



Chimpocentrism and reconstructions of human evolution (a timely reminder)



Krist Vaesen

Philosophy & Ethics, Eindhoven University of Technology, Den Dolech 2 (IPO 1.13), 5612 AZ Eindhoven, The Netherlands

ARTICLE INFO

Article history:

Received 25 September 2013

Received in revised form 10 December 2013

Keywords:

Human evolution

Phylogenetics

Kitcher

Comparative biology

ABSTRACT

Chimpanzees, but very few other animals, figure prominently in (recent) attempts to reconstruct the evolution of uniquely human traits. In particular, the chimpanzee is used (i) to identify traits unique to humans, and thus in need of reconstruction; (ii) to initialize the reconstruction, by taking its state to reflect the state of the last common ancestor of humans and chimpanzees; (iii) as a baseline against which to test evolutionary hypotheses. Here I point out the flaws in this three-step procedure, and show how they can be overcome by taking advantage of much broader phylogenetic comparisons. More specifically, I explain how such comparisons yield more reliable estimations of ancestral states and how they help to resolve problems of underdetermination inherent to chimpocentric accounts. To illustrate my points, I use a recent chimpocentric argument by Kitcher.

© 2013 Elsevier Ltd. All rights reserved.

When citing this paper, please use the full journal title *Studies in History and Philosophy of Biological and Biomedical Sciences*

1. Introduction

Let me start by setting up a straw man. The straw man believes that to reconstruct human evolution, there is one animal (other than the human animal) which should be privileged over all others: our closest relative, the common chimpanzee (*Pan troglodytes*). More specifically, the straw man's favored chimpocentric reconstruction consists of three steps (see Fig. 1).¹ In the first, the chimpanzee is used to single out those features that make humans unique, and thus are in need of reconstruction. So, from a direct comparison between us and chimpanzees, the straw man infers a uniquely human trait or character state T^* ; humans have it, whereas chimpanzees rather exhibit T . In the second step, extant chimpanzees serve to initialize the reconstruction. That is, their state T is assumed to adequately reflect the state of the last ancestor which humans have in common with them (*aka* the LCA, living some 6–7 mya). Third, the straw man now sets himself the task of identifying a mechanism which could have given rise to the transition from T (in the LCA) to T^* (in humans), say, a selective pressure S , which humans

faced but chimpanzees didn't. With that, the straw man would have reconstructed the evolution of T^* in our lineage.

To my mind, no serious philosopher (nor any scientist, for that matter) has endorsed our straw man's line of reasoning exactly, at least not as of late. Yet, one still finds unmistakable traces of it in the writings of many (including my own, see Vaesen, 2012, even though my aims there were not really reconstructive). In light of that, the primary purpose of this paper is to make explicit the sense in which chimpocentric reasoning undermines the credibility of reconstructions that rely on it. Second, the paper shows what can be done about it, by introducing an alternative model, the Comparative Convergence Approach. Finally, I illustrate the reality and threats of chimpocentrism as well as the merits of the Comparative Convergence Approach, by considering a representative case, namely a reconstruction offered by Philip Kitcher in his recent book *The Ethical Project* (2011).

There are two reasons for bringing up and elaborating these points. The first is that, although the points themselves are not new to this paper and have received attention outside philosophy

E-mail address: k.vaesen@tue.nl

URL: <http://home.ieis.tue.nl/kvaesen>

¹ Throughout the paper, chimpocentrism will refer to this three-step procedure, rather than to the idea that chimpanzees are much more clever than any other non-human animal (a common, alternative definition of the term).

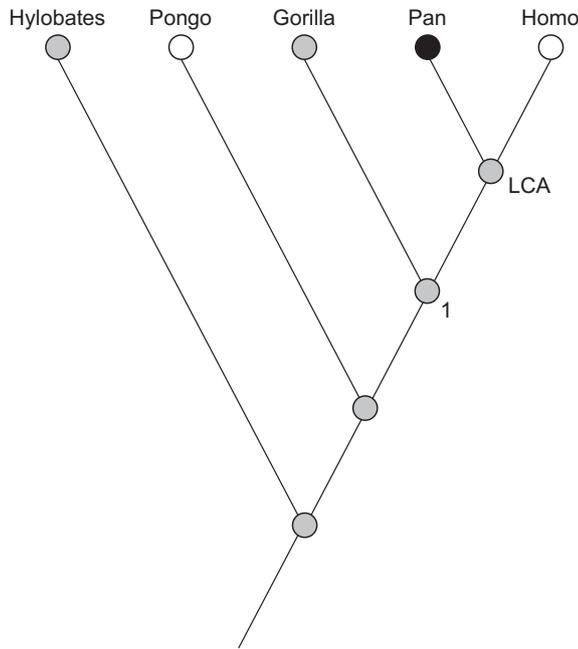


Fig. 2. Visual signs of ovulation in the apes. Black circles indicate exaggerated sexual swellings; gray circles indicate slight visual signs of ovulation; white circles indicate absence of visual ovulatory signals. Pan = chimpanzee and bonobo; Gorilla = gorilla; Pongo = orangutan; and Hylobates = gibbon. The picture is a redrawn detail of Sillén-Tullberg and Møller (1993) phylogenetic analysis, which in full used Tarsiioidea as outgroup. The analysis used a maximum-parsimony algorithm, which results in a tree that can account for the character state distribution at its tips with the fewest evolutionary changes. For instance, consider the LCA. If, as in the picture, the LCA is colored gray, only two changes are needed to get the observed distribution (namely one change from gray to black in between LCA and Pan; and one change from gray to white in between LCA and Homo). In contrast, if the LCA were black, one would need to invoke three changes (namely one change from gray to black in between point 1 and the LCA; one change from black to gray and one change from gray to white in between LCA and Homo). Hence, the maximum-parsimony algorithm will retain a tree in which the LCA is colored gray rather than black. Note that maximum-parsimony analyses have been largely superseded by maximum-likelihood and Bayesian approaches.

To summarize, when humans and chimpanzees differ in their state of a trait, step two in our model cannot be justified. Only broad taxonomic comparisons (to be detailed in Section 3) allow one to determine which of the two states is derived, and thus in need of reconstruction, and which one is ancestral.⁵

2.2. Step 3: Chimpanzee evolution as a baseline for human evolution

For the sake of the argument, let us assume that T is the ancestral state indeed. In our chimpocentric model, there are only two evolutionary trajectories, only one of which exhibits the transition of interest (from T to T^*). Consequently, in principle any pressure S that our lineage faced, but chimpanzees didn't, could have occasioned T^* . In other words, chimpocentrism only provides one criterion to screen out rivaling hypotheses: whether a hypothesized pressure S did or did not operate in both lineages.⁶

Consider the question why humans have such large brains. One hypothesis that seems to make sense is the social brain hypothesis, according to which the demands of group life favored higher encephalization (Humphrey, 1976). Construed in terms of our

chimpocentric model: early humans faced a challenge S (namely living in larger groups) which chimpanzees didn't, and that may explain the size of the human brain. But, our model is also consistent with the technical brain hypothesis, according to which the hominid colonization of savanna and more temperate habitats (shifts chimpanzees supposedly never made) demanded higher technical ingenuity (Washburn, 1960). Further, it is also consistent with the cultural brain hypothesis (Whiten & van Schaik, 2007), the cognitive buffer hypothesis (Allman, McLaughlin, & Hakeem, 1993; Deaner, Barton, & van Schaik, 2003) and with more recent versions of the technical brain hypotheses (Byrne, 1997).

Such underdetermination problems may be addressed by considering species other than humans and chimpanzees. If the state of interest, T^* , has emerged through independent evolution in other taxa, these cases do provide independent observations for testing one's hypotheses about the human case. A selective pressure S that we think may have favored T^* in us is a better contender if it has done more or less the same repeatedly and independently elsewhere (Harvey & Pagel, 1991; Pagel, 1994; for a recent philosophical treatment of the evidential status of convergence, see Currie, 2013). So in favor of the social brain hypothesis counts the finding that, across the primate order, evolutionary change as regards encephalization correlates with evolutionary change as regards group size (Dunbar, 1995). The hypothesis makes even more sense in the light of evidence of the same pattern in orders even more distant from humans, such as the Carnivora (Dunbar & Bever, 1998), Cetacea (Marino, 1996), and Ungulata (Shultz & Dunbar, 2005).

In Section 3, I return to the question as to when convergence (i.e. independent evolution of a trait in several species) will and will not illuminate human evolution. For now, it suffices to have pointed out the underdetermination problem associated with our chimpocentric model: the latter provides only one, highly indiscriminate datum to screen rivaling hypotheses. Consequently, apart from very likely suggesting incorrect starting points for one's reconstructions (as shown in the previous section), chimpocentrism faces tremendous difficulties in getting right the middle parts as well.

2.3. Step 1: Chimpanzees as a measure of humaniqueness

From the above, it follows quite straightforwardly that step one in our chimpocentric model suffers from myopia. First, if we need to perform phylogenetic analysis in order to be able to establish ancestral states, we evidently must first diagnose the trait in question in species outside *Homo-Pan troglodytes*. Second, if convergence may provide additional evidence for our hypotheses about human evolution, we evidently must first identify instances of convergence, and that *minimally* requires searching for T^* in species phylogenetically more distant to us than chimps. Additional procedures are needed to ensure that observations of T^* evidence convergent evolution rather than common ancestry, but diagnosing T^* in species other than humans and chimpanzees is a necessary and important first step.

To illustrate this second type of myopia, consider teaching. The absence of consistent evidence of chimpanzees facilitating learning in others, over more than 50 years of extensive study, has long sustained the idea that teaching is humanique. Yet, this kind of cooperative behavior has recently been reported, in various guises, in tamarin monkeys, meerkats, pied babblers, and even ants (for an

⁵ In fact, it is also possible that both states of the trait are derived. In a sense, this holds for the ovulatory signs of humans and chimpanzees. Supposing that the LCA indeed had slight ovulatory signs, not just the exaggerated sexual swellings of chimpanzees would be derived, but also the complete disappearance of these slight ancestral signs in humans. Importantly, that conclusion would be the result of applying a broad taxonomic comparison just as well.

⁶ Step two provides a convenient shortcut to implement this criterion. If, as per step two, one keeps fixed character states *and* selective environments in the chimpanzee lineage, one can retain any pressure S that extinct humans faced but extant chimpanzees currently do not.

overview, see Hoppitt et al., 2008; Thornton & Raihani, 2010).⁷ It is from these instances of convergent evolution that some general principles could be derived. For instance, it appears that teaching is more likely to be present in species in which pupils have few and/or only very risky opportunities to learn alone (Thornton & Raihani, 2008). Further, teaching seems disproportionately represented in cooperatively breeding animals (Hoppitt et al., 2008). This could mean that cooperative breeding promotes teaching, or that some other factor favors both cooperative breeding and teaching. Crucially, such patterns would have gone unnoticed in case one would not have taken advantage of the available evidence outside *Homo-Pan troglodytes*.

Generally, chimpanzee studies support claims about the human uniqueness of T^* only on the condition that we already know (which we typically don't) that chimpanzees are more human-like than any other species with respect to the trait in question. Our close relatedness to chimpanzees may give us some reason for assuming this condition to hold. Still, that reason is defeasible—as the example of teaching illustrates. Incidentally, in case broad taxonomic comparisons would identify T^* as zoologically unique indeed, underdetermination must be addressed by other means.

3. The Comparative Convergence Approach as an alternative to chimpocentrism

In this section, I introduce an alternative to the chimpocentric model I have been criticizing thus far—let us call it the Comparative Convergence Approach. The approach consists of four steps, and avoids the problems associated with chimpocentrism by, as I have hinted at already, taking advantage of comparative data from species other than humans and chimps. I first present the four steps, and then discuss the conditions under which this ideal procedure can and cannot be fruitfully applied.

Step 1: Pick a human trait or character state T^* that one wishes to reconstruct.

At this stage no comparative data are needed yet.

Step 2: Conduct a phylogenetic analysis to determine the state of the LCA.

So rather than taking extant chimpanzees as representative of the LCA, inferences are made based on, say, data of all the (great) apes or even of the entire primate order, plus data on the known phylogenetic relations between these species (for an example, see again Fig. 2; or see Sober, 1988, 2002). One should move to the third step only if one finds that, with some acceptable probability, the LCA exhibited T rather than T^* ; it is the transition from T (in the LCA) to T^* (in humans) one aims to reconstruct. Note that it is possible that chimpanzees and humans both exhibit T^* , but the LCA exhibits T . This may happen, for instance, when bonobos and gorillas exhibit T . That is the reason why I said that in the first step we do not need comparative data. Similarities between humans and chimpanzees may obscure independent evolutionary change in the two species; but it is only after step two that one is in a position to tell.

Step 3: Look for instances of convergent evolution, i.e. independent transitions from T to T^* in nonhuman animals.

Although these nonhuman animals may be either extant or extinct species, given our limited knowledge of the

environments in which the latter lived, these species are hardly useful once one moves to the fourth step. As regards extant species, the procedure would start by first finding animals exhibiting T^* , and next, checking that their ancestral state was T .

Step 4: Search for a cause (or a set of causes) that is invariably associated with transitions from T to T^* .

Repeated association of an environmental feature S with transitions from T to T^* makes it more likely that S was involved in the emergence of T^* in humans. In comparison to chimpocentrism, the Comparative Convergence Approach thus has an additional criterion for screening rivaling hypotheses. That is, in addition to evaluating whether or not a hypothesized pressure S operated both in human and chimpanzee evolution, the approach favors those pressures that appear to be generally conducive to the evolution of T^* .

Note that my presentation of the third and fourth step is an informal and highly simplified sketch of the quantitative convergence approach developed in comparative biology (for an excellent introduction, see chapters 6 and 7 of Nunn, 2011). For the purposes of the current paper, however, this sketch suffices. It represents an ideal that is much more easily attainable than its more rigorous, quantitative counterpart. Any allegation of not meeting it would thus be more charitable towards the putative offender, but also more serious if indeed true.

In order to assess the limitations of the Comparative Convergence Approach, I will answer the following question: What are the conditions under which it does not work (properly)? There are four conditions, one preventing us to establish the state of the LCA by means of phylogenetic analysis (Excuse 1), and three preventing us to deploy convergence for hypothesis testing (Excuse 2–4):

Excuse 1: There are insufficient reliable data outside *Homo-Pan troglodytes* to infer, by means of phylogenetic analysis, the state of the LCA;

Excuse 2: There are insufficient reliable data outside *Homo-Pan troglodytes* to properly detect instances of convergent evolution of T^* ;

Excuse 3: T^* really evolved only once, namely in our lineage.

Excuse 4: T^* has evolved several times, but these instances of convergent evolution do not seem to attest to repeated association with a common environmental feature S .

Note that while Excuses 1–4 are legitimate excuses for *not* using the Comparative Convergence Approach, they by themselves do not legitimize chimpocentrism. For instance, it is excusable to not carry out step two if insufficient comparative data are available. Yet, rather than to then use chimpocentrism as a fallback option, one arguably would better simply suspend judgment. Further, note that a fifth legitimate reason for not using the Comparative Convergence Approach may be our knowing the trait of interest to be a spandrel. This consideration is left out in the list above because we generally lack such knowledge. Both chimpocentrism and the Comparative Convergence Approach are adaptationist, and thus are both unable to detect evolutionary by-products—a serious but unavoidable shortcoming indeed. As a final remark, one of the easiest excuses to invoke, at least when it concerns discrete traits,

⁷ In animal studies, the standard operational definition of teaching is due to Caro & Hauser (1992, p. 153). Teaching occurs when: “An individual actor A [the *tutor*] can be said to teach if it modifies its behavior only in the presence of a naïve observer, B [the *pupil*], at some cost or at least without obtaining an immediate benefit for itself. A 's behaviour thereby encourages or punishes B 's behaviour, or provides B with experience, or sets an example for B . As a result, B acquires knowledge, or learns a skill earlier in life or more rapidly or efficiently than it might otherwise do so, or would not learn at all.”

seems Excuse 3. The finer-grained our descriptions of T^* , the less likely we will observe it in multiple species. Hence, by insisting on fine-grainedness, relieving oneself of the burden of applying the Comparative Convergence Approach comes quite cheap. Doing so, however, also implicates step two (i.e. establishing the state of the LCA through phylogenetic analysis). Insistence on fine-grainedness thus comes at a considerable price: that we can say very little about the evolution of T^* .⁸

With that we have a set of diagnostic tools for assessing comparative reconstructions of human evolution. In particular, we now have the means to identify a reconstruction as chimpocentric (see Section 2), the means to determine the extent to which it diverges from the Comparative Convergence Approach, and to assess the extent to which not deploying the latter is excusable (in terms of Excuses 1–4). I will now apply these diagnostic tools to a very recent reconstruction, offered in Philip Kitcher's book *The Ethical Project* (2011). The exercise is meant to demonstrate that chimpocentrism has not vanished, and as importantly, inexcusably so.⁹ Further, it illustrates how the Comparative Convergence Approach may help to settle questions about human evolution. To repeat an earlier remark, I find myself in the embarrassing position to have entertained at least in outlook chimpocentric thoughts myself (Vaesen, 2012). Even if I there provided pragmatic reasons for my focus on chimps, and even if my aims were not really reconstructive, I must level my charges against Kitcher with modesty.

4. Kitcher's chimpocentrism

Part I of Kitcher's book attempts to offer an analytical history of the evolution of our ethical practice; of how from the psychological capacities and socio-ecological conditions of our ancestors morality could emerge. Especially when reconstructing the beginnings of that story, Kitcher's argument bears some striking resemblances to the chimpocentric model presented in Fig. 1. Let me point out these resemblances, deferring until the next section questions of excusability.

In line with step one in Fig. 1, Kitcher defines his target by a direct comparison of humans and chimps. Based on Goodall's (1986) observation of an infant chimpanzee assisting its paralyzed mother, and on de Waal's (1996) story of a retarded mature female chimpanzee being helped by a conspecific in the Arnhem Zoo, he starts by arguing that chimpanzees may be attributed at least some altruistic desires (pp. 42–44). Still, chimpanzee and human altruism remain saliently different (pp. 69–72). More specifically, referring to studies by de Waal (1984, 1989), Kitcher argues chimpanzee altruism to be limited in range (the number of recipients) and scope (the different circumstances under which it occurs). While members that are a chimpanzee's principal allies may enjoy altruistic acts, others are just tolerated and/or treated with indifference (hence, limited range). Further, chimpanzee friendship is "situation linked"; even the most committed mutually altruistic bonds may be terminated in case one party gets the chance of a huge advantage (hence, limited scope). In humans, contrarily, these limitations appear to have been transcended (pp. 67–68). Our species has learned to interact peacefully with even unknown conspecifics, and to form markedly stable and complex cooperative relationships. Evidently, human altruism is far from

perfect. We haven't, writes Kitcher, "escaped entirely from the difficulties and tensions, the rivalries and conflicts, of chimpanzee social life" (p. 68).

The latter statement already suggests that Kitcher also takes the second step of the chimpocentric model: the fairly restricted altruistic dispositions of chimpanzees serve to initialize the reconstruction of the evolution of the altruism characteristic of humans, broad both in range and scope.¹⁰ Also chimpanzees' group size and composition is assumed ancestral. Like extant chimpanzees, our ancestors are assumed to live in bisexual groups of considerable size (30–70 individuals)—although to be fair, Kitcher backs up this claim by reference to archaeological and anthropological evidence (p. 18).

But perhaps the best evidence confirming that Kitcher takes chimpanzees as the model for our hominid past (words he himself uses, p. 59) would be absence of evidence of broader phylogenetic comparisons. Now, Kitcher actually *does* take a broader phylogenetic perspective once, albeit very briefly. In between his extensive discussion of chimpanzee life, he shortly describes the social lives of gibbons, orangutans and gorillas (p. 58), which he contrasts with the social lives of chimpanzees and bonobos. However, that excursion serves to establish the state of the ancestors of the LCA, rather than that of the LCA itself (which is arguably why no contrast is made with *Homo*).¹¹ In response, one may think that the excursion also could serve the latter purpose, in case one added data on humans. Would that immunize him from charges of chimpocentrism? Not entirely. Consider for instance male–female interactions, which Kitcher diagnoses in chimpanzees and bonobos (pp. 58–59), but omits to diagnose in gibbons, gorillas and orangutans (p. 58)—inclusion of humans should not be expected to fix this in outlook chimpocentric omission. Further, the issue is not just whether Kitcher considers species outside *Homo-Pan troglodytes*, but also whether he does so properly. Here the answer is no. As a supposed phylogenetic analysis, Kitcher's discussion falls short in three respects. First, it diagnoses incompletely several traits (e.g., as said, intersexual interactions are not diagnosed in gibbons, orangutans, and gorillas; intrasexual interactions are not diagnosed in gibbons) for which inferences are drawn nonetheless. Second, Kitcher misdiagnoses several traits. For example, chimpanzees and bonobos are said to exhibit cooperation among unrelated adults of both sexes (pp. 58–59). But, cooperative bonding between chimpanzee females is very rare, as is cooperative bonding between chimpanzee males and females, as is cooperation between bonobo males (see the overviews by van Schaik, Preuschoft, & Watts, 2004; Yamagiwa, 2004). Third, given these marked differences, in a phylogenetic analysis chimpanzees and bonobos should not be treated as if the same.

In conclusion, in quite some passages Kitcher's approach bears strong resemblances to step two of the chimpocentric model; and the one passage where the resemblance seems weaker still shows too little evidence of proper inclusion of data outside *Homo-Pan troglodytes*.

How, then, did our chimpanzee-like ancestors become human? Part of Kitcher's favored answer is that in the beginning of the ethical project our ancestors acquired a capacity for normative guidance, that is, the ability to apprehend and obey commands, an ability necessary to what we think of as ethical practice (p. 69). That ability would allow altruism to occur more readily, since it

⁸ Thanks to an anonymous reviewer for pressing me on these three points.

⁹ As said, some of the charges mounted against Kitcher may also be mounted against Dubreuil (2010), Joyce (2006) and Prinz (2007). See footnote 2.

¹⁰ Another quote to that effect (pp. 73–74): "Psychologically altruistic dispositions make it possible for these animals [i.e. chimpanzees] to live together, but the limitations of those dispositions subject their social lives to strain. Day after day, the social fabric is torn and has to be mended by hours of peacemaking. Once, that was the predicament of our ancestors, too."

¹¹ Another worry is that this excursion assesses strength of affiliative and cooperative bonding, which is not the same as assessing range and scope of altruism, the latter being Kitcher's principal explanandum, at least as it concerns the beginning of the ethical project. Evidently, this confuses not only Kitcher's discussion, but also mine, here and in the remainder. Unfortunately I see no way of avoiding inheriting such unclarity from Kitcher.

now could be issued both by genuinely altruistic motives *and* by recognition of the social expectations expressed in commands. Thus, following of orders would replace altruism failure by behavior that, at least from the outside, looks altruistic, and this in a broad variety of contexts. Peace and cooperation would become less hard-won.

In light of the fact that Kitcher aims to provide an *explanation*, even if just a “how possibly” explanation (see e.g., pp. 12–13, 61, 91), this evidently cannot be the whole story, for the evolution of normative guidance seems as mysterious as that of humanlike altruism. To qualify as an explanation, Kitcher needs to say something about the mechanisms which could have prompted these events. In other words, Kitcher must tell us *why* ameliorated altruism, issued by normative guidance, emerged in our lineage but not in that of our closest relative. On this score, Kitcher is much less explicit. He suggests that the original function of normative guidance (of ethics) was to remedy altruism failures; that more dependable forms of altruism relieved our ancestors from the tensions and rivalries of chimpanzee social life and to enable them to live more peacefully together (pp. 9, 98). But it remains unclear why our ancestors (but not those of chimpanzees) needed more peace and more stable cooperative dispositions in the first place, except perhaps because they experienced a pressure which Kitcher fairly consistently refers to, namely resource scarcity (see e.g., pp. 6, 35, 60, 104, 106, 107, 122).

What matters for our purposes is whether the latter hypothesis—i.e. resource scarcity putting a premium on human-like cooperation—results from application of step three of the chimpanzee model. There is some indirect evidence to believe it does. Recall that on the chimpanzee model, there is only one criterion to weed out evolutionary hypotheses: whether or not a hypothesized pressure acted both in *extinct* humans and *extant* chimpanzees. Kitcher, now, implicitly acknowledges this to be the only criterion indeed, when he identifies as source of uncertainty for his explanation the incompleteness of the human archaeological record (p. 11), but not the incompleteness of the chimpanzee archaeological record (betraying step two), nor absence of instances of convergent evolution which, if available, would perhaps allow him to narrow down the set of possible hypotheses (betraying step three). Consistent with this interpretation is the fact that Kitcher nowhere hints at the possibility of securing the credibility of his story by granting convergence evidential status.

5. Should Kitcher be excused?

Can Kitcher counter these charges, by invoking (at least some of) the four excuses presented in Section 3? To wit, could he argue

that his not deploying the comparative convergence approach (or at least a procedure more resembling it than resembling chimpanzee-centrism) is excusable?

5.1. Excuse 1: Insufficiency of data to establish ancestral states by means of phylogenetic analysis

Excuse 1 may partly apply as regards psychological altruistic dispositions. Our knowledge about psychological altruism among the (great) apes is limited indeed. Yet, it has been diagnosed properly in our other closest relative, the bonobo—or so assumes Kitcher: “psychological altruistic tendencies of the bonobo are more prominent and pervasive than in the (common) chimpanzee.” (p. 59) If this is so, and on the assumption that no other comparative data are available, a maximum-parsimony tree of *Homo*, chimpanzee and bonobo would dictate that, at least as regards altruism, the bonobo is a better model for the LCA than the chimpanzee.¹²

For aspects of sociality other than psychological altruism, our knowledge of the (great) apes is far more extensive, and Excuse 1 does not apply. Phylogenetic analyses have been performed taking into account data on affiliative and cooperative bonding (intra- and inter-sexual), mating system, dispersal, dominance relations, inter-group relations, paternal investment, and so forth. Some of these point to resemblances between chimpanzees and the LCA indeed (Ghiglieri, 1987; Wrangham, 1987), and fortunately, Kitcher’s portrayal of the LCA looks at least consistent with these findings.¹³ Still, the studies in question (and Kitcher too, see Section 4) largely ignore a feature which seems particularly relevant for reconstructing human altruism, namely long-term male–female relationships. While human pair-bonds may be fairly unique, they also fits a larger pattern: primates are highly unusual in that most of them (73% of primate species) exhibit year-round male–female associations (van Schaik & Kappeler, 1997; percentages for other well-studied and speciose mammalian genera vary between 12% and 32%).¹⁴ In such affiliative bonds, females usually provide most of the grooming and other services, whereas males may invest in protection and/or infant care (Kappeler & van Schaik, 2002). Interestingly, species that do not form long-term intersexual bonds include orangutans (but see Fox, 2002; Utami, Goossens, Bruford, de Ruiter, & van Hooff, 2002; Wich et al., 2009), muriquis, spider monkeys and, most important for present purposes, chimpanzees. Considering the apes, and relying on maximum-parsimony (as do Wrangham and Ghiglieri), one should infer the LCA to have formed reasonably strong male–female bonds, *unlike* extant chimpanzees (see Fig. 3; see also Foley, 1989; Geary & Flinn, 2001; Geary, Bailey, & Oxford, 2011).¹⁵ Hence, by modeling the LCA on extant chimpanzees, Kitcher may well have missed out on one likely conspicuous feature of LCA sociality; and insufficiency of data would hardly serve as an excuse. Further, as will

¹² True, Kitcher thinks to have an independent reason for preferring the chimpanzee over the bonobo as a model for our hominid past: if a compelling story can be told on the assumption of a chimpanzee-like LCA, it should be easier to defend a similar account when taking the much more peaceful bonobo as a starting point (p. 59). But, this line of reasoning is flawed in two respects. First if, per Kitcher, more dependable forms of altruism served to enable our ancestors to live more peacefully together, one would expect societies that are already peaceful, as those of bonobos, to be *less* likely to develop forms of altruism more dependable than those already present. Second, the argument ignores the fact that the marked differences between chimpanzee and bonobo sociality, some of which Kitcher acknowledges, are most likely shaped by different socio-ecological factors. For instance, stable affiliative associations in chimpanzees are primarily male–male, whereas in bonobos they are primarily female–female. Crucially, female–female gregariousness is plausibly governed by a combination of predation risk, food distribution, infanticide risk, and habitat saturation (Sterck, Watts, & van Schaik, 1997), whereas male–male bonding is a function of mating competition and dispersal pattern (Kappeler & van Schaik, 2002; van Hooff & van Schaik, 1994). Suppose now that the LCA were bonobo-like, and that in humans both strong male–male and female–female bonds occur. One of our principle tasks would be to explain affiliations among human males. In light of the determinants of male–male bonding just mentioned, changes in mating competition would perhaps be a plausible contender. Mating competition, however, would not be a salient explanans in case the LCA were chimpanzee-like. For the primary explanandum now would be female–female bonding, which is not governed by mating competition, but by, as said, a combination of predation risk, food distribution, infanticide risk, and habitat saturation. In sum, an explanation that would work for chimpanzees cannot be assumed to work for bonobos.

¹³ Since the findings of Wrangham and Ghiglieri have become common knowledge, they may have indirectly inspired Kitcher.

¹⁴ Pair-bonding refers to enduring affiliation between individuals. It is different from monogamy: the latter is a sexual relationship, the former a social relationship. These need not to coincide: monogamy may entail weak heterosexual attachment, and strong male–female bonds often occur in polygynous mating systems (Palombit, 1999). So cross-cultural evidence about polygyny in humans does not undermine the claim that human pair-bonds are unusually strong.

¹⁵ Foley’s study is somewhat ambiguous about male–female bonding in the LCA. His Fig. 6 suggests it was present in the LCA; the main text, however, is at least consistent with the interpretation that it emerged only in the first hominids. Further, interestingly, from their phylogenetic analysis (Geary & Flinn, 2001; Geary et al., 2011) infer that the LCA must have been more gorilla-like than chimpanzee-like. For the view that the LCA was more orangutan-like, see Schwartz (1987).

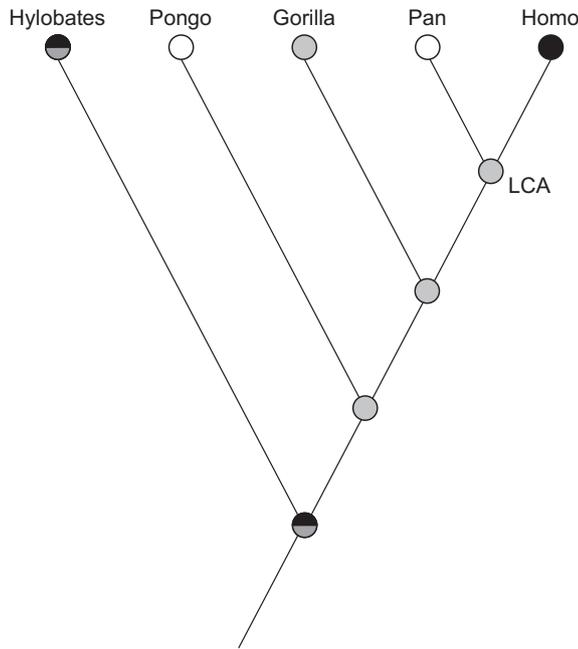


Fig. 3. Year-round male–female bonding in the apes. Black circles indicate very strong bonds; gray circles indicate bonds of intermediate strength; white circles indicate absence of year-round bonding. Pan = chimpanzee and bonobo; Gorilla = gorilla; Pongo = orangutan; and Hylobates = gibbon. The tree is based on maximum parsimony. Chimpanzee and bonobo are collapsed into one leaf. Even though bonobos more readily form long-term male–female bonds than chimpanzees, treating them as if they do not would yield the same result for the LCA.

become apparent later, this also affects the credibility of the rest of Kitcher's reconstruction.

5.2. Excuse 2: Insufficiency of data to detect instances of convergent evolution

Perhaps surprisingly, altruistic dispositions have been studied quite extensively in monkeys—more so than in most of the apes (gibbons, orangutans, gorillas, and even bonobos). And it is also in monkeys, more specifically in *Callitrichidae* (tamarin and marmoset species), that have been observed forms of altruism which approximate human altruism most, at least in the dimensions which interest Kitcher, i.e. range and scope. In terms of scope, unlike chimpanzees and bonobos, callitrichids do not just tolerate each other, acting altruistically only under threatening situations. Rather, they *spontaneously* share foodstuffs with their own offspring and the offspring of others; unsolicited help may also encompass infant carrying, babysitting and allonursing (Digby, Ferrari, & Saltzman, 2007). Regarding range, and again unlike chimpanzees and bonobos, callitrichids are known to act prosocially towards unrelated others (for tamarins: see Hauser, Chen, Chen, & Chuang, 2003; for marmosets: see Burkart, Fehr, Efferson, & van Schaik, 2007). Also in contrast to chimpanzee and bonobo societies, where altruistic acts are limited to close friends and bonded kin or depend on dominance, callitrichid societies are characterized by strong social bonds among *all* group members (Burkart, Hrdy, & van Schaik, 2009). Further, since we share with callitrichids a common ancestor 30 million years ago, it would be wildly implausible that callitrichid prosociality would not have evolved independently. So unless Excuse 3 and/or Excuse 4 apply (more on this below), callitrichids seem to provide us just with the kind of data the Comparative Convergence Approach demands.

I want to briefly return to male–female relationships. Any satisfactory reconstruction of human altruism would seem to need to say something about the domain where altruistic dispositions are expressed most strikingly, namely in human pair-bonds. Would Excuse 2 apply here? No. Gibbon pair-bonding has likely evolved independently from human pair-bonding; long-term male–female bonds are also present in chacma baboons, callitrichids, rodents (e.g., Malagasy giant rats, Arctic ground squirrels), birds (e.g., barn swallows, house wrens), and insects (e.g., burying beetles) (Palombit, 2000). So, again, unless Excuse 3 and/or Excuse 4 apply (more on this below), these instances of convergence could turn out to be very useful.

5.3. Excuse 3: T^* really evolved only once, namely in us

Undeniably, even if callitrichids come closest to exhibiting human-like prosociality, marked differences remain. For instance, while callitrichids frequently direct altruistic acts towards closely bonded kin, closely bonded non-kin and fellow group members, they (almost) never, unlike humans, direct their help towards true strangers (Burkart et al., 2009). And due to their limited theory of mind abilities, callitrichid monkeys are unlikely to engage in *psychological* altruism. Thus, if we define altruism sufficiently narrow, so that it picks out the human variant and the human variant alone, convergence approaches would seem to be blocked from the start; and we would have to make do with the history of our lineage, set against the chimpanzee baseline, in order to test evolutionary hypotheses. In other words, we would face the kind of underdetermination problem plaguing chimpocentrism.

However, since we are interested in explaining evolutionary *change*, we need to take into account not just similarity at the leaves of the phylogenetic tree, but also similarity as regards change. Consider again human encephalization. The human neocortex ratio (i.e. the ratio of the size of the neocortex to the rest of the brain) is, in absolute terms, the highest among primates: 4.1. So, in absolute terms, this neocortex ratio has evolved only once (at least in primates). By implication, if we were to measure similarity in terms of this absolute number alone, the primate order would not contain instances of convergence; all other primates would be denied evidential status. But, primates that are dissimilar from us as measured by neocortex ratio may still be similar with respect to *change* in neocortex ratio. While, due to phylogenetic constraints, a primate may not reach a ratio of 4.1, it still may have evolved a bigger brain, perhaps even in response to the very same selection pressure which produced the 4.1 ratio in humans. And as the results of Dunbar and others suggest (see above), this may indeed well have happened repeatedly in the primate order.

Applied to Kitcher, Excuse 3 would be valid only on the condition that we wouldn't find independent increases in altruism outside *Homo*. But in light of studies on callitrichids, this condition doesn't seem to hold. And similar considerations apply to intersexual associations: Excuse 3 is undermined by independent changes towards long-term male–female bonding in some primates, some rodents, some birds and some insects.

5.4. Excuse 4: Convergent evolution of T^* is not invariably associated with a common environmental feature *S*

Let us start with general altruistic dispositions, and put to test first the hypothesis I earlier attributed to Kitcher.¹⁶ According to that hypothesis, resource scarcity could have been one of the drivers of human altruism. The credibility of that hypothesis would improve in case we would have reason to believe the altruism of callitrichids

¹⁶ For present purposes, it doesn't really matter whether Kitcher really holds this hypothesis, for I just want to illustrate what convergence may do for us.

to have evolved in response to resource scarcity. Yet, if we compare callitrichids with the genus *Cebus* (the closest sister taxon) the hypothesis seems disconfirmed. For the altruism of *Cebus* is in general more limited than that of callitrichids, despite the fact that none of the two can be singled out as experiencing higher feeding competition (Brown & Zunino, 1990; Digby et al., 2007). So if we would focus on this particular hypothesis alone, Excuse 4 would seem valid.

However, callitrichids may also serve the purpose of hypothesis generation. For instance, a remarkable fact is that both callitrichids and humans, in contrast to chimpanzees and bonobos, are cooperative breeders (meaning that their offspring is taken care for and provisioned by individuals other than parents). This is particularly interesting given that in mammals cooperative breeding is fairly consistently associated with high and generalized (i.e. extending beyond infants) (pro)sociality. The latter observation is based on comparisons of the various callitrichid species with their independently breeding sister taxa, and on evidence of other cooperatively breeding mammals, most notably, canids and elephants (Burkart et al., 2009, 2010 and references therein). So, contra Excuse 4, evolution of higher prosociality actually *does* seem to be associated with a common pressure, namely cooperative breeding—which fuels the hypothesis that cooperative breeding was an important factor in the evolution of human altruism.¹⁷

Alternatively, higher prosociality and cooperative breeding are both favored by some other factor. If so, we need to determine whether convergent evolution of cooperative breeding is invariably associated with some environmental feature *S*. The answer is yes—and Excuse 4, again, doesn't apply. Pressures which are generally conducive to cooperative breeding include habitat saturation, high predation risk, high inter-group competition, unpredictable environments, and pressures issuing the colonization of new habitats (Clutton-Brock, 2006, and references therein; Hrdy, 2005, 2009; Isler & van Schaik, 2012, and references therein). Some of these are more likely than others to have played a role in the evolution of cooperative breeding in our lineage (estimated around *Homo erectus*, some 1.8 million years ago; see van Schaik & Burkart, 2010). For instance, in light of our best estimations of Pleistocene hominid population densities (for a review plus a discussion of the remaining uncertainties, see Hawkes, Hunley, Lee, & Wolpoff, 2000), the contribution of habitat saturation and inter-group competition should be expected to be minor. In contrast, it seems likely that shifts to more open habitats increased predation risk (Hart & Sussman, 2005) and that Pleistocene climatic harshness and/or instability and shifts to more seasonal habitats resulted in heightened unpredictability (Potts, 1998). Further, our predecessors are thought to have rapidly colonized large areas outside Africa some 1.9 to 1.7 million years ago, and some have argued that this is linked to our species' cooperative childcare (Hrdy, 2005, 2009; van Schaik & Burkart, 2010). In sum, some of the pressures which have repeatedly favored cooperative breeding also seem to have operated in human evolution.

Let me now turn to male–female bonding, and again consider the resource scarcity hypothesis first. As said, the hypothesis conflicts with the evidence of callitrichids (versus *Cebus*). More generally, primates are remarkable in that most of them exhibit year-round male–female associations (as said above), *despite* the considerable variation in feeding competition they experience. The relevant selection pressure is thus likely not scarcity.

Are there any other pressures that are invariably associated with the convergent evolution of strong male–female bonds (invalidating Excuse 4)? Several hypotheses have been proposed in this respect. According to a very prominent one, male–female associations serve to reduce the risk of infanticide by strange males (van Schaik & Kappeler, 1997). So in these associations, females tend to provide services to males, which in return provide protection for the female and her infants, thereby increasing the probability of survival of their putative young. The infanticide protection hypothesis finds support in burying beetles, barn swallows, house wrens, Arctic squirrels, mountain gorillas, and chacma baboons, but not in gibbons, and only equivocally in lemurs (Palombit, 2000). Further, Quinlan and Quinlan (2007) describe cross-cultural evidence inconsistent with the infanticide protection hypothesis, but consistent with the paternal investment and mate guarding hypothesis, the latter likely being implied also in gibbons, the former only in siamang gibbons (Palombit, 1996). Hence, convergence, contra Excuse 4, actually does shed interesting new light on the human case.

5.5. Final notes on excusability and the Comparative Convergence Approach

The above assessment shows the sense in which the four excuses can be deployed to diagnose the excusability of a putative case of chimpocentrism, or more accurately, of not applying the Comparative Convergence Approach. But it has also shown the merits of the latter, at least implicitly. Let me briefly sum up the results. First, by granting convergence evidential status, there appears to be little support for the hypothesis that human altruism was prompted by resource scarcity. In contrast, second, convergence seems to support the cooperative breeding hypothesis, according to which cooperative breeding played a substantial role in the evolution of our prosociality. Third, convergence suggested a set of hypotheses to account for the altruism evidenced in human pair-bonds, i.e., the infanticide protection hypothesis, the mate guarding hypothesis, and the paternal investment hypothesis. The first of these could subsequently be eliminated in light of cross-cultural data.

I take these results, however tentative, to be significant enough to be examined further and to deserve consideration in a story of how human morality evolved. More generally, they illustrate the way in which the Comparative Convergence Approach affords claims which chimpocentrism does not; and the way in which chimpocentrism generates claims that do not hold water on further inspection.

6. Concluding remarks

In the above, I hope to have made clear several things. First, I have pointed out three problems associated with chimpocentric reconstructions of human evolution. These problems, I subsequently argued, may be handled by pursuing what I called the Comparative Convergence Approach—an approach that should be favored unless the excuses provided in Section 3 apply. Finally, using a recent reconstruction offered by Kitcher, I illustrated the reality of chimpocentrism; how my work may help to diagnose the excusability of not applying the Comparative Convergence

¹⁷ Kitcher seems to hint at this hypothesis when he writes (p. 68): “Perhaps as hominid brain size increased, it was necessary for babies to be born at developmentally earlier stages (so their heads would still pass through the birth canal), with the consequence that they were more dependent for a longer period of time. The resulting selection pressure may have favored enhanced altruistic tendencies in the specific context of providing care for helpless young” Still, Kitcher doesn't further develop this thought, because: “Without underestimating the importance of steps like these, it is evident that neither hominids nor contemporary human beings have escaped entirely from the difficulties and tensions, the rivalries and conflicts, of chimpanzee social life. If human societies are less vulnerable to breakdown than those of our primate relatives, it is because other modifications have taken place.”

Approach; and how convergence, which the latter trades on, may illuminate human evolution.

In general, the exercise indicates that investigations of human nature may benefit greatly from phylogenetic comparisons much broader than commonly applied. Even quite distant species may reveal things (about ourselves) which under a strict chimpanzee approach would have gone unnoticed.

I acknowledge that philosophers will face great practical difficulties when trying to expand the scope of their comparisons: the literature is huge, traits of interest to philosophers may not have been of interest to comparative biologists, species that may be highly relevant are endangered, few species have been studied as systematically as chimpanzees, phylogenetic and convergence analyses are time- and resource-consuming. Nonetheless, even if practical issues would force one to pursue a chimpanzee approach, one should keep in mind and be explicit about its limitations. And if these have become even a little clearer, the aim of this paper would be accomplished.

Acknowledgments

Thanks to two anonymous reviewers and Wybo Houkes for comments on an earlier version of this paper.

References

- Alexander, R., & Noonan, K. (1979). Concealment of ovulation, parental care, and human social evolution. In N. Chagnon & W. Irons (Eds.), *Evolutionary biology and human social behavior* (pp. 436–453). Duxbury Press.
- Allman, J., McLaughlin, T., & Hakeem, A. (1993). Brain-weight and life-span in primate species. *Proceedings of the National Academy of Sciences*, 90, 118–122.
- Brown, A., & Zunino, G. (1990). Dietary variability in *Cebus apella* in extreme habitats: Evidence for adaptability. *Folia Primatologica*, 54, 187–195.
- Burkart, J., Fehr, E., Efferson, C., & van Schaik, C. (2007). Other-regarding preferences in a non-human primate: Common marmosets provision food altruistically. *Proceedings of the National Academy of Sciences*, 104, 19762–19766.
- Burkart, J., Hrdy, S., & van Schaik, C. (2009). Cooperative breeding and human cognitive evolution. *Evolutionary Anthropology*, 18, 175–186.
- Burkart, J., & van Schaik, C. (2010). Cognitive consequences of cooperative breeding in primates? *Animal Cognition*, 1, 119.
- Burley, N. (1979). The evolution of concealed ovulation. *American Naturalist*, 114, 835–858.
- Burt, A. (1992). “Concealed ovulation” and sexual signals in primates. *Folia Primatologica*, 58, 1–6.
- Byrne, R. (1997). The technical intelligence hypothesis: An additional evolutionary stimulus to intelligence. In A. Whiten & R. Byrne (Eds.), *Machiavellian intelligence II*. Cambridge University Press.
- Caro, T., & Hauser, M. (1992). Is there teaching in nonhuman animals? *Quarterly Review of Biology*, 67, 151–174.
- Clutton-Brock, T. (2006). Cooperative breeding in mammals. In P. Kappeler & C. van Schaik (Eds.), *Cooperation in primates and humans: Mechanisms and evolution* (pp. 172–190). Springer.
- Currie, A. (2013). Convergence as evidence. *British Journal for the Philosophy of Science*, 64, 763–786.
- Daniels, D. (1983). The evolution of concealed ovulation and self-deception. *Ethology and Sociobiology*, 4, 69–87.
- de Waal, F. (1984). *Chimpanzee politics: Power and sex among apes*. John Hopkins University Press.
- de Waal, F. (1989). *Peacemaking among primates*. Harvard University Press.
- de Waal, F. (1996). *Good natured: The origins of right and wrong in primates and other animals*. Harvard University Press.
- Deaner, R., Barton, R. A., & van Schaik, C. (2003). Primate brains and life histories: Renewing the connection. In P. Kappeler & M. Pereira (Eds.), *Primate life histories and socioecology* (pp. 233–265). University of Chicago Press.
- DeVore, I., & Washburn, S. (1963). Baboon ecology and human evolution. In F. Howell & F. Bourliere (Eds.), *African ecology and human evolution* (pp. 335–367). Aldine Publishers.
- Digby, L., Ferrari, S., & Saltzman, W. (2007). Callitrichines: The role of competition in cooperatively breeding species. In C. Campbell, A. Fuentes, K. MacKinnon, M. Panger, & S. Bearder (Eds.), *Primates in perspective* (pp. 85–106). Oxford University Press.
- Dubreuil, B. (2010). *Human evolution and the origins of hierarchies: The state of nature*. Cambridge University Press.
- Dunbar, R. (1995). Neocortex size and group size in primates: A test of the hypothesis. *Journal of Human Evolution*, 28, 287–296.
- Dunbar, R., & Bever, J. (1998). Neocortex size predicts group size in carnivores and some insectivores. *Ethology*, 104, 695–708.
- Foley, R. (1989). The evolution of hominid social behaviour. In V. Standen & R. Foley (Eds.), *Comparative socioecology: The behavioural ecology of humans and other mammals* (pp. 474–493). Blackwell Scientific Publishers.
- Fox, E. (2002). Female tactics to reduce sexual harassment in the Sumatran orangutan (*Pongo pygmaeus abelii*). *Behavioral Ecology and Sociobiology*, 52, 93–101.
- Geary, D., Bailey, D., & Oxford, J. (2011). Reflections on the human family. In C. Salmon & T. Shackelford (Eds.), *The Oxford handbook of evolutionary family psychology* (pp. 365–385). Oxford University Press.
- Geary, D., & Flinn, M. (2001). Evolution of human parental behavior and the human family. *Parenting: Science and Practice*, 1, 5–61.
- Ghiglieri, M. (1987). Sociobiology of the great apes and the hominid ancestor. *Journal of Human Evolution*, 16, 319–357.
- Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Harvard University Press.
- Hart, D., & Sussman, R. (2005). *Man the hunted: Primates, predators, and human evolution*. Westview Press.
- Harvey, P. H., & Pagel, M. (1991). *The comparative method in evolutionary biology*. Oxford University Press.
- Hauser, M., Chen, M., Chen, F., & Chuang, E. (2003). Give unto others: Genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proceedings of the National Academy of Sciences*, 100, 2363–2370.
- Hawks, J., Hunley, K., Lee, S., & Wolpoff, M. (2000). Population bottlenecks and Pleistocene human evolution. *Molecular Biology and Evolution*, 17, 2–22.
- Hoppitt, W., Brown, G., Kendal, R., Rendell, L., Thornton, A., Webster, M., et al. (2008). Lessons from animal teaching. *Trends in Ecology and Evolution*, 23, 486–493.
- Hrdy, S. (2005). Evolutionary context of human development: The cooperative breeding model. In C. Carter, L. Ahnert, K. Grossmann, S. Hrdy, M. Lamb, & S. Porges, et al. (Eds.), *Attachment and bonding: A new synthesis* (pp. 9–32). MIT Press.
- Hrdy, S. (2009). *Mothers and others: The evolutionary origins of mutual understanding*. Harvard University Press.
- Humphrey, N. (1976). The social function of intellect. In P. Bateson & R. Hinde (Eds.), *Growing points in ethology* (pp. 303–317). Cambridge University Press.
- Islar, K., & van Schaik, C. (2012). How our ancestors broke through the gray ceiling. *Current Anthropology*, 53, S453–S465.
- Joyce, R. (2006). *The evolution of morality*. MIT Press.
- Kappeler, P., & van Schaik, C. (2002). Evolution of primate social systems. *International Journal of Primatology*, 23, 707–740.
- Kitcher, P. (2011). *The ethical project*. Harvard University Press.
- Laland, K. N., & Brown, G. (2003). *Sense and nonsense: Evolutionary perspectives on human behaviour*. Oxford University Press.
- Marino, L. (1996). What can dolphins tell us about primate evolution? *Evolutionary Anthropology*, 5, 81–86.
- Moore, J. (1996). Savanna chimpanzees, referential models, and the last common ancestor. In W. McGrew, L. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 275–292). Cambridge University Press.
- Nunn, C. (2011). *The comparative method in evolutionary anthropology and biology*. University of Chicago Press.
- Pagel, M. (1994). The adaptationist wager. In P. Eggleton & R. Vane-Wright (Eds.), *Phylogenetics and ecology* (pp. 29–51). Academic Press.
- Palombit, R. A. (1996). Pair bonds in monogamous apes: A comparison of the siamang (*Hylobates syndactylus*) and the white-handed gibbon (*Hylobates lar*). *Behaviour*, 133, 321–356.
- Palombit, R. A. (1999). Infanticide and the evolution of pair bonds in nonhuman primates. *Evolutionary Anthropology*, 7, 117–129.
- Palombit, R. A. (2000). Infanticide and the evolution of male–female bonds in animals. In C. van Schaik & C. Janson (Eds.), *Infanticide by males and its implications* (pp. 239–268). Cambridge University Press.
- Pawłowski, B. (1999). Loss of oestrus and concealed ovulation in human evolution: The case against the sexual selection hypothesis. *Current Anthropology*, 40, 257–276.
- Potts, R. (1998). Variability selection in hominid evolution. *Evolutionary Anthropology*, 7, 81–96.
- Prinz, J. (2007). *The emotional construction of morals*. Oxford University Press.
- Quinlan, R., & Quinlan, M. (2007). Evolutionary ecology of human pair-bonds: Cross-cultural tests of alternative hypotheses. *Cross-Cultural Research*, 41, 149–169.
- Reader, S., & Hrolic, S. (2012). The limits of chimpanzee–human comparisons for understanding human cognition. *Behavioral and Brain Sciences*, 35, 238–239.
- Sayers, K., & Lovejoy, O. (2008). The chimpanzee has no clothes: A critical examination of *Pan troglodytes* in models of human evolution. *Current Anthropology*, 49, 87–114.
- Sayers, K., Raghantie, M., & Lovejoy, O. (2012). Human evolution and the chimpanzee referential doctrine. *Annual Review of Anthropology*, 41, 119–138.
- Schwartz, J. (1987). *The red ape: Orang-utans and human origins*. Houghton Mifflin.
- Shultz, S., & Dunbar, R. (2005). Both social and ecological factors predict ungulate brain size. *Proceedings of the Royal Society of London: Series B*, 273, 207–215.
- Sillén-Tullberg, B., & Möller, A. P. (1993). The relationship between concealed ovulation and mating systems in anthropoid primates. A phylogenetic analysis. *The American Naturalist*, 141, 1–25.
- Sober, E. (1988). *Reconstructing the past: Parsimony, evolution, and inference*. MIT Press.
- Sober, E. (2002). Reconstructing the character states of ancestors: A likelihood perspective on cladistic parsimony. *The Monist*, 85, 156–176.

- Sterck, E., Watts, D., & van Schaik, C. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, 41, 291–309.
- Thornton, A., & Raihani, N. (2008). The evolution of teaching. *Animal Behaviour*, 75, 1823–1836.
- Thornton, A., & Raihani, N. (2010). Identifying teaching in wild animals. *Learning and Behavior*, 38, 297–309.
- Utami, S., Goossens, B., Bruford, M., de Ruiter, J., & van Hooff, J. (2002). Male bimaturism and reproductive success in Sumatran orangutans. *Behavioral Ecology*, 13, 643–652.
- Vaesen, K. (2012). The cognitive bases of human tool use [target article]. *Behavioral and Brain Sciences*, 35, 203–218.
- van Hooff, J., & van Schaik, C. (1994). Male bonds: Affiliative relationships among nonhuman primate males. *Behaviour*, 130, 309–337.
- van Schaik, C., & Burkart, J. (2010). Mind the gap: Cooperative breeding and the evolution of our unique features. In P. Kappeler & J. Silk (Eds.), *Mind the gap: Tracing the origins of human universals* (pp. 477–496). Springer.
- van Schaik, C., & Kappeler, P. (1997). Infanticide risk and the evolution of male–female association in primates. *Proceedings of the Royal Society of London: Series B*, 264, 1687–1694.
- van Schaik, C., Preuschoft, S., & Watts, D. (2004). Great ape social systems. In A. Russon & D. R. Begun (Eds.), *The evolution of thought: Evolutionary origins of great ape intelligence* (pp. 190–209). Cambridge University Press.
- Washburn, S. (1960). Tools and human evolution. *Scientific American*, 203, 62–75.
- Washburn, S., & DeVore, I. (1961). Social behavior of baboons and early man. In S. Washburn (Ed.), *The social life of early man* (pp. 91–105). Aldine Publishers.
- Whiten, A., & van Schaik, C. (2007). The evolution of animal ‘cultures’ and social intelligence. *Philosophical Transactions of the Royal Society B*, 362, 603–620.
- Wich, S., Setia, T., Delgado, R., Utami, I., Singleton, S. S., & van Schaik, C. (2009). Social organization and male–female relationships. In S. Wich, S. Utami, T. Setia, & C. S. van Schaik (Eds.), *Orangutans: Geographic variation in behavioral ecology and conservation* (pp. 245–253). Oxford University Press.
- Wrangham, R. (1987). The significance of African apes for reconstructing human social evolution. In W. Kinzey (Ed.), *Primate models of hominid evolution* (pp. 51–71). SUNY Press.
- Yamagiwa, J. (2004). Diet and foraging of the great apes: Ecological constraints on their social organizations and implications for their divergence. In A. Russon & D. R. Begun (Eds.), *The evolution of thought* (pp. 220–233). Cambridge University Press.