100 ± 0.006	-0.140 ± 0.006
l(age^2)	0.0005 ± 0.0003	-0.0009 ± 0.0003	-0.0036 ± 0.0003	-0.0009 ± 0.0003	0.0022 ± 0.0003	0.0001 ± 0.0003	-0.0020 ± 0.0002	0.0022 ± 0.0002
LRT and significance level, fixed effect age	38 ***	20 ***	286 ***	5, P=0.026	266 ***	7 **	218 ***	307 ***
LRT and significance level, fixed effect l(age^2)	2 P= 0.14	7 **	128 ***	7 P=0.01	54 ***	0.12 P= 0.7	59 ***	51 ***
Random Effects: SD [correlation]								
Monkey (intercept)	0.435	0.513	0.196	0.368	0.474	0.312	0.384	0.494
monkey-age slope	0.035 [-0.74]	0.043 [-0.65]	0.040 [-0.69]	0.044 [-0.61]	0.032 [-0.82]	0.021 [-0.41]	0.022 [-0.82]	0.026 [-0.72]
rater intercept	0.00000	0.126	0.093	0.00000	0.079	0.00013	0.000046	0.111
# ratings	7928	7996	7996	7918	7995	7920	7843	7996
# monkeys	439	439	439	439	439	439	439	439
# raters	83	84	84	83	84	83	82	84

The raw data sets for these analyses are found in separate tabs of the file called “2_PersonalityRawData.xlsx”.

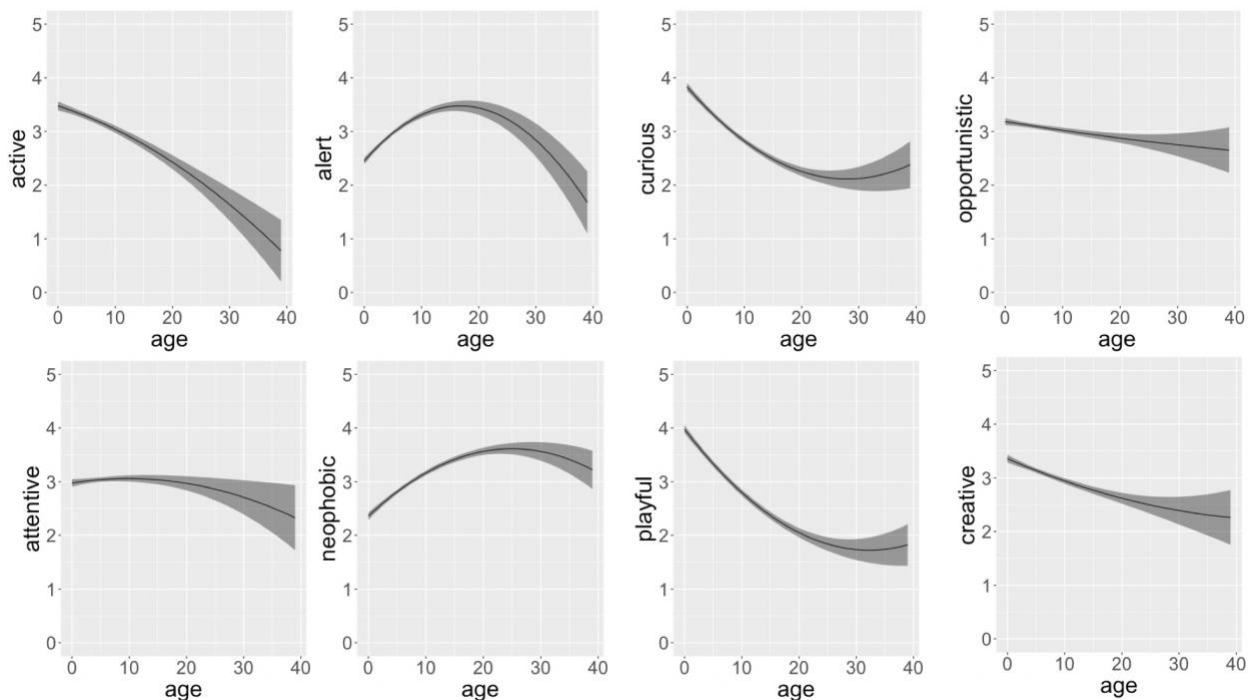
The R code used to run these models and create these graphics are found in the file called “2_Personality_Rcode.R”

Additional methodological notes about the models in section 2:

Several convergence warnings were generated when running these models in R version 3.6.1, using the lme4 package. Following the advice on <https://rdrr.io/cran/lme4/man/convergence.html>, the models were rerun using “allFit” with all available optimizers. Because all 5 optimizers (except, sometimes, nlminbwrap) converged to approximately equivalent values, the warnings were assumed to be false positives.

The three models with warnings about being singular had very low variance for the random effect “respondent” in the model version we used (attentive: $4e-5$, creative: $6.5e-5$, and neophobic: $7.3e-4$). Comparison of the full model with a model eliminating respondent as a random effect revealed virtually identical results.

Figure S1: Age-related changes in personality traits for quadratic mixed effect models including monkey identity, respondent identity, and monkey-age slope as random effects. X-axis is age in years, from 0 to 39 years of age. Y-axis is rating of that personality trait, from 0 to 5. Values are predicted estimates based on the quadratic model, and shaded areas represent 95% confidence intervals.



Section 3: How do capuchins change with age regarding their motivation to seek information about foraging from conspecifics?

Figure S2: Three juvenile capuchins peer at an adult male who is foraging on rare insects, while a fourth juvenile watches from a greater distance. They are emitting “scary food peep” vocalizations - a call normally produced when handling (or watching someone else handle) potential prey that can be hazardous in some way (e.g. wasps having particularly dangerous stings, maggots gleaned from others’ wounds or found in faeces, or dead prey).



The raw data, along with the code used to create the model described in the main text, are found in separate tabs of the file called “3_PeeringData_code.xlsx”

Section 4: What is the role of age in individuals' choices about whose foraging to observe?

Figure S3: Y axis shows age of the forager, X-axis shows age of the focal. Blue line (diamonds) shows mean age of foragers whom the focal ignored; red line (squares) shows mean age of foragers the focal watched. This is a plot of raw data, not model predictions.

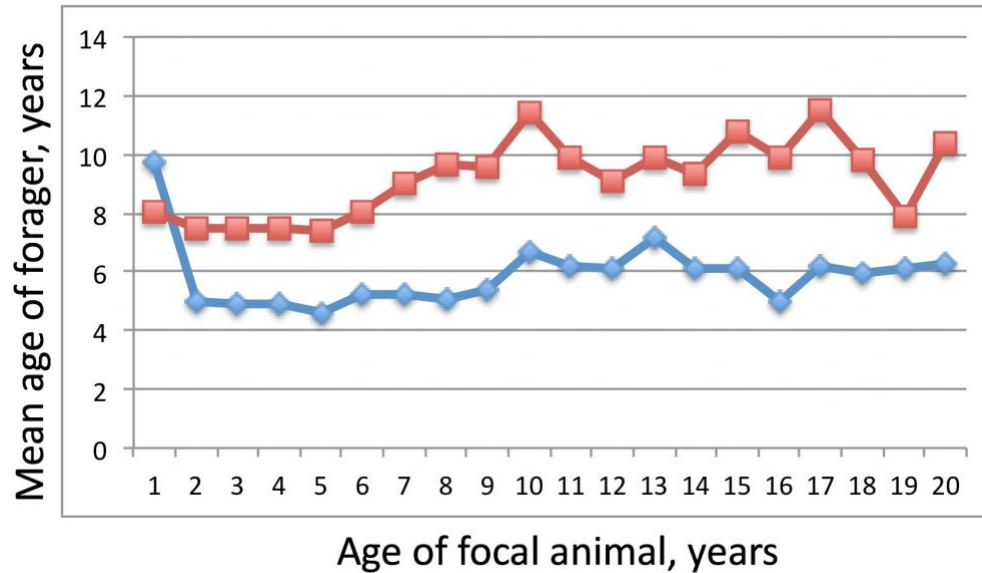
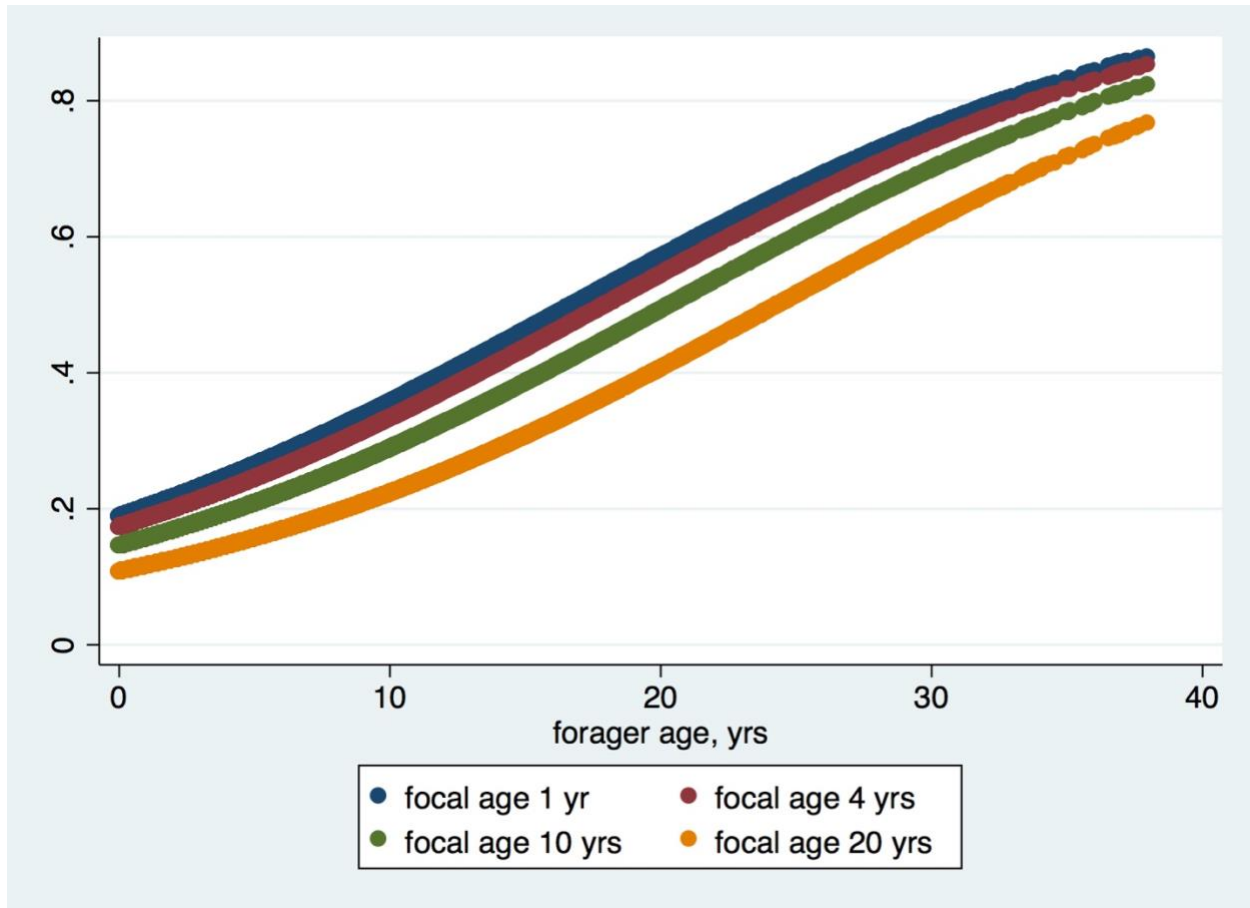


Table S3: Mixed-effects logistic regression model output demonstrating effects of focal monkey's age and foraging monkeys' age on probability that the focal animal will watch the forager's actions.*

	Odds ratio	SE	P	95% CI
Fixed effects:				
Focal age	0.966	0.004	<0.001	0.958 to .974
Forager age	1.091	0.005	<0.001	1.082 to 1.101
constant	0.238	0.016	<0.001	0.208 to 0.272
Random effects:				
Focal identity	0.158	0.027		0.112 to 0.222
Forager identity	0.371	0.041		0.298 to 0.461

*A model run exclusively on focal monkeys under age 21 (sample size of 71144 observations) yielded similar results (Odds ratio of 0.963 for focal age, and 1.094 for forager age, both $P < 0.001$), so the results seem not to have been biased by low sampling in the older age ranges.

Figure S4: Model predictions regarding impact of forager age on the odds of the forager being watched by the focal animal, for 4 different focal animal ages corresponding to infancy (age 1), juvenile (age 3), young adult (age 10), and middle-aged adult (age 20).



The raw data, along with the code used to create the model described in the main text and presented in SI Table 2 and SI Figure 4, are found in separate tabs of the file called "4_Dataset_Code_focal-forager_ages_watching.xlsx".

Section 6: Age-related changes in behavioural repertoires:

The raw data, along with the coding scheme and the code used to create the model described in the main text and described in SI Table 3, are found in separate tabs of the file called “6_Luehea_diversity_dataset_coding.xlsx”

Table S4: Model predictions for 4 Poisson models with cluster-robust standard error, in which age predicts # of techniques used to process *Luehea* fruits, using a different coding scheme for behavioral diversity. N=68 observations, SE adjusted for 37 clusters (in monkey).

Model		Coef.	SE	P> z	95% CI
Model 1: liberal coding					
	age	-0.090	0.020	<0.001	-0.130 to -0.051
	constant	1.397	0.131	<0.001	1.140 to 1.654
Model 2: conservative coding					
	age	-0.068	0.017	<0.001	-0.102 to -0.034
	constant	1.038	0.115	<0.001	0.812 to 1.264
Model 3: sensible techniques					
	age	-0.035	0.009	<0.001	-0.053 to -0.016
	constant	0.684	0.091	<0.001	0.506 to 0.862
Model 4: silly techniques					
	age	-0.408	0.161	0.01	-0.723 to -0.094
	constant	1.018	0.504	0.04	0.030 to 2.006

Figure S5: Age-related changes in diversity of techniques used to process *Luehea* fruits. This is a raw data plot using the more conservative coding scheme.

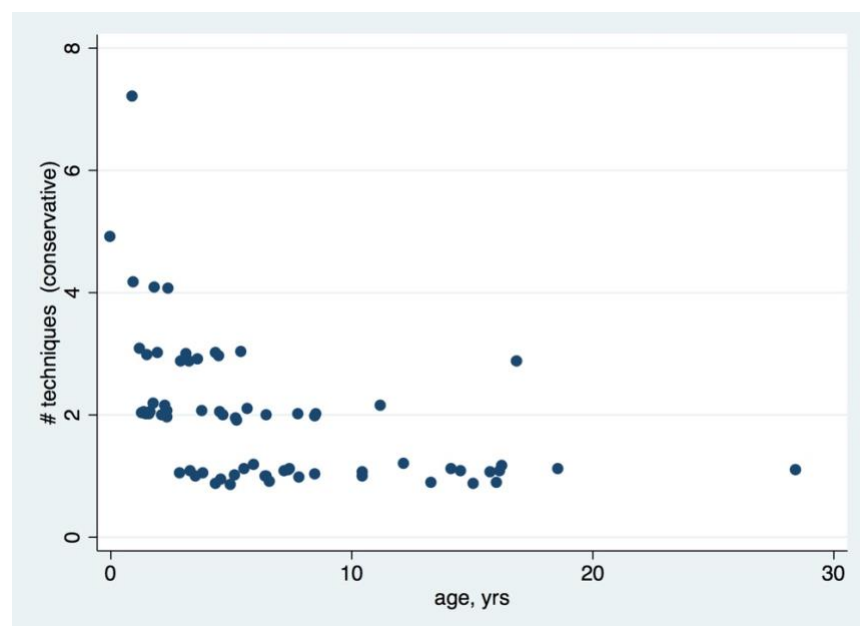


Figure S6: Age-related changes in diversity of techniques used to process *Luehea* fruits. This is a raw data plot of those behaviours coded as “sensible” (i.e. producing a high yield of seeds).

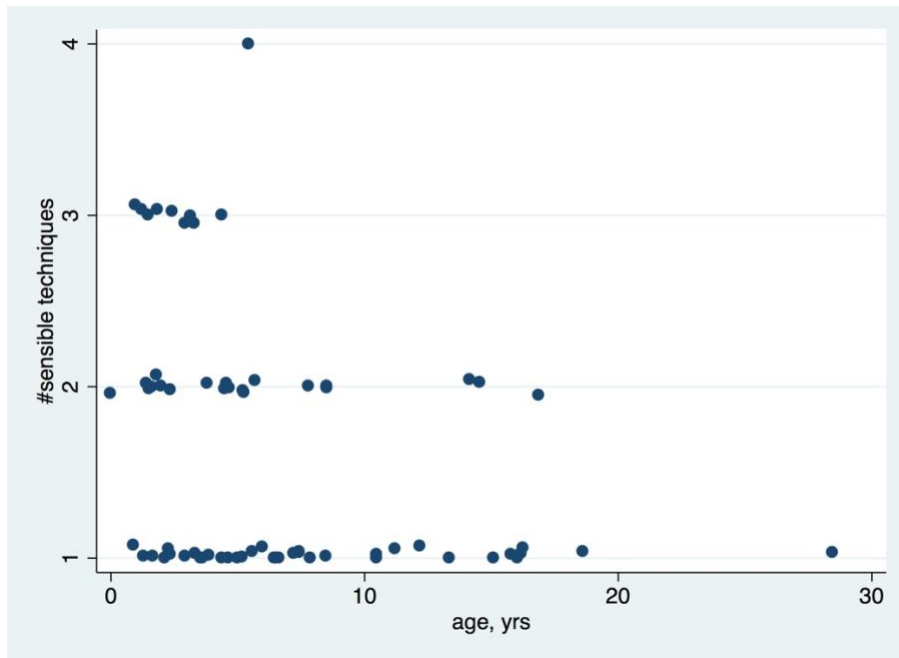


Figure S7: Age-related changes in diversity of techniques used to process *Luehea* fruits. This is a raw data plot of those behaviours coded as “silly” (i.e. producing a low yield of seeds and often involving extraneous movements).

