

## pigment loss, photoreceptor degeneration and eventual blindness.

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# Behavioral Development: Timing Is Everything

A new study has found that bonobos take longer to reach adult levels of two behaviors than do chimpanzees, providing empirical support for the ‘paedomorphism’ hypothesis among our closest relatives.

Sarah F. Brosnan

One challenge in evolutionary biology is explaining how relatively large changes between species can arise in a relatively short period of time. A potential mechanism for this change is heterochrony, in which development speeds up, slows down, or is truncated in one species relative to another [1]. The resulting effects on morphology and behavior can be dramatic. A well-known example of heterochrony exists among a group of foxes in Russia that have been part of a decades-long study of domestication [2]. Juvenilization is a hallmark of domesticated species [3,4], and geneticist Dmitry Belayev hypothesized that selection for a single behavior, tameness, could cause the plethora of changes seen during the process of domestication due to effects on developmental processes. Belayev chose a single criterion — willingness to interact with humans — to determine which foxes bred each generation. Within a few

generations, the foxes were not only domesticated, but had developed adult characteristics typical of juveniles, such as the piebald coats and large, floppy ears.

Heterochrony also exists outside of domestication. It has been proposed that some of the differences between bonobos and chimpanzees (and, in fact, humans and other apes [5]), can be explained by paedomorphism — the retention of juvenile traits into adulthood. Bonobos, in comparison to chimpanzees, show paedomorphism in anatomy [6,7] as well as some juvenilized behaviors [8–10]. Although this indicates that their behavior may also be paedomorphic with respect to chimpanzees, no study has been done to explicitly investigate this. In a new study reported in this issue of *Current Biology*, Wobber et al. [11] investigated whether the marked behavioral differences seen between chimpanzees and bonobos, the congeneric apes most closely related to humans, might be a result of changes in development speed.

Specifically, they investigated paedomorphism: whether changes in behavior may be due to slower — or the early curtailment of — development in one species as compared to the other.

In the initial study, Wobber et al. [11] examined food-sharing frequency in both apes. The apes were simultaneously given access to a food resource, which they could either monopolize or share. Tolerance around food is uncommon in adult primates [12], so willingness to share in adulthood may be a sign of juvenilization. Adult bonobos were more likely to share than were adult chimpanzees. Moreover, bonobos showed no change in tolerance as they aged; juveniles were just as likely as adults to share food. Chimpanzees, on the other hand, were as tolerant as bonobos when they were younger, but they became much less tolerant by adulthood (Figure 1). In other words, the two ape species started out with similar levels of tolerance, but while bonobos maintained their tolerance, chimpanzees became less so. Thus, in comparison with the chimpanzees’ behavior, bonobos’ behavioral development is paedomorphic.

Wobber et al. [11] next examined whether bonobos’ ability to inhibit was altered with respect to chimpanzees in another food situation. The authors first designed an inhibition



Figure 1. Two adult female chimpanzees look on as another eats a frozen fruit juice treat.

Although chimpanzees are generally tolerant of each other's presence, they share much less food as adults than as juveniles. On the other hand, bonobos share as frequently as adults as they did as juveniles, indicating different developmental trajectories between the species. This provides evidence in favour of behavioral paedomorphism in bonobos. Photograph by Sarah F. Brosnan, taken at the Keeling Center of MD Anderson Cancer Center.

task that could be used with juveniles. In an initial test, the apes had to choose from among three experimenters, only two of whom had food. If they requested food from the middle experimenter, who did not have food, the trial was over. Thus, the apes had to inhibit their tendency to ask each experimenter in turn, and instead skip over the middle individual, to get all of the food. The chimpanzees were very successful at this task at all stages of development. Older bonobos were equally adept as older chimpanzees; however, the younger bonobos were less capable than either the older bonobos or the chimpanzees. Thus, while bonobos and chimpanzees reached the same level of competence, the bonobos did so at an older age, indicating retarded development as compared to the chimpanzees.

To follow up, Wobber *et al.* [11] used a slightly more demanding inhibition task, a reversal learning paradigm, with an older group of apes. This allowed them to test whether there were differences in inhibitory skill which lingered into adulthood. The apes were initially exposed to one

experimenter who had food and one who did not. After their preferences were established, the experimenters switched roles, so the apes had to switch their preferences to get the food. Again, adult apes of both species reached similar levels of competence at this task, although chimpanzee adults were slightly, but not significantly, better in the first trials of the session than were the bonobos. Once again, the bonobos became adept at the task at a later age than did the chimpanzees. Taken together, these results indicate that bonobos' behavior is paedomorphic with respect to chimpanzees. They are more likely to retain juvenile traits (tolerance) into adulthood and to develop other cognitive skills (inhibition) at an older age than are chimpanzees.

Of course, when studying something as complex as the development of an organism, one of the challenges is to avoid oversimplification. Heterochrony can result from a variety of different mechanisms [1], and as with any evolutionary theory it is important to avoid just-so stories which are not empirically validated [13]. One example of a research area in which popular belief may outstrip scientific evidence is the case of the domestic dog. Although it is commonly assumed that, as a result of domestication, dogs are paedomorphic in comparison to wolves, the evidence for this is actually mixed [14,15]. One commonly cited example of paedomorphism in dogs, the truncated snout, is correlated with better vision: thus, this trait may have been selected for due to its benefits to the dogs, rather than being the byproduct of domestication ([16,17]; although see [18] for a developmental perspective). While this may seem like splitting hairs, if the goal is to understand evolutionary scenarios, it is actually quite important; if paedomorphism does not explain the evolution of some behavior, then we must seek out the mechanism which does [1].

The same holds true for our own evolution. In our quest to figure out what it is that sets humans apart from other apes, a common perception has developed that humans are paedomorphic. We appear to be extremely juvenilized as compared to the other apes, and arguments that we, too, are paedomorphic have been forwarded for at least a century [5,19]. However, this approach ignores other

evidence which indicates the opposite, or peramorphosis. In particular, the argument has been made that our brain is overdeveloped, with additional synaptic complexity, rather than being the result of plasticity due to juvenilization [1]. If we are to understand our own evolution, it is critical that we approach the evidence carefully.

One of the benefits of studies such as this new one [11] is that the heterochrony hypothesis is empirically validated. The authors demonstrate not only that adult chimpanzees and bonobos behave differently, but also that the developmental trajectories of the two species differ. Although future studies will undoubtedly complicate the picture, they would do well to take similar care in gathering the evidence. In this way, we may eventually tease apart which factors led bonobos and, by extension, other species, to be selected for altered developmental speeds, and understand how this affected their evolution.

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## Evolutionary Ecology: When Pollinators Are Also Herbivores

Plants often face a dilemma in attracting mutualists versus deterring antagonists. This dilemma may be exceptionally challenging when the mutualist and antagonist are the same visitor. It has now been demonstrated how plants can resolve this conflict through a novel change in flowering traits.

Rebecca E. Irwin

Plants interact with myriad visitors, including mutualists such as pollinators and antagonists such as herbivores. Although both pollinators and herbivores have played central roles in natural selection and plant evolution [1,2], there is increasing recognition that plant–pollinator and plant–herbivore interactions are not independent. For example, the dazzling floral traits that attract pollinators may also attract plant antagonists, including herbivores, florivores, nectar robbers, and seed predators. However, the arsenal of plant defensive traits that deters many of these antagonists may also come at a cost of deterring pollinators, especially if they are expressed in floral tissues or nectar [3]. Thus, plants may face a dilemma in attracting pollinators while at the same time defending against herbivores. This dilemma may be particularly acute when a plant's pollinators also act as herbivores in the same or different life-history stages [4]. However, as reported in this issue of *Current Biology*, Kessler *et al.* [5] document a novel mechanism by which plants overcome this conundrum by changing flowering phenology and thus relying on alternative pollinators.

While it might seem uncommon that a pollinator would also act as an herbivore on the same plant, such is not the case. Nature abounds with animals that act as both pollinators and consumers of their host plants [4]. For example, cabbage white butterflies pollinate wild radish but also oviposit

eggs on the same host plants [6,7]. Their larvae are known specialists on plants in the Brassicaceae and can cause damage that affects plant fitness. Similarly, hawkmoths often pollinate Solanaceous plants as nectar-feeding adults and lay eggs that develop into voracious herbivorous larvae in the same or different floral visits [4]. *Yucca* moths, which are specialized seed predators, simultaneously pollinate flowers while ovipositing their eggs into the floral ovary, thus ensuring that their developing larvae will have *Yucca* seeds as a food resource [8]. This conflict of mutualists consuming their hosts is not restricted to herbivorous pollinators; ants that tend aphids and consume their honeydew also consume the aphids under certain ecological conditions [9].

Given that some plants must cope with pollinators who also act as herbivores, how do plants defend against these antagonistic mutualists? The solution for plants is not straightforward, as traits that defend against antagonists may come at the cost of also dissuading, or being deleterious to, mutualists. Some of the best-known examples of tradeoffs in traits that affect both attraction and defense pertain to the production and distribution of secondary compounds in plants [10,11]. Many plant species produce secondary compounds that protect their leaves, but these defense chemicals are also found in their floral tissue, nectar, and pollen. While the expression of secondary compounds in leaves may benefit plants through reduced herbivore damage, their

expression in petal tissue and floral rewards may come at a cost of also deterring pollinators [3]. Alternatively, traits that increase pollinator attraction may come at a cost of increased herbivory. For example, augmented nectar production can result not only in higher pollinator visitation rates but also increased oviposition by antagonistic mutualists, given that nectaring and oviposition are often tightly coupled behaviors [5].

These tradeoffs in pollinator attraction versus plant defense may be rampant in natural systems, and Kessler *et al.* [5] report a novel mechanism by which plants can cope with interactions with pollinating herbivores. Wild tobacco (*Nicotiana attenuata*) is pollinated by night-flying hawkmoths (*Manduca quinquemaculata*), and after foraging for nectar, the moths oviposit eggs of their herbivorous larvae onto the same host plants. In a fascinating series of observations and experiments, Kessler *et al.* [5] document that plants damaged by hawkmoth larvae change their flowering phenology from night-opening flowers to morning-opening flowers. Morning-opening flowers are more attractive to hummingbird co-pollinators of wild tobacco, likely because the nectar has not been ravaged the night before by hawkmoths (Figure 1). This herbivore-induced shift in flower-opening time benefits plant seed production, a feat purportedly accomplished by substituting the system's nocturnal antagonistic mutualist, the hawkmoth, with an adequate replacement, the diurnal hummingbird. Also associated with the shift in flower-opening time following damage is a reduction in benzyl acetone production (a volatile emitted from flowers that is attractive to hawkmoths) and a change in flower shape. The authors speculate that the change in flower shape may provide an honest signal by which hummingbird