

*Chapter 2*

**NICHE CONSTRUCTION AND  
DEVELOPMENTAL BIAS IN CHIMPANZEES  
AND GORILLAS**

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## ABSTRACT

Examining the environment as a background condition for the vast degree of behavioural diversity observed within the clade of African apes has proven insufficient in explaining some of the most interesting and salient differences among our closest living relatives. In this review, we apply the framework of the Extended Evolutionary Synthesis to examine the relationship between great apes and their environments. We cite examples of wild chimpanzees and gorillas modifying their environments in ways that systematically influence selection pressures acting on current populations and their descendants. We also compare potential developmental biases within populations to determine if some kinds of variation may be more common than others and could therefore play a role in driving evolutionary change. Our aim is not only to broaden the consideration of niche construction to include great apes, but also to identify the “ecological legacies” that these species may bequest to future generations that facilitate scaffolding of complex skills.

**Keywords:** great ape, ecology, culture, learning, social inheritance

## INTRODUCTION

Understanding the immense variation across hominids in sociality and in technological skills has proven a formidable challenge for biological anthropologists. Research into both of these topics traditionally proceeds by considering the environment as a background condition for the vast degree of behavioural diversity observed within the clade of African apes. However, this approach has proven insufficient in explaining some of the most interesting and salient differences among our closest living relatives. In this study, we invoke the framework of the Extended Evolutionary Synthesis (EES) to examine the relationship between great apes and their environments and also the potential role of developmental bias. More specifically, we review field observations of sympatric chimpanzees (*Pan troglodytes troglodytes*) and western lowland gorillas (*Gorilla gorilla gorilla*) in the Goualougo Triangle of northern Republic of Congo to identify how these apes change their social and physical environments in

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ways that may systematically influence selection pressures acting on current populations and their descendants. We hypothesize that complex technical behaviours (such as tool-assisted foraging) modify the environment and generate “ecological legacies” that could help novice tool users to acquire technological skills. This may be a factor contributing to the maintenance of complex tool use of chimpanzees in this region over generations. We further hypothesize that both chimpanzees and gorillas dynamically adjust their social behaviour and patterns of association to functionally influence their social environment and that of conspecifics.

### **Extended Evolutionary Synthesis: A Broader View of Evolutionary Processes**

The EES highlights extragenetic influences that may contribute to inheritance (Gilbert, Opitz, & Raff, 1996; Pigliucci & Müller, 2010; Laland et al., 2014, 2015). While retaining fundamental tenets of evolutionary theory, the EES emphasizes the role of organismal agency and reciprocal pathways of causation in evolutionary changes. It provides a framework that includes not only the evolutionary processes that directly affect gene frequencies, but also those that bias the outcome of natural selection, as appears in Figure 1 (Laland et al., 2015).

Niche construction and developmental bias are two forces proposed to shape the direction and rate of evolution. “Niche construction” can be defined as the “process whereby the metabolism, activities and choices of organisms modify or stabilize environmental states, and thereby affect selection acting on themselves and other species” (Laland et al., 2015). Rather than taking the environment as the background condition that generates one-way selective pressure on organisms, the EES emphasizes how organisms make nonrandom modifications to environmental states and thus generate the very selective pressures to which they are subject (Odling-Smee, Laland, & Feldman 2003). Over multiple generations, these processes can facilitate long-term stability of environmental conditions and enhance the complementarity of organisms and their environments

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(Laland, 2015; Laland et al., 2015). “Developmental bias” includes processes that “systematically channel the generation of phenotypic variants along certain pathways, and thereby bias the direction and rate of evolution by, in part, determining the variants that are subject to selection”

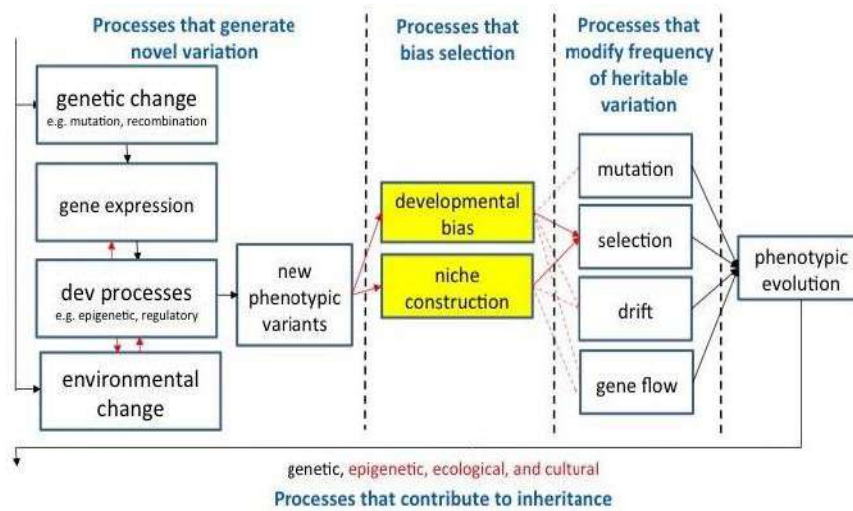


Figure 1. The structure of the EES. Adapted from “The Extended Evolutionary Synthesis: Its Structure, Assumptions and Predictions” by K. N. Laland, T. Uller, M. W. Feldman, K. Sterelny, G. B. Muller, A. Moczek, E. Jablonka, and J. Odling-Smee, (2015), *Proceedings of the Royal Society B*, 282 (1813), 20151019 p. 8. Copyright 2015 by Royal Society Publishing. Open access. Retrieved from <https://royalsocietypublishing.org/doi/full/10.1098/rspb.2015.1019>.

(Laland, 2015). These processes may involve the interaction of numerous biological, social, and environmental forces that effectively bias the expression and retention of specific phenotypes. Many of the best-known examples emphasize the role of developmental bias as a constraint on how different aspects of physical development can proceed (Maynard-Smith et al., 1985), or on what variants of body form are likely to evolve (Arthur, 2011). However, developmental bias may be essential in the generation of adaptive variants, and may even be pervasive across taxa (Laland, 2015; Uller et al., 2018). Further, developmental bias could play an important role not only for morphological features (e.g., the number of limbs), but also for the acquisition of learned behaviours (Laland et al., 2015). A

fundamental component of this process is “ecological inheritance.” This refers to the way environmental changes can accumulate, comprising a nongenetic legacy that is passed to, and can shape, the actions and development of descendant organisms as well as other species (Odling-Smee et al., 2003; Erwin, 2008).

Extended from ecological niche theory (Odling-Smee, Laland, & Felding, 1996; Laland, Olding-Smee, & Felding, 2000), the “social niche” is the set of social conditions required for species-typical social organization and structure as shaped by interactions and/or associations with conspecifics across multiple, overlapping social networks (Flack et al., 2006; Bergmüller & Taborsky, 2010). Therefore, “social niche construction” is the process by which individuals, dyads of individuals, or collective units “influence the composition and dynamics of their social environment” (Saltz et al., 2016). Social niche construction has the potential to positively affect the niche constructor(s) and their offspring’s abilities to adapt under various social pressures (Lipatov, Brown, & Feldman, 2011; Saltz et al., 2016). The flexible expression of social behaviour in response to local social or environmental pressures could confer numerous evolutionary advantages. For example, dynamic maintenance of social relationships could facilitate or improve transmission of information, access to social and ecological resources (e.g., coalition partners, consortships, food, sleeping sites), and the ability to navigate power structures (e.g., dominance hierarchies) (Flack 2012; Malone, Fuentes, & White, 2012).

## **Ecological Inheritance**

### *Nest Construction*

Each evening, great apes construct sleeping platforms. The proposed functions of these nests include decreasing the risk of predation, reducing exposure to disease, increasing thermoregulation, and improving sleep quality (Baldwin et al., 1981; Fruth & Hohmann, 1996; McGrew, 2004; Fruth, Tagg, & Stewart, 2018). Ape nests may be detectable for only a few

days to several years, depending on nest construction type, materials used, and rainfall. These nests have lasting impacts on the environment and possibly the ecology of future generations of apes as they comprise identifiable traces of ape presence and can facilitate the germination of ape foods. The specific vegetative structures (wooden basins created by interwoven twigs and branches, or leafy beds fashioned from herb stalks) of ape nests are highly salient in the environment and indicate ape residency and possibly even density in an area. Further, there is evidence that ground nest construction by gorillas facilitates the growth of seeds that are deposited in the nests within gorilla faecal deposits. Habitat choice can affect seedling development rates, which were found to be two to ten times higher within nests in open canopy forest versus other conditions (Haurez et al., 2015). Choices of habitat for nesting and foraging may also systematically channel the generation of phenotypic variants along certain pathways. Through nest building, apes can alter their environments in ways that influence evolutionary processes (Figure 2).



Figure 2. Nest construction as an organism-induced change in the environment.

### *Tool Sites*

All studied chimpanzee populations exhibit some form of tool-using behaviour (McGrew, 1992; Shumaker, Walkup, & Beck, 2011). However,

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there is variation in the size and complexity of their tool-using repertoires (Sanz & Morgan, 2007; Sanz & Morgan, 2010). Some chimpanzee communities rarely exhibit few tool behaviours, whereas others show diverse tool repertoires. In addition to ecological variables, social learning is proposed to influence the immense intraspecific variation observed among chimpanzees in tool-assisted foraging (e.g., McGrew, Tutin, & Baldwin, 1979; Whiten et al., 2001). Some of the physical impacts of tool use on the environment are detectable to subsequent visitors to the tool site. These environmental changes and tool traces could facilitate social learning through local enhancement and stimulus enhancement. Selection of particular types of plant materials for tool making, transport of these tool materials to a tool-using site, and leaving these tools inserted in the soil could also promote the increased availability of suitable tool materials for future tool users. In sum, we suggest that tool-use sites may include a variety of organism-induced changes in the environment (see Figure 3).

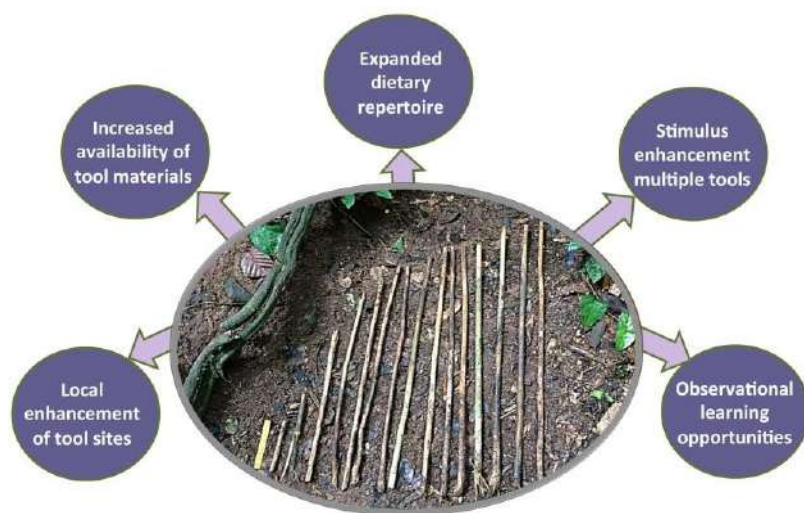


Figure 3. Tool-use sites as an organism-induced change in the environment.

Tool locations may be revisited over years by generations of chimpanzees, as has been shown at nut-cracking sites in West Africa with

archeological evidence dating back to 4,000 years (Mercader et al., 2007). Tool behaviours differ in the types of locations targeted and types of tools used, which means that tasks differ in their potential ecological legacies. While tools made from perishable materials (herbs, twigs, branches) are not amenable to long-term preservation, these materials and their changes in the environment are detectable and may provide important information to subsequent tool users over several days to months (depending upon the tool material and target location). Chimpanzees in Central Africa have some of the most diverse and complex tool-using behaviours documented among the animal kingdom (Sanz & Morgan, 2007). Our observations indicate that niche construction and developmental bias may facilitate such diverse and complex tool behaviors.

## **Social Niche Construction**

### *Chimpanzees*

Chimpanzee social organization is generally characterized by male philopatry, female emigration, minimal spatial-temporal cohesion across a larger community (which in total may be comprised of 20 to over 140 individuals; McGrew et al., 2004; Watts & Mitani, 2001), and fission-fusion social dynamics, which involves flexible formation of smaller foraging parties of variable membership (Boesch & Boesch-Achermann, 2000; Lehmann & Boesch, 2004). However, community social structure and party composition vary in relation to social and ecological variables (reviewed by Malone et al., 2012). Proponents of traditional socioecological models have attempted to identify rules for species-wide responses to ecological factors or competitive regimes, with varying degrees of success (van Schaik & van Hooff, 1983; c.f., Strier, 1994; Thierry, 2008). In contrast, a social niche construction framework considers how group members may preferentially select with whom and where to spend their time, and how this flexibility could facilitate adaptive responses to immediate environmental (e.g., food resource distribution) and social pressures (e.g., dominance instability, mating opportunities).

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Flexibility in constructing one's social niche likely enables individuals to maximize opportunities (i.e., for socializing, feeding, or mating) not only across variable settings, but also over the lifespan. For example, female chimpanzees immigrating to a new community often remain in the peripheral edges of the community range, occupy low dominance status, and persist in low-quality core areas. Developing affiliative relationships with more established residents is critical to integrating into a new community. Relative to the gradual socialization process in one's natal group during development, immigrant females must abruptly establish and maintain social relationships with potentially long-lasting consequences. For example, an immigrant female's reproductive success might partially depend on her ability to outcompete resident females to establish high-quality core areas and mating opportunities (Thompson et al., 2007). Forming social relationships with males also could be necessary to secure support in such conflicts with resident females (Kahlenberg, Thompson, & Wrangham, 2008). Formation of high-quality relationships with individuals of both sexes could also provide immigrant females, and their offspring in future years, with not only access to food resources and mating opportunities, but also information about the social customs specific to that group. Furthermore, a chimpanzee's social skills may reflect the social dynamics and opportunities that she was exposed to during ontogeny, largely via her mother's social niche. These considerations highlight an intergenerational component of social niche construction both in the development of social skills and in the construction of one's own social niche.

The termite-gathering context provides an example of one setting in which chimpanzees may moderate the frequency, duration, and context in which they associate with particular conspecifics (e.g., Aureli et al., 2008). Social tolerance in close proximity has been hypothesized to aid in facilitating the transfer of information among conspecifics (Coussi-Korbel & Frigaszy, 1995; van Schaik et al., 2003), thereby sustaining complex tool-using behaviours in a population (van Schaik & Pradhan, 2003; Sanz & Morgan, 2013). Selective association among conspecifics who share highly tolerant relationships could enable foraging in close proximity on

this high-quality resource (Fraser, Schino, & Aureli, 2008; Massen & Koski, 2014) and also facilitate the overlap in space and time that is necessary for social transmission of complex foraging skills. This may promote the horizontal transmission of information among peers, such as from immigrant subadults who can introduce new tool variants into a community (O'Malley et al., 2012). In addition, maternal choices of social associates in tool contexts could shape the social environment in which immature chimpanzees learn to use tools. Chimpanzees plan their tool use (Byrne, Sanz, & Morgan, 2013) and thus they could similarly be capable of planning with whom they use tools.

### *Gorillas*

Variation in the social organization of gorillas is influenced by predation pressure, food availability, reproductive opportunities, and other socioecological variables (Doran & McNeilage, 1998; Harcourt & Stewart, 2007). Understanding the characteristics of social systems such as group stability, structure, and composition can aid in clarifying the roles that these factors play in the social niche construction of gorillas. Group stability influences an individual's ability to make accurate predictions about outcomes of inter- and intragroup social interactions (Sascher, Durschlag, & Hirzel, 1998). Instability in a social system leads to pressures at both the individual and group level, which may have broader implications for sociality, health, and fitness.

Flexibility in constructing one's social niche likely enables individuals to maximize opportunities across variable settings and over the lifespan. Young adult male western lowland gorillas who emigrate have been found to remain in the vicinity of male kin, forming "neighbourhoods" where related males live close together. This creates a network of independent groups in which an individual may encounter a dispersed relative in another group during an intergroup encounter (Bradley et al., 2004; Forcina et al., 2019). Such extended male networks may aid younger males by providing opportunities to identify and attract reproducing females from other groups. As the potential competitors might be kin or a familiar individual, it has been suggested that associating within these

neighbourhoods may serve to decrease aggression during intergroup encounters (Bradley et al., 2004). Additionally, these extended male networks may provide support against peripheral silverbacks or solitary males who attempt to encroach on resources.

Intergroup encounters provide a window into how social niche construction can impact group dynamics in gorillas, with broader implications for individual fitness and population viability. Variability within and between gorilla populations is expected to influence the relative roles of resource and mate defense during encounters between groups of conspecifics and, consequently, the nature of intergroup encounters (Sicotte, 1993; Tutin, 1996; Bermejo, 2004; Bradley et al., 2004; Doran-Sheehy et al., 2004). Behaviours exhibited by individuals before and during intergroup encounters are expected to vary depending on group composition, familiarity of peripheral individuals, and age and size of the dominant silverback (Harcourt, 1978; Yamagiwa, 1987, Sicotte, 1993). Male gorillas typically engage in more frequent and intense aggressive interactions than females (Cavigelli & Caruso, 2015). Conversely, silverback males also may influence the composition and dynamics of their social environment by opting to not engage in encounters with peripheral males or family groups by avoiding other groups altogether. This could serve to reduce the likelihood of female transfer between groups and also the risk of infanticide.

Western lowland gorillas also may alter the rate, duration, and setting in which they encounter conspecifics through choices in foraging location and ranging. Western lowland gorillas are predominately folivorous, but they preferentially and opportunistically feed on fruits when available even if this requires additional travel to these ephemeral resources. Longer daily path lengths elevate the likelihood of interactions with conspecifics, thus potentially providing knowledge about peripheral individuals and increasing the likelihood of information transfer during interactions. We propose that gorillas are capable of altering their social niche in ways that may bias the direction and rate of evolution.

## **Interaction of Niche Construction and Developmental Bias**

Recent studies on ape nest building, tool sites, and habitat use prompt reconsideration of the relationship between apes, their environments, and the forces that generate behavioural variation. In this study, we review and synthesize our observations of African apes systematically changing their physical and social environments in ways that influence evolutionary processes. We examine these processes among Central chimpanzees and western lowland gorillas, which reside in sympatry throughout much of the Congo Basin. These species show a relatively high degree of dietary overlap and have been observed to co-feed on several food resources (Morgan & Sanz, 2006; Walsh et al., 2007). Their nesting behaviors also overlap, which has historically been an obstacle for efforts to precisely monitor these species through indirect traces. Odling-Smee et al. (2003) suggest that failure to detect character displacement in closely related sympatric species provides an opportunity to investigate whether there is evidence for organism-driven modification of the selective environment. The complex tool use exhibited by chimpanzees who are sympatric with gorillas, for example, could be a form of niche construction that facilitates access to high-quality food, expands the dietary repertoire, and reduces feeding competition. Here, we review the means by which chimpanzees and gorillas may modify their environments in flexible, dynamic ways to construct their ecological and social niches. We also consider how social niche construction may influence an individual's development in the social realm, and then use this information to address long-standing debates about the evolutionary forces involved in the emergence and maintenance of ape material culture.

## **METHODS**

This research was conducted in the Nouabalé-Ndoki National Park (2°05'–3°03'N, 16°51'–16°56' E), Republic of Congo. The Goualougo Triangle study area is part of the Sangha River Tri-National Protected Area

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Complex, which comprises 7,000 km<sup>2</sup> of contiguous forest spanning national parks and reserves across Republic of Congo, Cameroon, and Central African Republic. The Goualougo Triangle encompasses 380 km<sup>2</sup> of lowland forest with altitudes between 330 m and 600 m. The climate can be described as transitional between the Congo-equatorial and subequatorial climatic zones.

Direct observations of chimpanzees and gorillas in the Goualougo Triangle have been ongoing since February 1999. The main study group of chimpanzees is the Moto community, which at the time of this study consisted of 71 individuals, including 12 adult males and 24 adult females. Since 2013, a group of gorillas within the Moto chimpanzee community range has been habituated to researcher presence. The Loya gorilla group consisted of a dominant silverback, two females, a blackback, a juvenile male, and two infants during the time of this study. During daily follows of chimpanzee parties and the focal gorilla group, observers recorded location, forest type, group composition, activity patterns, feeding observations, and interactions between species.

Remote video recording devices with passive infrared sensors were used to determine chimpanzee and gorilla visitation at 12 fruiting trees over 46 months and 32 tool sites over 60 months. Detection of movement by the sensor caused the camera to record for 2-minute intervals until triggers ceased (Sanz, Morgan, & Gulick, 2004). Video footage was archived and converted to MPEG format for review, after which we coded videos using INTERACT software (Mangold, 2015). The footage was screened for time that large mammals were present.

We surveyed all ape nests encountered along systematically spaced line transects across the study area. We recorded nests of all ages during the first passage of all transects, but only fresh and recent nests were subsequently monitored for nest decay and used for survival rate analyses during subsequent passages (Morgan et al., 2016). We recorded the age class of the nest (fresh, recent, old, very old) during each passage following Tutin and Fernandez (1984). We designated each nest as built by chimpanzee or gorilla based on the presence of faeces, shed hair, odour, or other signs. We classified any nest without associated evidence of which

ape species built it as great ape, and later attributed each to either gorillas or chimpanzees using a logistic regression model based on a set of explanatory variables associated with known gorilla and chimpanzee nests detected in this study (Sanz et al., 2007; Stokes et al., 2010).

## RESULTS

### Ecological Inheritance

#### *Habitat Choice*

Gorillas and chimpanzees overlap in several types of habitats, including mixed-species forest, monodominant *Gilbertiodendron* forest, and swamp forest (Morgan et al., 2006). Each species shows preferences in using some types of habitats to a higher degree than the habitat's overall representation across their range (Morgan et al., 2006). Within these habitats, they consume many of the same foods (67% overlap in food species consumed), but differ in the importance of specific foods in their diets. This can be directly observed in their biased visitation to food resources. As shown in Figure 4, we observed that gorillas frequented particular fruiting tree species more often than chimpanzees.

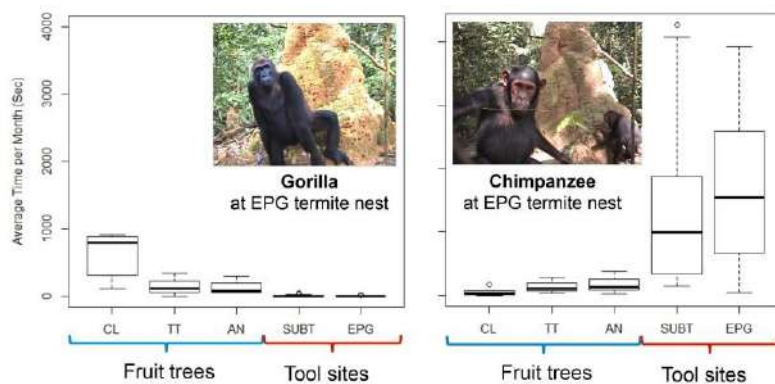


Figure 4. Habitat choice as developmental bias between chimpanzees and gorillas. Fruit trees included are CL = *Gambeya lacourtiana*, TT = *Tetrapleura tetraptera*, and AN = *Anonidium mannii*. Insect resources are SUBT = subterranean termite nests and EPG = epigeal termite nests.

Similarly, we rarely observed gorillas at *Macrotermes* nests, which chimpanzees frequented. Spending time at tool-using locations increases exposure to tools and tool users, which may directly and indirectly bias the interest of other individuals toward those localities and objects.

### *Nesting Behaviour*

We surveyed a total of 4,703 gorilla nests and 7,764 chimpanzee nests during transect surveys across the study area (Morgan et al. 2006, 2016, 2018). Survival analysis was conducted on a subset of 1,035 fresh and recent nests and yielded a mean longevity of 146.4 days (Morgan et al., 2018). Most gorilla nests were constructed on the ground (60.7%), whereas chimpanzee nests were nearly all arboreal (99.8%). Gorillas constructed nearly half of their nests from terrestrial herbaceous vegetation (47.7%), and 92% of these nests were associated with gorilla faeces. In a study of gorilla feeding ecology, we reported that 79.9% of gorilla faeces ( $n = 631$ ) contained remains of at least one fruit item (Morgan & Sanz, 2006). The average number of fruits per fecal sample was  $1.63 \pm 1.42$ , with up to eight species of fruit documented in a single faecal specimen. Other studies have shown that seeds deposited within gorilla nests have a higher chance of germinating, which would promote the growth of foods consumed by gorillas in particular habitats and areas of their home range (Petre et al., 2013; Haurez, Brostaux et al., 2015, Haurez, Dainou et al., 2015).

### *Tool Sites*

Within the Goualougo Triangle chimpanzee population, termite fishing takes place at earthen nests of *Macrotermes* spp. (Sanz et al., 2004). Chimpanzees manufacture probes from particular species of herbs by removing a stalk from a stand of herb stems and then removing the large leaf at the end of the stem. The tip of the herb stem is then pulled through the chimpanzee's teeth to create a brush tip, which has been shown to increase this type of tool's efficiency in gathering termites (Sanz, Call, & Morgan, 2009). In surveying such tool-use sites, we recovered an average of 3.0 fishing probes (685 sites, range = 1, 30) at epigeal (above-ground) termite nests. Subterranean termite nests were associated with a similar

number of fishing probes, but also included 4.1 puncturing sticks on average (94 sites, range = 1, 32). Puncturing sticks serve a different function than do fishing probes; they are inserted into the nest to create an access tunnel for the fishing probe. The chimpanzees' fishing and puncturing tools increase the saliency of these sites within the forest, as the tools are detached and modified, and represent a homogeneous assemblage of materials.

Both fishing probes and puncturing sticks accumulate with site visitations, as chimpanzees bring new probes (observed in 81% of tool using bouts) when they arrive to gather termites. They were observed reusing probes at the site in 10% of tool-using bouts and manufacturing fishing probes at the site in 9% of occasions. In contrast to the herbaceous fishing probes, which decay within days, wooden puncturing tools are durable and can be effective for months after manufacture. As such, it is common for chimpanzees to reuse puncturing tools deposited by other individuals during previous visits, and we documented reuse in 39% of bouts. Transport of new puncturing tools was observed in 57% of bouts, and tool manufacture at the nest in 4% of bouts. Chimpanzees sometimes left puncturing tools inserted in the termite nest matrix, which resulted in the growth of a sapling of the tool material plant species at the tool site.

We also identified and recovered tool assemblages from sites where chimpanzees had used saplings to perforate ant nests and herb wands to gather the insects. The use of a tool set to harvest army ants had not previously been documented in wild chimpanzees, but was indicated by tool assemblages at ant nests and then confirmed by direct observations (Sanz, Schoning, & Morgan, 2010). We found tool sets to perforate and dip for ants at 36% of tool sites (3.7 ant gathering tools per site,  $n = 284$  sites, range = 1, 18 tools).

While the tool repertoire of the Goualougo Triangle chimpanzee population comprises more than 20 different types of tools, not all of these leave detectable traces (Meulman et al., 2012). We thus suggest that tool use in arboreal settings may not provide as many avenues for either immediate (such as stimulus enhancement) or long-term social facilitation through ecological legacies as is the case with terrestrial tool use.

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Consistent with this prediction, we recovered relatively small tool assemblages from bee hives where chimpanzees had used wooden clubs to access honey (2.1 tools recovered, 14 sites, range = 1, 5).

## **Social Niches**

### *Chimpanzees*

We have previously documented variation in average foraging party size among Goualougo Triangle chimpanzees. Across contexts, average party size was  $4.47 \pm 1.47$  individuals. Parties in the termite-gathering context are intermediately sized ( $2.23 \pm 1.57$ ) relative to the larger parties observed for chimpanzees feeding on fruit, leaves, or flowers and the smaller parties observed in the context of feeding on meat, bark, or pith (Sanz & Morgan, 2013). This flexibility in social grouping may reflect the differing priorities and opportunities across settings. For example, in the termite-gathering setting, mother-offspring parties and parties that contain at least some immatures (e.g., multiple mother-infant dyads) are more commonly observed than mixed-sex parties (Sanz & Morgan, 2013). Smaller parties that comprise close social associates could be more amenable to foraging in close proximity. In addition, it could also allow for safe exploratory behavior by immature chimpanzees, while maximizing opportunity for vertical and oblique transmission of technical skills between mothers or other skilled adults to immature chimpanzees. Nonetheless, we also routinely observed that even among adult and subadult peers, individuals in the termite-gathering setting often use tools in close proximity to other individuals and observe each other's tool use, providing opportunities for horizontal transmission.

The termite-gathering setting is instructive for understanding how social niche construction may influence individual feeding ecology and degree of technical specialization. For example, in remote video footage, we have observed that there may be differences in how often or for how long particular individuals visit specific termite-gathering localities. For females, such preferences could influence the termite-gathering behaviour

of their offspring as adults, generating characteristic patterns of mother-infant similarity (Laland et al., 2015). Anecdotally, we also observed that particular means of facilitation could be socially inherited. An orphaned subadult female, when younger, was the frequent recipient of tool transfers from her mother; these tool transfers function as a form of teaching (Musgrave et al., 2016). A younger male chimpanzee who was also orphaned, as an infant, began to extensively associate with this orphan female and routinely gathered termites with her. We have since documented tool transfers from this orphan female to the younger orphan male, including observations of multiple transfers of newly manufactured fishing probes in the same visit. Therefore an individual's social niche may impact tool-using behaviour as well as the modes of intergenerational transmission of these learned behaviours.

### *Gorillas*

Gorillas tend to have a stable social system, yet the composition of gorilla groups differs between species. Maximum group size in mountain gorillas (*Gorilla beringei*) has been observed to exceed 20 individuals, while western lowland gorilla groups are typically observed in groups smaller than 20 individuals (Yamagiwa, Kahewa, & Basabose, 2003). Gorillas reside in one of three group structures: a family group consisting of one or more silverbacks, females, and their offspring; a bachelor group where there are multiple nonbreeding males; or a solitary silverback who has either left his natal group or departed a bachelor group. Mountain gorilla groups often include multiple silverbacks, with one of the males being dominant over the other silverbacks (Robbins, 1999). Western lowland gorillas live in groups with one silverback who is solely responsible for protecting resources. This dominant male may experience increased pressure (and thus increased stress), even though younger subordinate males may participate in mate and resource guarding (Bradley et al., 2004). Dominance and longer tenure lengths are correlated with reproductive success for males. However, the costs associated with sex and social position for single versus multimale groups remain to be assessed.

In gorillas, both males and females disperse upon reaching sexual maturity. Silverback males show less tolerance toward adolescent males as they mature and will expel younger individuals before they reach silverback status (between 10 and 15 years). Mountain gorilla males approaching silverback status are more likely to remain in their natal group and assist in group protection efforts, whereas western lowland gorillas almost always disperse from the natal group but may remain in its vicinity. Variability in male coalitions suggests that gorillas may have species-specific adaptations with regard to social organization, but the specific selective pressures and adaptive advantages remain to be determined.

## **DISCUSSION**

The EES framework provides a way to understand how extragenetic inheritance may facilitate information transfer across multiple generations. This study aimed to summarize and synthesize our observations of chimpanzees and gorillas in the Goualougo Triangle, so as to determine the extent to which these apes may bias the selection pressures they face through various forms of ecological and social niche construction. In the ecological realm, we cite evidence of habitat choice, which may channel the generation of phenotypic variants along certain pathways. Nest construction and tool-use sites provide evidence of niche construction among apes, resulting in nonrandom modifications to the environment in advantageous ways (e.g., growth of tools or germination of preferred foods). Furthermore, flexibly adaptive social niches may have intergenerational effects and be associated with specific types of advantageous interactions in certain settings (e.g., tolerance in termite gathering, tolerant interactions between gorilla groups). In addition to broadening consideration of niche construction to include specific examples from great apes, we have also highlighted the “ecological legacies” that these species may bequest to future generations and their potential adaptive significance.

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## Ecological Inheritance and Task Complexity

Ecological legacies have the potential to facilitate scaffolding of skill acquisition and task complexity. Within the tool kit of the chimpanzees in the Goulougo Triangle, there may be a positive relationship between complexity of a task and the amount of information that learners inherit via the environment (see Figure 5). By inventorying the tools at different types of tool sites, we have found that there are differences in the nonrandom modifications of environmental states associated with different tool tasks that may vary in how much they facilitate ecological inheritance. For example, gathering of subterranean termites requires different types of tools, the most specific tool materials, and particular tool-using techniques.

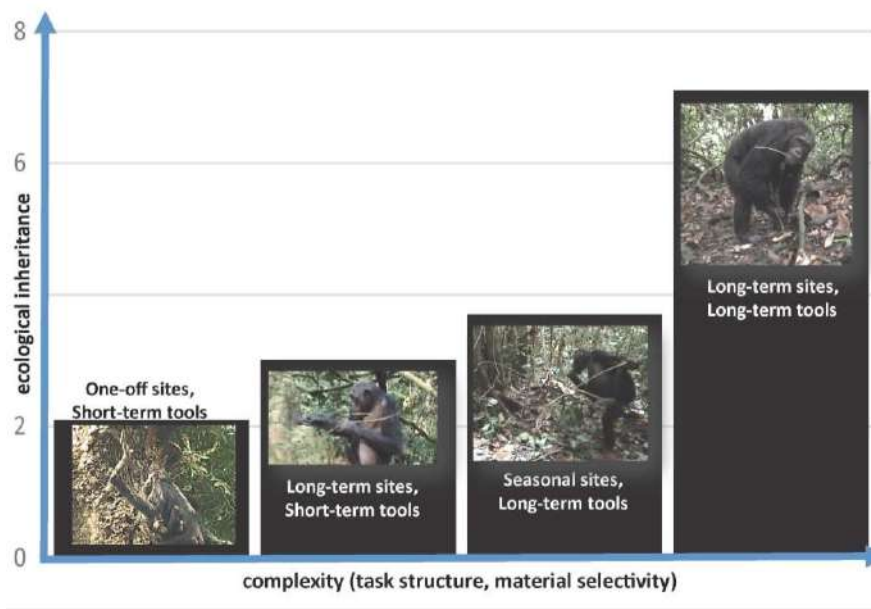


Figure 5. Relationship between ecological inheritance and tool complexity. The vertical axis indicates average number of tools recovered in tool sites. One-off sites with short-term tools are represented by honey gathering. Long-term sites with short-term tools are represented by gathering of insects at epigeal termite nests. Seasonal sites, with long-term tools include ant gathering behaviour observed within the Goulougo Triangle, Republic of Congo. Long-term sites with long-term tools are represented by gathering of insects at subterranean termite nests.

Chimpanzees revisit subterranean tool sites where changes in the nest substrate, accumulation of tools, and possible intersection with conspecifics may facilitate the maintenance of these particular foraging skills. Intergroup encounters among gorillas may also facilitate opportunities to maintain knowledge or transfer skills among individuals, with the degree of tolerance related to the type of information gained or exchanged between individuals (Forcina et al., 2019).

### **Variation in Ecological Inheritance**

Despite adequate ecological opportunities for niche construction, habitat choice and social structure may intervene to amplify or reduce the likelihood of expression of tool behaviors across a landscape. Ecological inheritances were influenced by proximate factors such as the longevity of the tool site and perishability of the materials. Further, target resources (e.g., insect prey, honey, or water) differ in whether they can be repeatedly exploited and in the rate at which previously deposited tools are encountered. In addition to the goal-directed nature of the tool use itself, this variation highlights the non-random nature of the landscape modifications that chimpanzees impose through enactment of their tool traditions. An emerging field of research focuses on the “archeology of the perishable,” which examines not only the form and material of stone tools, but also the rich diversity of tools made from perishable materials and environmental traces of gathering materials on the landscape (Pascual-Garrido, 2018).

A key insight of the EES, and one of its principal emphases in contrast to the traditional evolutionary approach revolves around the important role of the organism in directing modifications of the physical or social environment and the impact these modifications can have in canalizing the development of future generations. One of the most important components of chimpanzee tool sites as constructed environments is the accumulation of tools, particularly at subterranean termite mounds. In the subterranean termite nest setting, the robust wooden puncturing tools used by

chimpanzees to create puncturing tunnels are the frequent targets of infant attention. So, too, are the brush-tipped fishing probes used to gather termites, which illustrates that the use of these objects as tools likely influences their perception by young tool users. Herbaceous material is often present in proximity to tool sites, but manufactured tools differ from these raw materials in that they have been selected by conspecifics and are often modified from their original form (e.g., as an attached herb stalk) (Fragaszy et al., 2013). Brush-tipped fishing probes are emblematic of how such raw material is transformed. While a number of species with suitable flexibility and diameter exist in the environment and can be used successfully to gather termites, we have found that chimpanzee infants rarely attempt to acquire other materials such as twigs or vines to fish for termites (Musgrave et al., forthcoming). Instead, they receive tools from conspecifics, or they use discarded fishing probes near the termite mounds. Depending on the age of the tool, these herb tools occasionally still exhibit a brush tip. The choices of past tool makers with respect to raw material selection and tool modifications thus scaffold the learning of novice learners. Younger generations of tool users go on to select the same species and to follow the same manufacturing template for these brush-tipped probes, as the prior generation.

Subterranean termite nests also illustrate how conspecifics' past tool-using actions scaffold novices' activities. Puncturing subterranean nests is a physically challenging task, the difficulty of which precludes infants and juveniles from capably puncturing new access tunnels. However, these youngsters nonetheless have the opportunity to explore, fish from, and practice puncturing at the tool sites created by others. We often have observed young chimpanzees inserting puncturing sticks into the tunnels created by older chimpanzees. As youngsters grow, they progress to using puncturing tools with greater aptitude in partially created tunnels or reopening old tunnels that have become partially filled in. Access to the tools and tool sites of competent tool users is thus the foundation for skill development in these settings when youngsters neither manufacture their own tools nor have the skill or strength to access the underground termite nest chambers independently. In addition to shaping the general skill

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development of young chimpanzees, this may also lead to parent-offspring similarity (Laland et al., 2015), as young chimpanzees are routinely exposed particularly to the technical variants or preferences of their mothers and their mothers' associates.

Undoubtedly, specific, tool-assisted foraging skills could have immediate fitness benefits, and here we have discussed niche construction and developmental bias as they may manifest in one specific tool context. For chimpanzees (and potentially many other species) more broadly, however, developmental bias likely supports flexible and powerful learning abilities that enable novices to acquire a range of skills, the exact nature of which is biased in part by the constructed niche in which they develop (Flynn et al., 2013; Frigaszy et al., 2013). Indeed, chimpanzees' flexibility and aptitude for learning a wide range of behaviours, rather than rigidly adhering to any particular foraging variant, intersects with ecological variation to produce the diverse foraging behaviours documented in different populations.

The intergenerational persistence of tool behaviours can lead to long-term environmental modifications, which in turn, could increase the accessibility of this information to novice learners. Further, by providing additional information than might otherwise be available via individual exploration or observation of others, ecological inheritance could accelerate learning and acquisition in ways that increase the likelihood that cumulative cultural variants will emerge, be maintained, and potentially be expanded upon (Fragaszy et al., 2013). A rich portfolio of behavioural variants could be a necessary precondition for the accelerating development of human cumulative cultural abilities, i.e., selection for enhanced social learning capacities is more likely if there are a substantial array of beneficial behaviours that can be learned, offsetting the associated costs of increased brain size, maternal investment, and extended life histories (Henrich, 2017). Thus, understanding how niche construction and developmental bias intersect to scaffold learning in our closest living relatives offers unique insights into the emergence of cultural behaviour in the hominin lineage.

## Insights and Future Directions

The framework of the EES and social niche construction in particular are well suited for examining the flexibility observed within great ape social systems. Social niche construction theory is parsimonious with many models of hominin brain, language, and sociocognitive expansion (Fuentes, 2018). Further, it is ideal for evolutionary modeling because it considers processes whereby emergent and self-reinforcing aspects of social systems can feedback to improve the constructor's fitness. Our consideration of social niche construction suggests a number of research directions that will aid in addressing long-standing questions about the evolution of social systems in hominids. For example, understanding the underlying mechanisms, or hierarchically structured simple rules, that entice individuals or groups to favour one (or more) flexible response(s) over others is an enduring pursuit within evolutionary biology (Aureli et al., 2008). Research on social niche construction in captive settings may provide useful comparative evidence for this endeavour, given captivity represents an independent suite of social and environment pressures through which individuals and groups persist. This may be of particular interest for chimpanzees, given the wide variety in observed social systems of captive chimpanzees (e.g., Cronin et al., 2014; Funkhouser et al., 2018) and the intriguing differences in social structure observed across contexts (e.g., Kanngiesser et al., 2011; Clark, 2011). Similarly, social niche construction may be useful in attempts to understand variation in the suitability and persistence of captive gorilla groups of certain compositions (e.g., Maestripieri, Ross, & Megna, 2002; Gartland et al., 2018).

Standardized approaches to identifying and comparing social niches have the potential to advance studies in comparative cognition on a number of topics, including understanding differences in hierarchical structure (across individuals, dyads, and groups); classifying relationships or individual's social roles; deciphering between relationships of certain types; and inferring evolutionary advantages of those relationships. More specifically, this approach could also aid in answering questions about the divergence of chimpanzee and bonobo social systems (Furuichi et al.,

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2015; Gruber & Clay, 2016). To operationalize models of social niches and their construction during ontogeny, we suggest that multidimensional social network analyses could be useful to simultaneously examine the effects of individuals, dyads, polyadic motifs, or ecological contexts on the network whole (Barrett, Henzi, & Lesseau, 2012; Flack, 2012; de Domenico et al., 2015; Smith-Aguilar et al., 2018).

Social niche construction may also provide important insights for understanding how populations face anthropogenic disturbance and conservation crises. Social niches are not expected to be uniformly affected by all individuals; rather, certain individuals are expected to have disproportionate effects on the social niches to which they belong (i.e., keystone individuals; Modlmeier et al., 2014). Investigating the flexibility with which social niches are reconstructed following the deterioration or removal of keystone individuals may assist conservationists in predicting and protecting the rate, flow, and direction of recuperative efforts (Morgan et al., 2006; Cameron et al., 2016). Simulations of social niche deterioration, fragmentation, and the suppression of cultural variation could further demonstrate the effects of human disturbance, logging, disease epidemics, or selective removals (e.g., poaching) on critically endangered primate populations (Junker et al., 2012; Morgan et al., 2018; Kühl et al., 2019).

## REFERENCES

- Arthur, W. (2011). *Evolution: A developmental approach*. Wiley-Blackwell, New York.
- Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., . . . van Schaik, C. P. (2008). Fission-fusion dynamics: new research frameworks. *Current Anthropology*, 49(4), 627–654.
- Baldwin, P. J., Sabater Pi, J., McGrew, W. C. & Tutin, C. E. G. (1981). Comparisons of nests made by different populations of chimpanzees (*Pan troglodytes*). *Primates*, 22(4), 474–486.

Complimentary Contributor Copy

- Barrett, L., Henzi, S. P. & Lusseau, D. (2012). Taking sociality seriously: The structure of multi-dimensional social networks as a source of information for individuals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1599), 2108–2118.
- Bergmüller, R. & Taborsky, M. (2010). Animal personality due to social niche specialisation. *Trends in Ecology & Evolution*, 25(9), 504–511.
- Bermejo, M. (2004). Home-range use and inter-group encounters in western gorillas (*Gorilla g. gorilla*) at Lossi Forest, North Congo. *American Journal of Primatology*, 64(2), 223–232.
- Boesch, C. & Boesch-Achermann, H. (2000). *The chimpanzees of the Tai Forest: Behavioural ecology and evolution*. Oxford University Press.
- Bradley, B. J., Doran-Sheehy, D. M., Lukas, D., Boesch, C. & Vigilant, L. (2004). Dispersed male networks in western gorillas. *Current Biology*, 14(6), 510–513.
- Byrne, R. W., Sanz, C. M. & Morgan, D. B. (2013). Chimpanzees plan their tool use. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology*, (pp. 48–64).
- Cameron, K. N., Reed, P., Morgan, D. B., Ondzié, A. I., Sanz, C. M., Kühl, H. S., . . . Mundry, R. (2016). Spatial and temporal dynamics of a mortality event among Central African great apes. *PloS One*, 11(5), e0154505.
- Cavigelli, S. & Caruso, M. (2015). Sex, social status and physiological stress in primates: The importance of social and glucocorticoid dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1669), 1–13.
- Clark, F. E. (2011). Space to choose: Network analysis of social preferences in a captive chimpanzee community, and implications for management. *American Journal of Primatology*, 73(8), 748–757.
- Coussi-Korbel, S. & Fragazy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour*, 50(6), 1441–1453.
- Cronin, K. A., Van Leeuwen, E. J., Vreeman, V. & Haun, D. B. (2014). Population-level variability in the social climates of four chimpanzee societies. *Evolution and Human Behavior*, 35(5), 389–396.

- de Domenico, M., Nicosia, V., Arenas, A. & Latora, V. (2015). Structural reducibility of multilayer networks. *Nature Communications*, 6, 6864.
- Doran, D. M. & McNeillage A. (1998). Gorilla ecology and behavior. *Evolutionary Anthropology*, 6(4), 120-131.
- Doran-Sheehy, D., Greer, D., Mongo, P. & Schwindt, D. (2004). Impact of ecological and social factors on ranging in western gorillas. *American Journal of Primatology*, 64(2), 207–222.
- Erwin, D. H. (2008). Macroevolution of ecosystem engineering, niche construction and diversity. *Trends in Ecology & Evolution*, 23(6), 304–310.
- Flack, J. C. (2012). Multiple time-scales and the developmental dynamics of social systems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1597), 1802–1810.
- Flack, J. C., Girvan, M., de Waal, F. B. & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature*, 439(7075), 426.
- Flynn, E. G., Laland, K. N., Kendal, R. L. & Kendal, J. R. (2013). Target article with commentaries: Developmental niche construction. *Developmental Science*, 16(2), 296-313.
- Forcina, G., Vallet, D., Le Gouar, P. J., Bernardo-Madrid, R., Illera, G., Molina-Vacas, G., . . . Vila, C. (2019). From groups to communities in western lowland gorillas. *Proceedings of the Royal Society B-Biological Sciences*, 286(1896), 20182019.
- Fragaszy, D. M., Biro, D., Eshchar, Y., Humle, T., Izar, P., Resende, B. & Visalberghi, E. (2013). The fourth dimension of tool use: Temporally enduring artifacts aid primates learning to use tools. *Philosophical Transactions of the Royal Society B*, 368(1630), 20120410.
- Fraser, O. N., Schino, G. & Aureli, F. (2008). Components of relationship quality in chimpanzees. *Ethology*, 114(9), 834–843.
- Fruth, B. & Hohmann, G. (1996). Nest building behavior in the great apes: The great leap forward? In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies*, (pp. 225–240). Cambridge, UK: Cambridge University Press.

- Fruth, B., Tagg, N. & Stewart, F. (2018). Sleep and nesting behavior in primates: A review. *American Journal of Physical Anthropology*, 166(3), 499–509.
- Fuentes, A. (2018). How humans and apes are different, and why it matters. *Journal of Anthropological Research*, 74(2), 151–167.
- Funkhouser, J. A., Mayhew, J. A., Sheeran, L. K., Mulcahy, J. B. & Li, J. H. (2018). Comparative investigations of social context-dependent dominance in captive chimpanzees (*Pan troglodytes*) and wild Tibetan macaques (*Macaca thibetana*). *Scientific Reports*, 8(1), 13909.
- Furuichi, T., Sanz, C., Koops, K., Sakamaki, T., Ryu, H., Tokuyama, N. & Morgan, D. (2015). Why do wild bonobos not use tools like chimpanzees do? *Behaviour*, 152(3–4), 425–460.
- Gartland, K., McDonald, M., Braccini Slade, S., White, F. & Sanz, C. (2018). Behavioral changes following alterations in the composition of a captive bachelor group of western lowland gorillas (*Gorilla gorilla gorilla*). *Zoo Biology*, 37(6), 391–398.
- Gilbert S. F., Opitz, J. & Raff, R. A. (1996). Resynthesizing evolutionary and developmental biology. *Developmental Biology*, 173(2), 357–372.
- Gruber, T. & Clay, Z. (2016). A comparison between bonobos and chimpanzees: A review and update. *Evolutionary Anthropology*, 25(5), 239–252.
- Harcourt, A. (1978). Strategies of emigration and transfer by primates, with particular reference to gorillas. *Zeitschrift für Tierpsychologie*, 48(4), 401–420.
- Harcourt, A. H. & Stewart K. J. (2007). *Gorilla society: Conflict, compromise, and cooperation between the sexes*. Chicago: University Of Chicago Press.
- Haurez, B., Brostaux, Y., Petre, C. & Doucet, J. (2015). Is the western lowland gorilla a good gardener? Evidence for directed dispersal in Southeast Gabon. *Bois et Forêts de tropiques*, 324(2), 39–50.
- Haurez, B., Dainou, K., Tagg, N., Petre, C. A. & Doucet, J. L. (2015). The role of great apes in seed dispersal of the tropical forest tree species *Dacryodes normandii* (Burseraceae) in Gabon. *Journal of Tropical Ecology*, 31(5), 395–402.

- Henrich, J. (2015). *The secret of our success: How culture is driving human evolution, domesticating our species, and making us smarter*. Princeton: Princeton University Press.
- Junker, J., Blake, S., Boesch, C., Campbell, G., Toit, L. D., Duvall, C., . . . Kühl, H. (2012). Recent decline in suitable environmental conditions for African great apes. *Diversity and Distributions*, 18(11), 1077–1091.
- Kahlenberg, S. M., Thompson, M. E. & Wrangham, R. W. (2008). Female competition over core areas in *Pan troglodytes schweinfurthii*, Kibale National Park, Uganda. *International Journal of Primatology*, 29(4), 931.
- Kanngiesser, P., Sueur, C., Riedl, K., Grossmann, J. & Call, J. (2011). Grooming network cohesion and the role of individuals in a captive chimpanzee group. *American Journal of Primatology*, 73(8), 758–767.
- Kühl, H. S., Boesch, C., Kulik, L., Haas, L., Arandjelovic, M., Dieguez, P., . . . Kalan, A. K. (2019). Human impact erodes chimpanzee behavioral diversity. *Science*, 363(6434), 1453–1455.
- Laland, K. N. (2015). On evolutionary causes and evolutionary processes. *Behavioural Processes*, 117, 97–104.
- Laland, K. N., Odling-Smee, J. & Feldman, M. W. (2000). Niche construction, biological evolution, and cultural change. *Behavioral and Brain Sciences*, 23(1), 131–146.
- Laland, K. N., Uller, T., Feldman, M. W., Sterelny, K., Müller, G. B., Moczek A., Jablonka, E. & Odling-Smee, J. (2015). The extended evolutionary synthesis: Its structure, assumptions and predictions. *Proceedings of the Royal Society B-Biological Sciences*, 282(1813), 20151019.
- Laland, K., Uller, T., Feldman, M., Sterelny, K., Gerd, Müller, G., . . . Futuyma, D. (2014). Does evolutionary theory need a rethink? *Nature News*, 514 (7521), 161–164.
- Lehmann, J. & Boesch, C. (2004). To fission or to fusion: Effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organisation. *Behavioral Ecology and Sociobiology*, 56(3), 207–216.

- Lipatov, M., Brown, M. J. & Feldman, M. W. (2011). The influence of social niche on cultural niche construction: Modelling changes in belief about marriage form in Taiwan. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1566), 901–917.
- Maestriperi, D., Ross, S. K. & Megna, N. L. (2002). Mother-infant interactions in western lowland gorillas (*Gorilla gorilla gorilla*): Spatial relationships, communication and opportunities for social learning. *Journal of Comparative Psychology*, 116(3), 219.
- Malone, N., Fuentes, A. & White, F. J. (2012). Variation in the social systems of extant hominoids: Comparative insight into the social behavior of early hominins. *International Journal of Primatology*, 33(6), 1251–1277.
- Mangold. *INTERACT 14 User Guide*. (Ed, Mangold International GmbH) (2015).
- Massen, J. J. & Koski, S. E. (2014). Chimps of a feather sit together: Chimpanzee friendships are based on homophily in personality. *Evolution and Human Behavior*, 35(1), 1–8.
- Maynard-Smith, J., Burian, R., Kauffman, S., Alberch, P., Campbell, J., Goodwin, B., . . . Wolpert, L. (1985). Developmental constraints and evolution. *Quarterly Review of Biology*, 60(3), 265–287.
- McGrew, W. C. (1992). *Chimpanzee material culture: Implications for human evolution*. Cambridge, UK: Cambridge University Press.
- McGrew, W. C. (2004). *The cultured chimpanzee: Reflections on cultural primatology*. Cambridge, UK: Cambridge University Press.
- McGrew, W. C., Ensminger, A. L., Marchant, L. F., Pruetz, J. D. & Vigilant, L. (2004). Genotyping aids field study of unhabituated wild chimpanzees. *American Journal of Primatology*, 63(2), 87–93.
- McGrew, W. C., Tutin, C. E. G. & Baldwin, P. J. (1979). Chimpanzees, tools, and termites: Cross-cultural comparisons of Senegal, Tanzania, and Rio Muni. *Man*, 14(2), 185.
- Mercader, J., Barton, H., Gillespie, J., Harris, J., Kuhn, S., Tyler, R. & Boesch, C. (2007). 4,300-year-old chimpanzee sites and the origins of percussive stone technology. *Proceedings of the National Academy of Sciences*, 104(9), 3043–3048.

Complimentary Contributor Copy

- Meulman, E. J. M., Sanz, C., Visalberghi, E. & van Schaik, C. P. (2012). The role of terrestriality in promoting primate technology. *Evolutionary Anthropology*, 21(2), 5868.
- Modlmeier, A. P., Keiser, C. N., Watters, J. V., Sih, A. & Pruitt, J. N. (2014). The keystone individual concept: An ecological and evolutionary overview. *Animal Behaviour*, 89, 53–62.
- Morgan, D., Mundry, R., Sanz, C., Ayina, C. E., Strindberg, S., Lonsdorf, E. & Kühl, H. S. (2018). African apes coexisting with logging: Comparing chimpanzee (*Pan troglodytes troglodytes*) and gorilla (*Gorilla gorilla gorilla*) resource needs and responses to forestry activities. *Biological Conservation*, 218, 277–286.
- Morgan, D. & Sanz, C. (2006). Chimpanzee feeding ecology and comparisons with sympatric gorillas in the Goualougo Triangle, Republic of Congo. In G. Hohmann, M. Robbins, & C. Boesch, (Eds.), *Primate feeding ecology in apes and other primates: Ecological, physiological, and behavioural aspects*, (pp. 97–122). Cambridge, Cambridge University Press.
- Morgan, D., Sanz, C., Onononga, J. R. & Strindberg, S. (2006). Ape abundance and habitat use in the Goualougo Triangle, Republic of Congo. *International Journal of Primatology*, 27(1), 147–179.
- Morgan, D., Sanz, C., Onononga, J. R. & Strindberg, S. (2016). Factors influencing the survival of sympatric gorilla (*Gorilla gorilla gorilla*) and chimpanzee (*Pan troglodytes troglodytes*) nests. *International Journal of Primatology*, 37(6), 718–737.
- Musgrave, S., Morgan, D., Lonsdorf, E., Mundry, R. & Sanz, C. (2016). Tool transfers are a form of teaching among chimpanzees. *Scientific Reports*, 6, 34783.
- Odling-Smee, F. J., Laland, K. N. & Feldman, M. W. (1996). Niche construction. *American Naturalist*, 147(4), 641–648.
- Odling-Smee, F. J., Laland K. N. & Feldman, M. W. (2003). *Niche construction: The neglected process in evolution*. Princeton, Princeton University Press.
- O'Malley, R., Wallauer, W., Murray, C. & Goodall, J. (2012). The appearance and spread of ant fishing among the Kasekela chimpanzees

- of Gombe: A possible case of intercommunity cultural transmission. *Current Anthropology*, 53(5), 650–663.
- Pascual-Garrido, A. (2018). Scars on plants sourced for termite fishing tools by chimpanzees: Towards an archaeology of the perishable. *American Journal of Primatology*, 80(9), e22921.
- Petre, C. A., Tagg, N., Haurez, B., Beudels-Jamar, R., Huynen, M. C. & Doucet, J. L. (2013). Role of the western lowland gorilla (*Gorilla gorilla gorilla*) in seed dispersal in tropical forests and implications of its decline. *Biotechnologie Agronomie Societe Et Environnement*, 17(3), 517–526.
- Pigliucci, M. & Müller, G. B. (2010). *Evolution: The extended synthesis*. Cambridge, MA: MIT Press.
- Robbins, M. (1999). Male mating patterns in wild multimale mountain gorilla groups. *Animal Behaviour*, 57(5), 1013–1020.
- Saltz, J. B., Geiger, A. P., Anderson, R., Johnson, B. & Marren, R. (2016). What, if anything, is a social niche? *Evolutionary Ecology*, 30(2), 349–364.
- Sanz, C., Call, J. & Morgan, D. (2009). Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biology Letters*, 5(3), 293–296.
- Sanz, C. & Morgan, D. (2007). Chimpanzee tool technology in the Goualougo Triangle, Republic of Congo. *Journal of Human Evolution*, 52(4), 420–433.
- Sanz, C. & Morgan, D. (2010). The complexity of chimpanzee tool-use behaviors. In E. Lonsdorf, S. R. Ross, & T. Matsuzawa (Eds.), *The mind of the chimpanzee: Ecological and experimental perspectives*, (pp. 127–140). University of Chicago Press.
- Sanz, C. M. & Morgan, D. B. (2013). Ecological and social correlates of chimpanzee tool use. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1630), 20120416.
- Sanz, C., Morgan, D. & Gulick, S. (2004). New insights into chimpanzees, tools, and termites from the Congo Basin. *American Naturalist*, 164(5), 567–581.



- Sanz, C., Morgan D., Strindberg S. & Onononga J. R. (2007). Distinguishing between the nests of sympatric chimpanzees and gorillas. *Journal of Applied Ecology*, 44(2): 263-272.
- Sanz, C., Schöning, C. & Morgan, D. (2010). Chimpanzees prey on army ants with specialized tool set. *American Journal of Primatology*, 72(1), 17–24.
- Sascher, N., Durschlag, M. & Hirzel, D. (1998). Social relationships and the management of stress. *Psychoneuroendocrinology*, 23(8), 891–904.
- Shumaker, R. W., Walkup K. R. & Beck B. B. (2011). *Animal tool behavior: The use and manufacture of tools by animals*. Baltimore, MD: Johns Hopkins University.
- Sicotte, P. (1993). Inter-group encounters and female transfer in mountain gorillas: Influence of group composition on male behavior. *American Journal of Primatology*, 30(1), 21–36.
- Smith-Aguilar, S. E., Aureli, F., Busia, L., Schaffner, C. & Ramos-Fernández, G. (2018). Using multiplex networks to capture the multidimensional nature of social structure. *Primates*, 60(3), 1–19.
- Stokes, E. J., Strindberg, S., Bakabana, P. C., Elkan, P. W., Iyenguet, F. C., Madzoké, B., . . . Rainey, H. J. (2010). Monitoring great ape and elephant abundance at large spatial scales: Measuring effectiveness of a conservation landscape. *PloS one*, 5(4), e10294.
- Strier, K. B. (1994). Myth of the typical primate. *American Journal of Physical Anthropology*, 37(S19), 233–271.
- Thierry, B. (2008). Primate socioecology, the lost dream of ecological determinism. *Evolutionary Anthropology*, 17(2), 93–96.
- Thompson, M. E., Kahlenberg, S. M., Gilby, I. C. & Wrangham, R. W. (2007). Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. *Animal Behaviour*, 73(3), 501–512.
- Tutin, C. E. G. & Fernandez, M. (1984). Nationwide census of gorilla and chimpanzee populations in Gabon. *American Journal of Primatology*, 6(4), 313–336.
- Tutin, C. (1996). Ranging and social structure of lowland gorillas in the Lope´ Reserve, Gabon. In W.C. McGrew, L. F. Marchant, & T.

- Nishida (Eds.), *Great ape societies*, (pp. 58–70). Cambridge: Cambridge University Press.
- Uller, T., Moczek, A. P., Watson, R. A., Brakefield, P. M. & Laland, K. N. (2018). Developmental bias and evolution: A regulatory network perspective. *Genetics*, 209(4), 949–966.
- van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., . . . Merrill, M. (2003). Orangutan cultures and the evolution of material culture. *Science*, 299(5603), 102–105.
- van Schaik, C. P. & Pradhan, G. R. (2003). A model for tool-use traditions in primates: Implications for the coevolution of culture and cognition. *Journal of Human Evolution*, 44(6), 645–664.
- van Schaik, C. P. & van Hooff, J. A. (1983). On the ultimate causes of primate social systems. *Behaviour*, 85(1–2), 91–117.
- Walsh, P. D., Breuer, T., Sanz, C., Morgan, D. & Doran-Sheehy, D. (2007). Natural history miscellany: Potential for Ebola transmission between gorilla and chimpanzee social groups. *American Naturalist*, 169(5), 684–689.
- Watts, D. P. & Mitani, J. C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour*, 138(3), 299–328.
- Whiten, A., Goodall, J., McGrew, W., Nishida, T., Reynolds, V., Sugiyama, Y., . . . Boesch, C. (2001). Charting cultural variation in chimpanzees. *Behaviour*, 138(11–12), 1481–1516.
- Yamagiwa, J. (1987). Intra- and inter-group interactions of an all-male group of Virunga mountain gorillas (*Gorilla gorilla beringei*). *Primates*, 28(1), 1–30.
- Yamagiwa, J., Kahekwa, J. & Basabose, A. K. (2003). Intra-specific variation in social organization of gorillas: Implications for their social evolution. *Primates*, 44(4), 359–369.