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Parrots and People: A Morphodynamic Convergence

Zusammenfassung

Die rund 398 lebenden Papageienarten (Aras, Sittiche, Kakadus usw.) bilden eine mehr oder weniger homogene Gruppe von Vögeln, die hauptsächlich in tropischen und subtropischen Regionen vorkommen. Keine andere Gruppe von Wildvögeln hat ein so starkes menschliches Interesse auf sich gezogen, und folglich sind Papageien unter den Vögeln die beliebtesten Haustiere auf der ganzen Welt, von den Tropen bis zu den gemäßigten Zonen. Was interessiert uns an Papageien? In diesem Artikel stelle ich die These auf, dass Papageien viele morphologische, Entwicklungs- und Verhaltensmerkmale mit Menschen teilen. Während ihre Intelligenz, ihre Fähigkeit, die menschliche Stimme nachzuahmen und die starken familiären Bindungen bekannte Merkmale sind, die mit menschlichen Eigenschaften übereinstimmen, weise ich auf zusätzliche, bisher übersehene menschenähnliche Eigenschaften der Papageien hin, von ihrem kugelförmigen Kopf bis zu ihrer hoch entwickelten Greiffähigkeit. Diese Greiffähigkeit des Papageienfußes – die es den Vögeln ermöglicht, Nahrung handzuhaben und Gegenstände zum Schnabel zu bringen – ist bei modernen Vögeln einzigartig und konvergiert mit der Geschicklichkeit der menschlichen Hand. Darüber hinaus besteht eindeutig ein Zusammenhang zwischen Intelligenz bzw. kognitiven Fähigkeiten und der Greiffähigkeit. Neben Papageien werden weitere Tierbeispiele in der Arbeit kurz diskutiert. Die schiere Anzahl der Ähnlichkeiten zwischen Papageien und Menschen erfordert eine Neubewertung der evolutionären Dynamik. Dementsprechend ist die Evolution nicht nur das Ergebnis der kumulativen Reaktion und Anpassung des Organismus an sich verändernde äußere Bedingungen der Umwelt, sondern auch der internen Integration und Kohärenz dynamisch interagierender anatomischer, morphologischer Verhaltens- und Entwicklungsprozesse. Als phänomenologischer und konzeptioneller Rahmen dieser Arbeit ist die konvergente Morphodynamik gut geeignet, diese dynamischen Zusammenhänge zu beleuchten.

Summary

The approximately 398 species of living parrots (macaws, parakeets, cockatoos, etc.) comprise a more or less homogeneous group of birds found mostly in tropical and subtropical regions. No other group of wild birds has attracted such strong human interest, and consequently parrots are the most popular avian pets around the world, from the tropics to the temperate zone. What is it about parrots that draws our interest? In this paper I propose that parrots share many morphological, developmental, and behavioral features with humans. While parrot intelligence, ability to mimic human speech, and strong family bonds are well-known features that converge with human characteristics, I point out additional overlooked humanlike traits of parrots, from their spherically-shaped head to their highly developed grasping ability. Regarding the latter, the prehensility of the parrot's foot – which enables birds to manipulate food and bring items to the mouth – has no equal among modern birds and is convergent with the dexterity of the human hand. Furthermore, there is evidently an association between intelligence, i.e., cognitive ability, and prehensility, and additional animal examples are discussed briefly. The sheer number of similarities between parrots and people calls for a reconsideration of evolutionary dynamics. Accordingly, evolution can be understood as not only the result of the organism's cumulative response and accommodation to shifting external conditions of the environment but also to the internal integration and coherence of dynamically interacting anatomical, morphological, behavioral, and developmental processes. The phenomenological and conceptual framework of convergent morphodynamics is well suited to shed light on these dynamic relationships.

Introduction

There are about 398 species of parrots in the Order Psittaciformes, comprised of families Strigopidae (3 spp.), Cacatuidae (21 spp.), and Psittacidae (374 spp.), living today (Winkler & al. 2015), most found in tropical and subtropical regions (Juniper & Parr 1998). Undoubtedly, more than any other wild birds, parrots – including macaws, parakeets, cockatoos, cockatiels, budgerigars, lories, etc. (hereafter collectively called »parrots«) – have captured the imagination and admiration of people around the world. Accordingly, parrots are popular pets globally and, consequently, have been subjected to the international pet trade perhaps more than any other group of birds (Pruett-Jones 2021). Clearly, their intelligence, behavioral antics, ability to mimic human speech, colorful plumage, and tendency to bond closely with their human companions have endeared them to us (Bond & Diamond 2019). What I hope to show is that the suite of characteristics that we find so intriguing about this group of birds points to a dynamic and unique evolutionary convergence between parrots and people: We each give expression to a similar web of morphological patterns, respectively among birds and among primates (and mammals in general). In other words, parrots are the most humanlike birds though, of course, expressed in a caricatured motif.

To be clear, I am *not* implying the parrot-human relationship in a *metaphorical* sense but as an actualization, or manifestation, of similar evolutionary themes and trajectories. Moreover, these expressions, I propose, are not random, that is, not the result of stochastic genetic combinations subjected to natural selection, so-called convergent evolution as conventionally understood. My perspective is that the parrot-human relationship is not a »fluke of nature«, as implied by Bond & Diamond (2019: 6), but goes much deeper, and thereby requires a reorientation to evolutionary dynamics. In other words, we need to allow the phenomena to guide our observation and understanding to new and perhaps unorthodox concepts and ideas if we wish to understand how nature takes form and how evolution unfolds. To accomplish this, I will draw on the phenomenological tradition of the poet and scientist J. W. von Goethe (1749–1832), who pioneered a methodology of mindful and engaged observation to decipher, among other things, the language of plant and animal morphology (Miller 1995), and whose influence would likely be familiar to previous readers of »The Yearbook«. Accordingly, guided by this approach, I will frame my observations in a morphodynamic context, explained in the next section.

Methods

In this paper, I describe phenomenologically (that is, relating what is clearly observable) various morphological and behavioral characteristics of parrots within the group itself, and I also compare and contrast these with parallel features in humans and other organisms. Besides drawing from the growing literature on studies of wild and captive parrots, my observations and conclusions are based on my field experience of wild parrots in Latin America, especially in Peru and the Brazilian Pantanal, and in Australia and East Africa, as well as observations of captive birds. To estimate the relative percentage of color patterns seen in parrots, I referred to illustrations in various books, especially Lynx Edicion's »All the Birds of the World« (del Hoyo 2020).

What I hope to demonstrate is that the sheer number of covarying features between parrots and humans raises important questions regarding the nature of evolutionary dynamics. In other words, the probability that these parallel suites of covarying characters emerged in unrelated groups through random mutation and subsequent selection is diminishingly small and therefore points to another explanatory framework, such as that of »convergent morphodynamics«. Lockley (2007), in his exploration of dinosaur fossils and their trackways, and Lockley & Jackson (2008), in their study of the convergence between sauropod and human feet and limbs, ground their approach in a »morphodynamic« context, couched in the paradigm constituted by evolutionary developmental biology (so-called evo-devo; Hall & Olson 2003, Carroll 2005, Sassoon 2020). Note that it was Goethe who coined the term »morphology«, and his conception already engaged a dynamic, and comparative, way of seeing natural forms, which is especially evident in his notion of metamorphosis (Goethe 1790/2009, Bortoft 2012, Riegner 2013). But since this dynamic quality of cognition is no longer assumed today in the conventional study of morphology, morpho*dynamics* is the preferred term used here. Although the word has various contemporary applications, »morphodynamics« was historically first applied in a biological context by Seilacher to the study of the transformation in ontogenetic and phylogenetic time of fossil marine invertebrates (recounted in Seilacher & Gishlick 2020). From a Goetheanistic perspective, at the center of a morphodynamic approach to understanding, i.e., cognizing, biological processes exists the identification of recursive morphological and behavioral features presumably based on recursive developmental trajectories that come to expression in seemingly unrelated phenomena and in distantly related taxa (such as the expression of similar morphotypes across the diversity of mammals, explicated by Schad 1977, 2020, or of converging trackways and morphologies among dinosaurs, explored by Lockley 2007, or of similar avian plumage patterns across the diversity of birds, described by Riegner 2008; for an in-depth discussion of recursion, see Bird 2003 and West-Eberhard 2003, especially chapter 19).

General Biology and Morphology of Parrots

Parrots exhibit remarkable morphological uniformity and are easily recognized (Juniper & Parr 1998), though body length can vary 12-fold (Collar 1997) from the tiny *Micropsitta* pygmy parrots of Papua New Guinea and nearby islands to the Hyacinth Macaw (*Anodorhynchus hyacinthinus*) of South America. All parrots have a relatively large head, which gives them a juvenile appearance, like a large-headed human baby. Furthermore, with their strongly hooked beak, parrot heads are rounded more so than that of any other bird (*Fig. 1*), which likewise portrays a humanlike appearance. Among mammals, the spherical adult human skull is the most juvenile in form, departing the least from fetal proportions, and thus is considered paedomorphic, a result of neoteny (Gould 1977, McNamara 1997, Verhulst 2003). Ancient cultures in Mexico depicted parrots with rounded heads and steep humanlike foreheads (*Fig. 2*). This youthful theme is also reflected in parrots' typical diet: the undeveloped seeds, that is, the embryos, of trees and palms. (Accordingly, many parrots do not serve their host plants by dispersing their seeds but, instead, are destructive »seed predators«, though recent studies are finding otherwise: e.g., Blanco & al. 2018; Tella & al. 2020.) Wild Cockatiels (*Nymphicus hollandicus*), for example, which feed on grass seeds, select »the soft immature seeds over the hard ripe ones« (Toft & Wright 2015: 63). Moreover, when animal food is occasionally consumed, for example by various species of cockatoos, it often consists of beetle grubs (Toft & Wright 2015), that is, the *immature* larval stage of the coleopteran life cycle. The New Zealand Kaka (*Nestor meridionalis*), for instance, includes longhorn beetle (Cerambicidae) larvae in its diet (Bond & Diamond 2019). Note that some parrots, e.g., the lorikeets, eat nectar and pollen.

Thus, morphologically, in respect to the spherical head, both parrots and humans exhibit a juvenile-like form, with parrots in addition amplifying this quality in their diets. Furthermore, regarding the humanlike head, some species, specifically the large macaws, have a featherless face; when excited or agitated, the birds, such as Blue-and yellow Macaws, actually blush (Munn 1994, Bertin & al. 2018; *Fig. 3*)! Cockatoos, in addition, raise their elongated crest feathers to express emotional states of excitement, while Keas smooth or fluff their body feathers (Bond & Dia-

Fig. 1: Note angular head profile of chicken (*left*), circular head profile of macaw (*middle*), and ovoid-shaped skull of small parrot species (*right*). (Skull from collection at American Museum of Natural History, New York, USA)

Unless otherwise indicated, all photos are by the author.

Fig. 2: Pre-Hispanic cultures in Mexico often depicted parrots with a humanlike head (*left*: from Oaxaca, Mexico; *right*: from Palenque, Mexico).

mond 2019). Note that parrots, again like humans, are mostly sexually monomorphic, that is, males and females look alike in color pattern and are more or less similar in body size, and they perch in a vertical position, mimicking human uprightness (see *Fig. 6*).

Unlike humans, however, parrots have short legs. Their toe arrangement is zygodactyl, that is, two toes point forward and two back, which is considered »superaltricial« (Botelho & al. 2015), in other words, highly juvenilized. This arrangement, besides displaying an anterior-posterior balance with equal number of toes pointing in opposite directions, enables parrots to manipulate food and other objects, discussed in a later section. It also allows them to move easily among tree branches but, somewhat comically, only waddle on the ground »rather like a child learning to walk« (Bond & Diamond 2019: 6). In this regard, note that parrot hind limbs are morphologically and functionally *opposite* to those of humans: Parrots have short legs not adapted for walking and long toes adapted for grasping, while humans have long legs highly adapted for walking and running but short toes that are mostly useless for grasping. Obviously, parrots have wings to propel them through space, so legs are not required for long-distance travel.

Parrot tail feathers can appear stubby or very long, the latter trailing in flight. The smaller species fly with continuous rapid wingbeats while the large forms, like the macaws, fly with intermittent wingbeats and horizontal gliding, often above the forest canopy or along rivers (personal observation). From my experience, parrots often call raucously to each other in flight. To our ears, parrots emit irritating, sometimes ear-splitting, vocalizations, especially when they take flight together from a feeding tree, or when a predator approaches, or when caged individuals seek attention. At other times, birds will chatter incessantly at a roost. Parrots can, however, remain silent and undetected. While searching for birds in neotropical forests, I've occasionally approached large fruiting trees, craned my neck to see to the canopy (sometimes over 40 meters above the ground), and then, after convincing myself the tree crowns were empty, moments later hearing loud cries and then an abrupt departure of a parrot flock.

In conclusion of this section, in keeping with a Goetheanistic perspective, it is illuminating to ask: What group of birds displays an opposite morphological, and perhaps opposite ecological, expression to that of parrots? We may expect this group to possibly be generally sympatric with parrots, that is, co-inhabiting forests where parrots are found. In the Neotropics there is a group of canopy-dwelling birds that, morphologically, exhibit a dramatically different, even what can be considered a polar opposite, gesture in their beaks, which are exceptionally long and broad, often colorful, and extend somewhat perpendicular to the body's axis when the birds are perched. The toucans comprise a family (Ramphastidae) of 50 species (Winkler & al. 2015) which, besides their elongated bill, also have, like parrots,

Fig. 3:

Blushing Great Green Macaw (*Ara ambiguus*). (Photo: Eric Kilby, license: CC BY-SA 2.0, Wikimedia Commons)

Fig. 4: *Left*: Blue-and-yellow Macaw (*Ara ararauna*); *right*: Chestnut-mandibled Toucan (*Ramphastos ambiguus* , Sarapiquí, Costa Rica). Compare opposite beak forms and orientations. (Painting by Walt Anderson; used with permission.)

Fig. 5: The metamorphosis from a spherical (»involuted«) to an extended (»evoluted«) form parallels the shift in beak morphology from the Hyacinth Macaw (*Anodorhynchus hyacinthinus*) to the Toco Toucan (*Ramphastos toco*), the largest (longest) members of their respective avian families. In addition, note that the macaw's beak grows in a logarithmic spiral, noted by Thompson (1961: 215). (Drawing from Elsner 2013; used with permission. Skull replicas are at same scale.)

short legs and a zygodactyl toe arrangement, though they lack the dexterity typical of parrots (*Fig. 4*); like parrots they also nest in tree cavities. The extended bill of toucans is the opposite gesture of the involution seen in the spherical-tending bill of parrots when viewed within the dynamic geometric context of metamorphosis, coincidentally depicted by Elsner (2013) (*Fig. 5*). Furthermore, whereas the parrot bill is a tool to manipulate and crack open hard seeds, the toucan bill is simply a grasping tool to reach and pluck fruits and other food items. Ecologically, the two groups are also divergent: Whereas parrots eat mostly seeds, cracking and thus killing the plant embryos, toucans gulp whole fruits with seeds intact, subsequently regurgitating the unharmed seeds and thereby serving as seed dispersers in tropical forests. Unlike parrots, toucans also eat animal food, such as the young of nesting birds, including parrot chicks!

Social Behavior, Nesting, and Development

Almost all parrots form permanent monogamous pair bonds (Toft & Wright 2015; *Fig. 6*). Both parents care for the young, and family groups exhibit strong cohesiveness over extended time periods. To strengthen social bonds, individuals often groom each other, so-called allopreening. For example, various cockatoos are known to practice mutual grooming bouts that can last 40 minutes or longer (Bond & Diamond 2019). Although the required research is difficult to undertake, there is some evidence that flock members remember and recognize individuals (Bond & Diamond 2019) and stay together over many years, with mated pairs and family members living within the context of a larger group. In this regard, most species are gregarious (Juniper & Parr 1998). Monk Parakeets (*Myiopsitta monachus*) take social living to the extreme, as they live in communal nests with separate compartments occupied by the mated pairs (*Fig. 7*). This co-op housing, however, is not without social tensions: Pairs regularly steal construction materials from their neighbors (Toft & Wright 2015)!

Most parrots nest in tree hollows, while others nest in excavated termite nests and on cliff ledges (Juniper & Parr 1998). Courtship displays, enacted by both partners, take place near the nest. Larger species, such as macaws, lay one to three eggs, while smaller species lay more; it is typically only the female that incubates (Collar 1997). Most medium- to large-bodied parrots develop slowly, require extended periods of parental care, and exhibit delayed maturation (that is, reproductive maturity is postponed); this developmental mode also parallels that of humans (Kipp 2005). Hyacinth Macaw fledglings may be fed by their parents for up to a year (Collar 1997). The extended fledgling period underscores the fact that »parrots depend a great deal on learning and mentoring from their parents, just as humans do« (Toft & Wright 2015: 200). The slow developmental rates, of course, resonate with a key life-history context, that is, parrots live a long time, up to 50 years or longer in the wild (Toft & Wright 2015, Wirthlin & al. 2018).

In recent years, parrots have been likened to primates based on their impressive cognitive abilities and associated parallel neurological development. For example, a recent study found that »parrots and primates have convergently evolved increased connectivity between the telencephalon and the cerebellum, but have done so through different neural pathways« (Gutiérrez-Ibáñez & al. 2018: 5). Moreover, parrots and corvids (crows, ravens, jays) have been shown to possess more neurons in their forebrains than primates with larger brains (Olkowicz & al. 2016), as well as larger brains and forebrains than most other birds (Iwaniuk & al. 2005). Disregarding owls, enhancement of brain volume in birds is often correlated with social complexity (Burish & al. 2004, Emery & al. 2007). On that point, parrots and corvids exhibit social play behavior (Diamond & Bond 2003), which is especially developed in the New Zealand Kea (*Nestor notabilis; Fig. 8*). Thus, because play behavior releases the participants from the immediate necessities of life maintenance, it is an expression of biological autonomy, which has evolved convergently in humans and in these other groups of endotherms (Rosslenbroich 2014).

Parrot developmental dynamics exhibit, in a sense, the harmonizing of the inherent polarity of the altricial-precocial developmental spectrum. Altricial birds, such as most songbirds, hatch in an underdeveloped condition with relatively small brains, and are carefully attended by their parent(s); as they grow, they are fed a protein-rich diet, which supports accelerated brain development and ultimately results in adults with disproportionately large brains. Precocial birds, such as chickens, in contrast, hatch with relatively large brains to perform the many immediate survival tasks – such as pecking for food – in the absence of much parental care. As they grow, their brain enlarges disproportionately less than their body and, as adults, they have a disproportionately small brain (for discussion of the altricial-precocial spectrum in birds, see Starck & Ricklefs 1998, and Iwaniuk & Nelson 2003, and references therein). As an apparent anomaly, parrots hatch in an altricial condition, yet their brains are relatively large, like those of newly hatched precocial birds. Furthermore, unlike precocial birds but similar to altricial birds, the brain of a parrot grows significantly throughout postnatal development (Ehrlich & al. 1988: 585 and 587). Specifically, parrots (and songbirds) exhibit a delay in the growth of the telencephalon and thus »the brains of parrots (…) are relatively immature at hatching« (Charvet & Striedter 2011: 3). In other words, parrot chick brains are paedomorphic. The obvious result, as the bird matures, is a highly intelligent bird capable of a marked degree of behavioral adaptability. Among primates, humans, too, are born with an exceptionally large brain, which still grows at a relatively accelerated rate throughout childhood, compared to the proportionally smaller neonatal brains of other primates that grow disproportionately slower (Verhulst 2003). Thus, another morphodynamic convergence is evident between parrots and humans. In addition, a recent study found that wild nestling Green-rumped Parrotlets (*Forpus passerinus*) exhibit vocal babbling, »a potentially convergent scenario with (…) human infant language development« (Eggleston & al. 2022: 7).

Intelligence and Vocal Learning

The remarkable intelligence of parrots is legendary, and they »appear to be geared to the learning process throughout their lives« (Collar 1997: 298), another parallel to human behavior. For example, a population of Sulphur-crested Cockatoos (*Cacatua galerita*) discovered how to open bin lids in three suburbs of Sydney, Australia, before 2018. By late 2019, the behavior spread by social learning to 44 suburbs (Klump & al. 2021)! In recent decades, Alex, the African Gray Parrot (*Psittacus erithacus*) trained by animal cognitive scientist Irene Pepperberg, demonstrated an ability to identify shapes and colors of objects and thereby exhibited a »category concept« (Pepperberg 2008, Toft & Wright 2015). He also had an extensive vocabulary of about 150 words, which he employed in sophisticated ways (that is, not simply mimicry), equivalent to the language ability of a five-year-old child (Pepperberg 2008). Most captive parrots can be taught to »speak«, that is, to imitate the human voice, an example of so-called vocal learning. Interestingly, with the exception of free-ranging African Gray Parrots, there are no observations of parrots mimicking non-parrot sounds in the wild (Toft & Wright 2015). In a potentially revelatory discovery, Chakraborty & al. (2015: 1) »(…) found that the parrot brain uniquely contains a song system within a song system«. This expression of a *system within a system* apparently points to a remarkable example of neurological and behavioral recursion. In humans, the parallel is seen in our uniquely recursive thinking activity: We are presumably the only organisms that can think about thinking (Corballis 2007). For example, it is well known that many animals can use and even fashion tools, as observed in such diverse species as tuskfish, Woodpecker Finches, Egyptian Vultures, sea otters, and chimpanzees. Humans, however, regularly create tools in order to make *other* tools – an example of applied recursive thinking (Corballis 2007). And previous readers of »The Yearbook« would likely be familiar with the human ability to place thinking itself as the object of thoughtful contemplation (Steiner 1995).

Fig. 6: *Left*: Pair of Red-and-green Macaws (*Ara chloropterus*); note similarity in appearance and more or less vertical posture. (Mato Grosso do Sul, Brazil)

Fig. 7: *Right*: Monk Parakeets (*Myiopsitta monachus*) in communal nest; note pairs in separate compartments. (Pantanal, Brazil)

Fig. 8: *Left*: The Kea (*Nestor notabilis*), found on South Island, New Zealand, exhibits a high degree of social play. (Photo: Gabriel Riegner)

Fig. 9: *Right*: Hyacinth Macaw (*Anodorhynchus hyacinthinus*) using stick as a tool (see white arrow) to prevent seed from slipping as bird bites down; also note use of foot to manipulate food. (Pantanal, Brazil)

Fig. 10: *Left*: Red-and-green Macaws (*Ara chloropterus*) visiting clay bank. (Tambopata National Reserve, Peru)

Fig. 11: *Right*: Peach-fronted Parakeet (*Eupsittula aurea*) uses foot to hold a relatively large food item as the bird feeds. (Pantanal, Brazil)

Regarding straightforward tool use, some species of parrots have been observed using various natural implements. Palm Cockatoo (*Probosciger aterrimus*) males will select a stick or stone to use as a drumstick to tap against a hollow tree to advertise territory; this has been likened to human instrumental music (Heinsohn & al. 2017). In the Pantanal of Brazil, I observed a Hyacinth Macaw holding a short stick in its beak pressed against a large palm seed to keep it from slipping as the bird bit down on it (*Fig. 9*). This behavior has previously been reported only in captive birds (Borsari & Ottoni 2005). Perhaps even more impressive, in a recent experimental study, Goffin's Cockatoos (*Cacatua goffiniana*) exhibited the use of tool sets, that is, anticipating the need for two tools to solve a future problem and transporting the paired tools together (Osuna-Mascaro & al. 2023). Though not specifically tool use, several species of neotropical parrots regularly visit clay banks to bite off and ingest chunks of clay, presumably to neutralize the mildly toxic secondary plant compounds contained in their diet (*Fig. 10*). Accordingly, this can be considered an example of self-medication! Furthermore, according to avian ecologist Donald Brightsmith, the macaws and other parrots may be ingesting clay to acquire sodium in the salt-deficient western Amazonian basin (Drake 2014).

Prehensility

As mentioned earlier, parrots possess a zygodactyl toe arrangement. This lends itself to an exceptional degree of prehensility (though other birds with zygodactyl toes, e.g., woodpeckers, lack the grasping ability of parrots). Accordingly, parrots can grasp food items with their feet, manipulate the items, bring them to the beak for further handling and processing and, with the aid of the thick tongue, then ingest the food (*Fig. 11*). No other birds are capable of this foot-to-beak transfer, with the exception of some owls (Marks & al. 1999: 122), which notably also have a flat face, strongly downcurved upper beak, and zygodactyl feet (but with reversible fourth toe).

Thus, as a group, parrots have evolved the greatest dexterity and foot prehensility among all birds. Interestingly, this parallels the evolution of the human hand, a key morphodynamic convergence that, surprisingly, typically goes unnoticed. Wirthlin & al. (2018), for example, identify eight attributes of parrots that are shared by humans, but advanced prehensility is not one of them! Among mammals in general, and primates specifically, humans have the most developed grasping ability. The relatively long thumb (Almécija & al. 2015) and high position (and directional orientation) of the thumb on the hand, slightly below the level of the other fingers, as well as three unique and additional small muscles (Bryson 2019), enable humans to apply the precision grip, such as in gripping a pencil, which no other primate can accomplish because, during fetal development, their thumbs are displaced disproportionately lower on the hand (Verhulst 2003: 121).

As an interesting correlate of the foot's prehensility and use in eating, the parrot's beak can be used for multiple purposes besides feeding. For example, when moving through a tangle of vines or branches, parrots will use their beak as a »foot« to assist in climbing (*Fig. 12*). They carefully grasp branches with their beak, which has a hinged joint (Bond & Diamond 2019), and then move their body and feet toward the head, pulling their way through the vegetation. This behavior is also readily displayed by captive parrots when they climb the bars or the mesh of their enclosure. In this regard, the »beak and head of parrots have been co-opted to function biomechanically as a third limb« (Young & al. 2022: 3). Thus, parrots can be considered to use their beak as an aid in climbing and their foot as an aid in eating, i.e., both feet and beak are dual purpose.

Coloration

Although parrots appear in a rainbow of colors – perhaps the most colorful group of birds (Bond & Diamond 2019, Merwin & al. 2020) – the group is remarkable in that green is expressed in significant degrees in the majority of species – at least 72% of species by my estimate – especially in neotropical parrots (Juniper & Parr 1998; *Fig. 13*). Except for a handful of bird families (e.g., hummingbirds, trogons, todies, jacamars, Asian barbets, green broadbills, and leafbirds) and scattered examples from otherwise multicolored bird families (e.g., some tanagers, turacos, bee-eaters, Australian catbird, toucanets), green is an uncommon color among birds. Is there a special relationship between parrots and the color green?

According to Goethe's color theory, colors arise as an expression of the tension between darkness and light represented by the polarity of, respectively, black and white (Miller 1995: 170, and elsewhere). The primal phenomenon is seen in the alternation of night and day or, as Goethe shows, in the further manifestations of atmospheric phenomena in the blue of the sky and yellow of the Sun. In the former, the blackness of space, when observed through Earth's illuminated slightly turbid atmosphere in daytime, appears blue (Miller 1995: 191–192, Löbe & al. 2022). In contrast, the white light of the Sun, when seen through the same slightly turbid atmosphere, appears yellow; when the Sun sets (that is, when we observe the Sun through a greater depth of atmosphere), or when we observe the Sun through a humid haze or through pollution (such as smoke from a fire), the yellow color shifts to orange and even to red-orange if the atmosphere is significantly turbid (Miller 1995: 191–192). Thus, by observing »darkness through light and light through darkness«, we apprehend the colors blue and yellow, respectively, which constitute a fundamental polarity (Miller 1995: 195). (A discussion of the origin of other colors and color intensification would fall outside the scope of this article; see Miller 1995: 245–246, and Löbe & al. 2022.)

Note that Goethe described the color green as a unity, »a phenomenon that hints at an accord« (Miller 1995: 268). Those readers familiar with Goethe's color theory will recall that he viewed the origin of green in a different manner from that of blue and yellow and their associated colors. Goethe, in opposition to Newton who saw green as just another color within the spectrum, maintained that green arises not as an independent color but only as a *combination* of blue and yellow, which creates a *unity* (Miller 1995: 268). This observation derives from Goethe's prism experiments in which he described not one but two separate color spectrums which, when they coalesce and blue and yellow overlap, produce green.

Returning to birds, how are colors, and specifically green, produced in avian plumage? First, beginning with blue, it is easily demonstrated that, if one finds a blue feather from, for example, a Blue Jay (*Cyanocitta cristata*), Woodhouse's Scrub Jay (*Aphelocoma woodhouseii, Fig. 14*), or a Eurasian Blue Tit (*Cyanistes caeruleus*), and grinds it up, what remains is a gray powder. In other words, there is no blue residue. This is based on the fact that there is no blue pigment; in these cases, blue arises as a structural color (Hill 2010). A blue feather's microstructure reveals a central cluster of dark melanin (i.e., black) granules surrounded by semi-hollow, spongy cells embedded in a keratin matrix (the same substance that composes your fingernails; *Fig. 15*). Light entering the feather microstructure is scattered in all directions – a phenomenon called diffusion – and, according to the conventional explanation, all colors are absorbed by the melanin, except blue, which is reflected. The parallels with Goethe's explanation of the origin of blue become apparent if the components of the feather microstructure, that is, the melanin granules, are seen as »darkness viewed through light«, that is, through an illuminated slightly turbid medium – the surrounding semi-hollow spongy cells, which scatter the light.

Yellow, orange, and red, in contrast to blue, are derived from pigments, typically carotenoids, which are synthesized only in plants (Hill 2010; *Fig. 16*). Consequently, birds displaying these colors must acquire the pigments in their diet, although some species have the biochemical ability to transform yellow pigment into red. Note that parrots, uniquely, can synthesize their own form of yellow and red pigments called psittacofulvins (Hill 2010, Tinbergen & al. 2013; *Fig. 16*).

Now what about those green feathers? Essentially, green plumage arises most often as a combination of blue structure and yellow pigment. The Australian Bud-

Fig. 12: Red-shouldered Macaw (*Diopsittaca nobilis*) climbing through vegetation using feet and beak. (Photos: Micah Riegner; Roraima, Brazil)

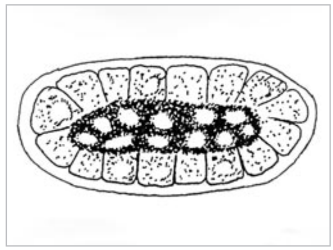

Fig. 13: *Left*: At least 72% of parrot species exhibit significant degrees of green plumage, such as in this pet Festive Parrot (*Amazona festiva*). (Amazon, Brazil)

Fig. 14: *Middle*: Woodhouse's Scrub Jay (*Aphelocoma woodhouseii*) exhibiting blue, gray, and white feathers; blue arises as a structural color. (Prescott, Arizona, USA)

Fig. 15: *Right*: Highly magnified feather microstructure of »blue« feather barbule showing central cluster of melanin granules surrounded by semi-hollow, spongy cells embedded in keratin matrix. (Drawing: Mark Riegner)

Fig. 16: The yellow pigment of the Yellow Warbler (*Setophaga aestiva; left*) is derived from carotenoids in the bird's diet, the more common source regarding yellow coloration in birds. In the Golden Parakeet (*Guaruba guarouba; right*) the yellow coloration derives from psittacofulvin, which is a pigment uniquely synthesized by parrots. (*Left:* photo by Mdf, license: CC BY-SA 3.0, Wikimedia Commons; *right:* photo by Micah Riegner; Amazon, Brazil)

gerigar (*Melopsittacus undulatus*), which is a popular pet (often misnamed a »parakeet«), occurs in the wild in a mostly green plumage with yellow head. However, artificial selection of captive birds has produced both blue (with white head) and all-yellow variants; in the former, a mutation hinders the deposition of yellow pigment (i.e., psittacofulvins) in the feathers, while in the latter a mutation disrupts the formation of feather microstructure that would otherwise produce blue (Cooke & al. 2017). In other birds of the world, occasionally green feathers are the result solely of structure, and there are rare cases where green plumage can result from synthesized pigments (such as turacoverdin in many African turacos, Musophagidae; Turner 1997). Thus, green typically arises from the harmonization of the polarity of blue and yellow, the first colors to manifest out of, respectively, darkness and light. According to Goethe, green is pleasing to the human eye and offers a sense of tranquility and balance (Miller 1995: 283); it is the central color in Newton's color spectrum as well as in Goethe's coalescence of his two color spectrums. Returning to parrots which, again, display green plumage in a majority of species (72% by my count), is there a relationship between the central position of green in the color spectrum and the constitution of this order of birds?

Evolution

As mentioned in various descriptions above, parrots tend to harmonize polarities. They use their beak as a foot when climbing and use their foot as a feeding tool. In addition, the Kaka (*Nestor meridionalis*), when about to crack open a nut, will wrap its toes around the end of its upper and lower beak and squeeze as the beak closes, providing extra »bite« force (Bond & Diamond 2019). As discussed above, although parrots hatch in an altricial condition, their brain is disproportionately large, like that of a precocial bird. Furthermore, although they hatch with an enlarged brain, it still grows at an accelerated rate, like that of an altricial bird's brain. In addition, parrots have been traditionally situated in the middle of the avian evolutionary tree, that is, in the middle of avian phylogeny between the earliest birds to evolve and those that have evolved more recently (Jetz & al. 2012), though one phylogenetic study using molecular markers has placed them at the crown of the tree next to songbirds (Suh & al. 2011). Thus, based on fossil evidence, parrots probably appeared roughly midway in avian evolution, somewhere between the more ancestral species, like waterfowl, and the more recent species to appear, such as the songbirds. Interestingly, their most closely related avian group has traditionally been considered the pigeons (family Columbidae), some of which, like parrots, exhibit a strong relationship to human life and culture, and even display a mammalian physiological feature. For example, the Rock Dove (*Columba livia*) is found in many cities and towns around the world, the white dove is often symbolized in religious themes, and »pigeon milk« is produced in the crop and fed to chicks (König 2013); moreover, the prominent vertical forehead of many of the world's pigeons and doves resembles the human forehead. Also, more than 25% of the world's 357 species of pigeons and doves possess at least significant patches of green plumage, including 31 species of the genus *Treron*, the green-pigeons, 10 species of the *Ramphiculus* fruit-doves, and 45 species of the *Ptilinopus* fruit-doves (estimated from examining color plates in del Hoyo 2020). Returning to the theme of morphodynamic convergence between parrots and people, it is notable that, within the mammalian tree of life, the primates occupy a central position between the more ancient mammals and those that evolved more recently, with humans situated within the primates (Gómez & al. 2016). According to Schad (1993: 387), the human being »does not stand at the peak of the genealogical tree, but right among the lower branches of the genealogical bush of the placental mammals«. Thus, parrots and humans evidently exhibit a parallel midway placement in their respective evolutionary tree of life.

In another example of parrot-human morphodynamic convergence, one can extract clues from morphological evolution. A century ago, it was believed that the large human brain, and its housing in the skull, led the way in human evolution. However, more recently, thanks to well-known fossil discoveries in South Africa and Ethiopia, we now conclude that upright walking, and associated pelvic bone and leg modifications, preceded large brain development in early hominins. Thus, standing and walking, and specialized feet and legs – not modifications of the brain and skull – were primary and instrumental in early hominin evolution. Similarly, fossil bones found in Europe of what appear to be ancestral parrots, roughly 35-55 million years old (Eocene), exhibit the specialized zygodactyl foot but, regarding the skull, the characteristic hooked beak is absent (Waterhouse 2006). Accordingly, fossil evidence shows that in both humans and parrots, in their respective evolutionary trajectories, limb specialization preceded skull, and presumably brain, development. This evolutionary pattern was previously identified in the transitional stages of the vertebrate classes by Schad (1993).

Morphodynamic Convergence among Parrots and other Animals

For this final section, we can ask, Do other animals display a similar morphodynamic convergence with parrots (and thus are by association convergent with humans)? It may seem an odd comparison, but I propose that elephants fit the bill.

First, like parrots, these massive mammals have a flat skull with an elevated forehead (*Fig. 17*). Correlated with the foreshortening of the skull is the evolution of the most remarkable prehensile organ in the animal kingdom: the trunk! The flexibility, grasping ability, and strength of the elephantine trunk are legendary (see Holdrege 2003, 2021) and new discoveries of its biomechanical functionality are made regularly (e.g., Schulz & al. 2022). Thus, the human hand, the elephant's trunk, and the parrot's foot each expresses a remarkable degree of prehensility, which is, of course, further correlated with a high degree of intelligence and concomitant large brain (though note that bird brains are differently structured than mammal brains). Like parrots and humans, elephants are highly social, maintain life-long bonds (but not between mates), rely on complex vocal and visual communication to express internal state (or »mood«), invest an inordinate amount of time and energy into parental care (only elephant cows), exhibit vocal learning, are exceptionally long lived, exhibit delayed maturation, and even use tools (for discussion of elephant-human parallels, see Schad 1977, 2020 and Holdrege 2003, 2021).

Regardless of how disparate these organisms may appear, through the process of recursive evolution (for definition and discussion of »recursion«, see Bird 2003), nature, in a sense, expresses similar motifs among evolutionarily distantly related species. Ralph Waldo Emerson once remarked: »Nature (…) delights in startling us with resemblances in the most unexpected quarters« (Emerson 1883: 7). Of course, these are *resemblances* and not exact copies; as Goethe already noted, natural phenomena are infinitely variable but, paradoxically, also limited by constraints (Riegner 2013). In this vein, and somewhat playfully, we can look even further afield to discover »parrot-like« motifs in ever more distantly related species.

If we go so far as to examine the invertebrates, there is a group/class that does, in fact, share certain parrot-like features. The Cephalopoda – which includes the octopuses, squids, cuttlefish, and nautiloids in the phylum Mollusca – have remarkable dexterity in their multiple grasping arms, especially the octopus (Kennedy & al. 2020), whose arm movements have been described as »humanlike« (Sumbre & al. 2006). The so-called tentacles, often lined with »suckers«, can grab and manipulate prey, such as fish or crabs, and even attempt to pull the regulator from a diver's mouth (Anderson 2007)! And once the prey is captured it is rapidly drawn to the mouth, where what is typically described as a »parrot-like beak« (*Fig. 18*) quickly dispatches the item.

In addition, the intelligence of cephalopods in general is well known, and the octopus specifically can be trained to identify visual patterns, utilizing a complex eye that was earlier thought to be convergent, but more recently homologous, with the eyes of vertebrates (Carroll 2006). This »deep homology« is attributed to the presence of the *PAX6* gene, which is associated with eye development from fruit flies to humans, and has also been isolated from squids (Carroll 2006). Further-

Fig. 17: African elephant. Note flat, vertical forehead and, that most prehensile of organs, the trunk. (*Left*: Maasai Mara National Reserve, Kenya; *right*: skull from an elephant that lived in the Berlin Zoological Garden; photo: Roselies Gehlig).

Fig. 18: *Left*: The »beak« of the octopus and squid resembles the parrot beak (compare with *Fig. 5*). (Beak of Giant Squid, *Architeuthis dux*; London Natural History Museum; photo: The Trusties of the Natural History Museum, London, license: CC BY-SA 4.0, Wikimedia Commons)

Fig. 19: *Right*: Note the humanlike shape of the »head« of this octopus. (Newly discovered unnamed octopod species; photo: National Marine Sanctuaries, license: public domain, Wikimedia Commons)

more, as noted above, parental care is highly developed in parrots, which begins with brooding the clutch of eggs. Although this behavior is rare in cephalopods, which typically lay eggs on the seafloor and then soon abandon them, a recent study has found that a female Deep-sea Octopus (*Graneledone boreopacifica*) brooded her clutch of eggs for an almost unbelievable 53 months, much longer than shallow-water octopuses (1–3 months) and in fact the longest recorded egg-brooding period for any animal (Robison & al. 2014)! Note that octopuses, like parrots, primates, and elephants, also have a flat »face« and a vertical »forehead« (*Fig. 19*). And finally, consider that all cephalopods are capable of instantaneous color change to reflect outwardly their internal »mood«, the expression of which implies a higher (especially for a mollusc!) cognitive ability. Of course, there are many differences, too, between cephalopods and parrots, but that doesn't diminish the remarkable suite of morphodynamic convergent features displayed by these vastly distantly related taxa separated by perhaps over 100 million years of evolution.

Conclusions

As I hope to have shown, there exists a remarkable number of congruencies between parrots and humans, such as paedomorphic/juvenile morphology (especially head shape), similar developmental trajectory (e.g., brain development), delayed maturity, vocal learning, vocal babbling in nestlings, intelligence and cognition, proclivity to learn throughout a lifetime, expressions of »selfless« (i.e., unrewarded) behavior (in African Gray Parrots; Brucks & von Bayern 2020), lifelong social bonds and the semblance of »personalities«, extended longevity, advanced degree of prehensility, and even position within respective phylogenies. Examined in isolation, these convergences are notable and have inspired researchers to remark that »parrots are the most human of birds« and that »the bulk of scientific studies on parrots point to (…) evolutionary parallels with humans« (Toft & Wright 2015: 262). However, the sheer number of parallels points beyond mere coincidence to questions about the broader context of evolutionary dynamics. What is at work in evolution to generate such remarkable convergences between these two groups? Are random mutation and natural selection adequate to generate such suites of covarying similarities? Evidently, these phenomena implore us to consider the parallel expression of similar dynamic evolutionary trajectories, as articulated by Lockley & Jackson's (2008) notion of convergent morphodynamics, discussed under »Methods«. Thus, evolution is not only the result of the organism's cumulative response and accommodation to shifting *external* conditions of the environment but also to the *internal* integration and coherence of dynamic interacting anatomical, morphological, behavioral, and developmental processes, which can be expressed similarly in disparate life forms (for example, among unrelated mammals: Schad 1977, 2020 and Riegner 1998; or color pattern among distantly related birds: Riegner 2008).

In conclusion, our strong fascination with parrots, and the close association between these birds and ourselves, especially in regard to the worldwide keeping of parrots as pets (or today called »companions«), is that we see a striking reflection of ourselves in these remarkable birds. »It is inevitable that people should see in these birds a familiar presence, a distorted mirror image of themselves« (Bond & Diamond 2019: 6). Not only can they learn to speak to us verbally, they speak to our subconsciousness, to the resonance of a shared bond that grows out of similar evolutionary trajectories. In a certain sense, perhaps even more so than monkeys and apes, parrots embody humanlike features and offer us the opportunity to learn about ourselves. Tragically, however, our relationship with parrots is not without consequences. A number of species have declined precipitously due to the illegal collection of wild birds for the pet trade (Pruett-Jones 2021), and the fragmentation of habitat and loss of forest due to large-scale agriculture and logging have also taken their toll on populations of wild parrots (Forshaw 2017; *Fig. 20*). By cultivating an appreciation of their unique constellation of attributes, such as through various studies and perhaps your own observations, and by informing oneself of the plight of particular species and supporting conservation initiatives, we can work to ensure a future for these most humanlike birds.

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Fig. 20: A pair of critically endangered Blue-throated Macaws (*Ara glaucogularis*) at an artificial nest box in central Bolivia. With probably no more than 400 individuals in the wild, it is one of the rarest birds in the world. (Photo: Micah Riegner; Laney Rickman Nature Reserve, Beni Department, Bolivia)

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