



CrossMark
click for updates

Review

Cite this article: van Schaik CP. 2013 The costs and benefits of flexibility as an expression of behavioural plasticity: a primate perspective. *Phil Trans R Soc B* 368: 20120339. <http://dx.doi.org/10.1098/rstb.2012.0339>

One contribution of 15 to a Theme Issue 'Flexibility and constraint in the evolution of mammalian social behaviour'.

Subject Areas:

behaviour, evolution

Keywords:

geographical variation, local adaptation, flexibility

Author for correspondence:

Carel P. van Schaik
e-mail: vschaik@aim.uzh.ch

The costs and benefits of flexibility as an expression of behavioural plasticity: a primate perspective

Carel P. van Schaik

Anthropological Institute and Museum, University of Zurich, Winterthurerstrasse 190, Zurich 8057, Switzerland

Traditional neo-Darwinism ascribes geographical variation in morphology or in behaviour to varying selection on local genotypes. However, mobile and long-lived organisms cannot achieve local adaptation this way, leading to a renewed interest in plasticity. I examined geographical variation in orang-utan subsistence and social behaviour, and found this to be largely owing to behavioural plasticity, here called flexibility, both in the form of flexible individual decisions and of socially transmitted (cultural) innovations. Although comparison with other species is difficult, the extent of such flexibility is almost certainly limited by brain size. It is shown that brains can only increase relative to body size where the cognitive benefits they produce are reliably translated into improved survival rate. This means that organisms that are very small, face many predators, live in highly seasonal environments, or lack opportunities for social learning cannot evolve greater flexibility, and must achieve local adaptation through selection on specific genotypes. On the other hand, as body and brain size increase, local adaptation is increasingly achieved through selection on plasticity. The species involved are also generally those that most need it, being more mobile and longer-lived. Although high plasticity buffers against environmental change, the most flexible organisms face a clear limit because they respond slowly to selection. Thus, paradoxically, the largest-brained animals may actually be vulnerable to the more drastic forms of environmental change, such as those induced by human actions.

1. Introduction

Evolutionary biologists are interested in how organisms achieve adaptation to local conditions. The traditional neo-Darwinian 'modern synthesis' assumed highly canalized development, and thus a rather direct relationship between genotype and phenotype. In such a scenario, natural selection can produce a tight fit between local conditions and a species' genotype, and thus achieve local adaptation. Pronounced geographical phenotypic variation within a species has often been ascribed to this process. Indeed, many studies, especially of smaller vertebrates, conducted under this paradigm suggested genetically based local or regional adaptation [1]. Although such work mostly involved morphology, behavioural variation can often be interpreted in the same way [2].

This pathway to local adaptation is foreclosed where local conditions vary extensively over distances routinely covered by individuals' range use or where gene flow owing to immigration from other places with other conditions prevents optimum adaptation to local conditions [3]. This pathway is also closed where the local conditions vary over time, especially when a single individual encounters fluctuating conditions during its lifetime. Thus, organisms that are both more mobile and long-lived are less likely to achieve local adaptation through selection on directly genetically based traits [4]. As a result, attention has increasingly focused on the interaction between the genotype and the nature of development. Developmental plasticity is often the adaptive means to fine-tune adaptation to local conditions, as shown by numerous examples of adaptive plastic responses [5,6].

Nonetheless, plasticity must also have some upper limit, because it will inevitably have costs and an upper limit of effectiveness [1]. First, the organism must pay a price for maintaining the physiological mechanisms to perceive the state of the environment and to change its phenotype in response to this. Surprisingly, however, empirical studies have found little evidence that these costs limit the expression of plasticity [7]. Second, there should be limits to how effective plasticity is [8], because many phenotypic changes are irreversible, and thus can be made only once in a lifetime, and because there is often a delay between sensing the environment (e.g. *in utero* in a mammal) and the expression of the modification in the phenotype (e.g. in the adult). The longer the delay, the less likely the environmental signal used for the plastic response predicts the conditions during the stage where the phenotypic trait concerned most affects fitness [8]. For these reasons, plastic responses in some environments may actually be maladaptive. Accordingly, we expect plasticity to reach optimum phenotypes only within a limited range of conditions. This conclusion should not be surprising because otherwise it would be difficult to explain the high species diversity in natural communities. Coexistence should be especially rare for congeners, for whom even fairly moderate plasticity could produce similar phenotypes.

There is one form of plasticity to which these limitations of irreversibility and delayed response do not apply to the same extent: behaviour. The function of learning is exactly to provide a reversible form of plasticity that can also be effective with relatively short delays. Thus, it would appear that behavioural plasticity, which I will refer to here as *flexibility*, is a key tool for organisms to achieve optimum local adaptation, although it may fail where environments change too rapidly [8]. Flexibility is the opposite of modular cognitive adaptations [9], which are developmentally canalized.

This argument ignores the first limitation to earlier-mentioned plasticity: the costs of behavioural plasticity. Flexible behaviour derives from learning by various mental mechanisms that vary in cognitive complexity and vary in the extent of social inputs [9]. These processes are normally considered part of intelligence by cognitive psychologists [10,11], and recent work has shown them to be tightly linked to brain size [12,13], which suggests that the costs to flexibility amount to the costs of supporting a larger brain. Thus, flexibility may well be limited by the brain size a species can evolve.

This study has two aims. First, I will review fieldwork showing that orang-utans (genus *Pongo*), which are among the largest-brained primates, use this flexibility to fine-tune their adaptation to local conditions. Second, I will review recent comparative work on the evolution of brain size to identify the nature of the costs of brain size. This allows us to identify several limitations to cognitive adaptations, and thus recognize the kinds of species that are prevented from going down the high-flexibility pathway. The discussion examines the consequences of this variation in flexibility.

2. Geographical variation in orang-utan behaviour

At present, orang-utans only occur on the islands of Sumatra and Borneo, where they show a substantial geographical variation in morphology, behaviour and probably physiology. A collective effort involving dozens of fieldworkers at more

than a dozen orang-utan study sites, compiled in Wich *et al.* [14], recently made it possible to produce an overview of geographical variation in orang-utan behaviour and biology [15]. Table 1, based on Wich *et al.* [14] but supplemented with more recent work, divides their natural behaviour into two main categories that may vary in their responsiveness to external conditions or conspecifics, and as a result could vary in the degree of flexibility: subsistence behaviours and social behaviours.

Table 1 is organized by subspecies: (i) the northern Sumatran (*Pongo abelii*), (ii) the western and central Bornean (*P. pygmaeus wurmbii*) and (iii) northeast Bornean *P. p. morio* (there is virtually no information on another Bornean subspecies, *P. p. pygmaeus*). These subspecies are arranged from west to east, in the direction of a major ecological gradient of increasing cloudiness and thus warm nights, resulting in lower forest fruit production, and increased impact of recurrent El-Niño-related events [16,24].

The three units differ in morphology, with the Bornean females showing more robust mandibles but smaller brains, and faster-paced life history, expressed in faster development; these differences are most pronounced in the northeast Borneans. They also vary in diet. Mean fruit and insect content of the diet declines from west to east, whereas temporal variability, and therefore reliance on non-fruit fall-back foods of lower nutritional quality, increases. In the same direction, we see a decrease in population density, female mobility and home range size. Perhaps as a result of the less favourable energy budgets, the units also differ in the number of nests built during the day (though not in that of night nests, which is always one).

The absence of tigers on Borneo allows flanged adult males (defined in Utami *et al.* [25]) to travel on the ground there, but not on Sumatra. Similarly, ground nests, invariably built by flanged males, are found only on Borneo.

Social organization varies in the same direction, with clusters of female relatives decreasing in size from the west to the east, along with time spent in friendly association. Although females in Sumatra associate closely and share food [26,27], those in west Borneo avoid each other and are more competitive [28] (there is no information on those from the northeast). Male–female relationships differ, probably because the monopolization by dominant males is highest in Sumatra and lowest in northeast Borneo [29]. Flanged males compete much more directly and violently on Borneo, and direct their long calls more at rivals than to attract females [30]. Sumatran males, by contrast, call more often spontaneously, and females in all reproductive states approach these calls [31]. Moreover, females form earshot associations with the dominant flanged male in the area, in which they actively regulate their distance to him [22]. Mating relations are different, with close male–female mating associations lasting weeks in Sumatra, but only days, if that, in northeast Borneo [27]. Forced matings are higher on Borneo [32], and perhaps the norm in northeast Borneo [30,33]. The development of the full complement of secondary sexual characteristics (with cheek flanges and long calls) is arrested in Sumatra, with some males waiting for at least two decades [25], but far less so on Borneo. This difference can be linked to the reduced ability of the dominant flanged males on Borneo to monopolize mating access to fertile females [34].

Overall, then, this compilation reveals substantial geographical variation in orang-utan subsistence and social

Table 1. Overview of geographical variation in the behavioural ecology, comfort behaviour and social organization of orang-utans. Largely after Wich *et al.* [14], supplemented with recent references.

	Sumatra <i>P. abelii</i>	Borneo <i>P. p. wurmbii</i>	Borneo <i>P. p. morio</i>	source (other than [14])
habitat				
forest productivity	higher	lower	lower	[16]
interannual variability in production	less	more	most?	
tigers	present	absent	absent	
morphology				
mandibles	gracile	robust	very robust	(+ C. P. van Schaik 2010, unpublished data)
average female brain size (cm ³)	388	374	364	
life history				
birth intervals (mean, years)	8.75	7.7	6.1	C. P. van Schaik 2010, unpublished data
age at reduced association with mother	from <i>ca</i> 10 years	from <i>ca</i> 6 years	from <i>ca</i> 6 years	
age at first birth	15–16	13–15	less than 13	
subsistence behaviours				
mean frugivory (% feeding time)	<i>ca</i> 67%	<i>ca</i> 68%	<i>ca</i> 58%	
variation in fruit intake	low	higher	highest	[17]
reliance on non-fruit fallbacks	very rare	common	commonest	
mean insectivory (% feeding time)	<i>ca</i> 11%	<i>ca</i> 6%	<i>ca</i> 1.5%	
meat eating	present	rare	absent?	[18]
female home range size	larger	intermediate	smaller	
female daily travel distance (m)	<i>ca</i> 820	<i>ca</i> 760	<i>ca</i> 230	
population density	higher	usually lower	among lowest	
terrestrial travel by flanged males	very rare	common	common	
comfort				
number of day nests built/day	<i>ca</i> 0.8	<i>ca</i> 0.4	<i>ca</i> 0.05	
nest-building styles/elements per nest	many	fewer	?	[19]
ground nesting	absent	present	present	C. P. van Schaik 2010, unpublished data
social behaviours				
clusters of female relatives	large	variable	small	[20]
sociability	highest	lower	lower	
susceptibility to social stress	lower	higher	higher	[21]
earshot associations (fl. male–female)	present	absent	absent?	B. Spillmann 2012, personal communication
flanged male monopolization	high	low	low	L. Dunkel 2012, personal communication
% long calls elicited	<i>ca</i> 15%	greater than 40%	?	[22]
duration of consortships	weeks	days	shorter	
presence of forced matings	lower	higher	higher	
male developmental arrest	present	weak	absent?	[23]

behaviour, as well as life history and morphology. Much of this variation reflects the environmental gradient, but there is obviously also much between-site variation within each of the three units [14]. This variation allows us to examine patterns in the differences between pairs of sites.

3. Explaining variation in orang-utan behaviour

(a) The role of genetic differences

Orang-utans cover a large geographical region, on two islands that were separated much of the time by either sea or unsuitable habitat. Each island also has mountain ranges

Table 2. Percentage of variance in orang-utan behavioural differences between pairs of sites explained by Mantel correlations with genetic or environmental differences between these sites (using two different ways of estimating genetic differences: non-protein-coding HVR-I and sequences of three concatenated coding genes, both in mtDNA). Partial values, which control for the effect of the other independent variable, are placed in italics. After Krützen *et al.* [24].

	HVR-I				coding genes			
	genetic diff.		environmental diff.		genetic diff.		environmental diff.	
	direct	<i>partial</i>	direct	<i>partial</i>	direct	<i>partial</i>	direct	<i>partial</i>
behavioural ecology/subsistence	13.5**	4.0	35.2***	28.0**	13.0**	2.5	35.2***	27.4**
social organization	12.3	6.9	29.6*	25.4*	7.4	5.6	29.6*	28.3*

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

and impassable rivers. Thus, spatially structured genetic differentiation is to be expected, providing an opportunity for selection to produce local adaptation. In the absence of local or regional selection, this differentiation reflects the effects of genetic drift because the now-distinct populations were separated from a common ancestor.

Two processes may serve to limit meaningful genetic differentiation. First, the population on Borneo has faced a near-extinction during the last glacial maximum between 60 and 20 kya, followed by expansion and substructuring during the subsequent warming and expansion of closed forests [35,36]. It is therefore not clear whether there was enough time for adaptation to arise, given the slow generation time of orang-utans of around 25 years [37]. Second, there is a dramatic sex difference in dispersal distance. Females show very strong philopatric tendencies [20,38], whereas males, by contrast, tend to move over long distances [39]. As a result, although at the mtDNA level, a very strong population structuring is found, this patterning is much weaker at the autosomal level [36]. Occasional male dispersal movements during periods of low sea level have even served to limit the genetic differences between the metapopulations of the two islands [36].

This structuring enables examination of the relation between genetic variation and variation in various aspects of behaviour. However, this analysis is not straightforward. Only in the rarest of cases is there information on the genes responsible for the occurrence of a particular behaviour pattern. Moreover, for behaviour, we know that in most cases the traits are polygenic, that is, affected by numerous loci [40], making it impossible to link geographical variation in behavioural traits directly to that in particular genes. We must therefore take an alternative approach.

The logic of this alternative is as follows. When two populations separate, they will gradually diverge genetically. The degree of genetic divergence on non-coding loci is affected by the time since separation, and thus the opportunity for selection to make them different. We can therefore relate pair-wise differences between sites in behaviour to those in non-coding genes. This approach is justified if the traits involved are polygenic, because genetic differentiation measures based on neutral markers are quite similar to those based on quantitative trait loci, regardless of the selection on the latter [41]. The reason for this is that each locus of a polygenic trait behaves as if it evolved nearly neutrally, even under selection [42].

If selection produced the differences, we should see a correlation between the genetic and the behavioural difference.

The absence of a correlation would therefore be indicative of some form of flexibility (behavioural plasticity), especially if there is independent evidence in favour of this alternative. This approach has been applied to call features of birds and frogs. In frogs, where there is no evidence for call learning, dialect differences in calls covary with genetic differences between populations, which diverged since the Pleistocene [43], whereas in songbirds, where songs are generally learned, such covariance is usually not found [44]. The approach thus assumes that not so much time has elapsed since divergence that genetic differences owing to selection have reached equilibrium. In the case of orang-utans, this assumption is warranted, because species with very low rates of mortality cannot sustain strong selection pressures [45], and, given the orang-utan's generation time of around 25 years [37], achieving local adaptation through selection would take numerous generations.

The absence of a correlation between behavioural and genetic differences thus leads to the conclusion that flexibility is present. However, behavioural variation could reflect random behavioural variation (drift) rather than behavioural adaptation to local conditions, i.e. flexibility. In an additional analysis, one could thus correlate pair-wise differences in behavioural profiles in subsistence ecology and social organization with pair-wise differences in environmental conditions. Because genetic differences and environmental differences are both affected by geographical distance and will thus inevitably be correlated, we must partial out the effect of genetic differences on those of environmental differences, and vice versa. When this was done for the orang-utans [24], environmental differences explained about 27 per cent of the variation in orang-utan subsistence and social behaviours, more than five times the proportion of variance explained by genetic differences (table 2). Even direct correlations, uncorrected for the effect of geographical distance on genetic distance, showed the same pattern. In sum, genetic variation, while pronounced, explains only a very modest amount of the behaviour variability seen in this taxon. Instead, the latter reflects flexibility.

(b) Evidence for flexibility (behavioural plasticity)

These results, while implicating flexibility as the mechanism of local adaptation, do not reveal whether the source of flexibility is individual innovation or social learning. Individual flexibility reflects solutions to ecological or social problems acquired independently by the individual during its own lifetime, i.e. learned responses. These responses can be very

minor deviations from the natural repertoire and be biologically prepared, such as switching to tree bark when food is scarce. But they can also be major and less predictable, and thus represent innovations [46], such as the technique of extracting seeds from the *Neesia* fruit using tools [47]. Each species has a repertoire of potential innovations, the zone of latent solutions [48], which could be seen as a list of the potential innovations its members can produce along with the probability of each occurring. The value of this approach will become apparent when one compares species: even closely related species tend to show some clear differences in their innovation repertoires [49]. The more improbable the innovation, the more likely social learning is involved in its acquisition by maturing individuals.

The method used earlier does not allow one to distinguish between these two sources of flexibility. However, one indirect way to do so is to examine behavioural variants that have previously been claimed to be cultural, i.e. innovations that have spread and are maintained primarily by social learning. Dispersal barriers should then produce geographical patchiness similar to that produced by genetic or environmental differences [50].

There are reasons to believe that behavioural variation in orang-utans may have an important cultural component. The behavioural repertoire is known to contain around 30 of such variants [51], but it is not known how much of each individual's repertoire is actually acquired through some form of socially supported learning. When we subject these putatively cultural elements to the same statistical analysis, we find that genetic and environmental differences explain only a small, statistically insignificant proportion of their variation [24], approximately 5 per cent and 8 per cent, respectively. This suggests that social learning of innovations plays a role in explaining the geographical variation in behaviour.

This conclusion is reached by eliminating alternative interpretations through the analysis of correlations and therefore is not entirely satisfying. However, it is consistent with detailed behavioural evidence [24]. Experiments have shown that orang-utans can imitate [52], allowing successful social transmission of novel techniques [53]. In the wild, immatures pay close, selective attention to foraging activities by their mother or their mother's associates, especially when they are rare or not yet acquired by them, but refrain from much independent exploration [54]. The latter is also suggested by the striking absence of response to novelty in natural conditions [55], including novel foods [56]. Such strong avoidance of novelty is not found in many species [57].

More localized comparisons show that the diet of two sites separated by an impassable river but with large overlap in flora can differ substantially. Bastian *et al.* [58] found that while the main fruit species selected by Bornean orang-utans at Tuanan and nearby Sungai Lading, across the river, were identical, the fallback foods, which are taken when preferred fruits are rare, were not. The most plausible explanation is that fallback foods may vary little in their profitability and give poor sensory feedback as to their actual profitability. Thus, a near-random subset is chosen from among the potentially suitable fallback foods. What is of course striking is that animals at the same site end up taking largely the same subset, consistent with a cultural explanation. It is impossible to exclude that subtle ecological differences, for example, taste or quality differences between sites in items of the same plant species [59], independently

lead individual animals to discover their own optimum diet, but the observed lack of individual exploration and the strong propensity to rely on earlier-noted social information, suggest this is the less parsimonious explanation. The latter is also supported by experiments showing that animals preferentially rely on information by more experienced individuals over that of their own [60].

Overall, then, we must conclude that a sizeable amount of geographical variation in orang-utans' ecological and social behaviour arises owing to flexibility, which is partly acquired through social transmission of innovations. Moreover, detailed behavioural studies support the idea that this variation is actually adaptive [27,47].

(c) How about other taxa?

This conclusion almost certainly generalizes to chimpanzees, for whom there is both extensive geographical variation in behaviour [61] that is accompanied by evidence for much cultural variation [62,63] and clear evidence for developmentally based flexibility in the form of large innovation repertoires ([62], cf. [64]). One study found genetic correlates for much purported cultural variation among chimpanzee populations ([65], but see [66]) but did not examine subsistence or social behaviours not thought to be cultural.

In some other primates, geographical variation in social organization is documented (*Papio* [67]; *Varecia* [68]), but it is not known how much of this is accompanied by genetic differences (but see [69]). Different species in the genus *Eulemur* show plasticity in ecology but not in social behaviour [70], suggesting overall less flexibility than among orang-utans or chimpanzees. In non-primate organisms, by contrast, geographical variation in behaviour is still often interpreted as being anchored in genetic differences [71,72], although we should of course expect similar flexibility in other culture-bearing birds and mammals [73,74].

Studies of large animals generally focused on plasticity of various kinds, whereas those of small animals focused on genetic variation. Moreover, ordinary experiments comparing subspecies or populations permit estimation of plasticity, but such experiments are logistically difficult with large and large-brained organisms, and have not been carried out for primates. Thus, the information available for conclusions is biased. Nonetheless, although other interpretations cannot be excluded, the available evidence supports the view that flexibility is greater in species known for their behavioural variability, including innovation repertoires or cultural variation, than in others.

4. Evolutionary limitations on brain size

In order to compare flexibility across lineages, we need a proxy measure. All the aspects of flexibility, from innovation repertoires to learning ability, show a strong correlation with brain size, or measures of brain size corrected for the effects of body size, in birds and mammals, including primates [12,13,75–78]. Moreover, the more demanding observational forms of social learning are concentrated in species with larger brains [75,79,80]. A plausible interpretation of these correlations is that a species' brain size, properly controlled for body size, is causally related to its flexibility.

Recent work suggests that brain size may be constrained owing to the unusual energetic costs and the developmental and reproductive price the organism must pay, if it evolves

larger brain size. First, brain tissue is energetically expensive [81]: per unit mass its caloric demands are among the highest in the body, perhaps because synaptic signalling is energetically very expensive [82]. Worse, brains that are still growing and differentiating require even more energy per unit mass [83]. Second, the energy needs of brains are inflexible, and thus cannot temporarily be reduced [84]. Third, the activity of brains does not depend much on the degree of external stimulation or perceived need [85]. As a result, brain enlargement is only possible where this generates the extra energy needed for it, or where energy can be shunted from other demands.

Awareness of these costs has led to the idea that a species' brain size, and thus its potential flexibility, is determined by the extent to which organisms can overcome these constraints. For instance, great apes are among the largest-brained lineages, relative to body size, found among mammals, but they are certainly not unique in having to face variability in ecology when they move or as they age. This suggests that something must be holding brain size back, despite the presence of numerous potential cognitive advantages.

There may be four general conditions preventing selection on increased brain size, in spite of potential cognitive benefits: (i) small body size; (ii) the inability to achieve a stable increase in net energy intake; (iii) the inability to improve survival through cognitive performance; and (iv) limited opportunities for social learning [49,80].

One obvious, but fundamental limitation may be sheer body size. Because sense organs and brains are relatively much larger in small organisms than in large ones [86], there may simply not be enough space to fit optimum-sized sense organs and brains in the head of a small animal.

The next two limitations are related to the two fundamental pathways for selection to enlarge brain size (relative to body size): a direct one and an indirect one [87]. The direct pathway is taken when the organism increases its overall metabolic turnover. Bigger brains pay for themselves if energy intake stabilizes on a higher plane than before. This is effective but it comes with a risk, because it requires that the animals can acquire a sufficiently nutrient-dense diet intake despite fluctuating food abundance in the environment [88]. The opportunities to generate such a stable increase in net energy intake may depend on external conditions, for example, the extent to which seasonal troughs in intake are inevitable, and thus will vary across species.

The indirect pathway is not exclusive, but rather may complement the direct one: reduced allocation to maintenance or production. There is evidence for both [87]. The involvement of the latter pathway is revealed by a fitness cost in terms of slower development and reduced reproductive rate [89–91], and the ubiquity of this effect suggests that in most lineages larger brains are bought at the expense of reduced immature growth and development and adult reproduction. In such lineages, the larger brain size must have improved adult survival sufficiently to be favoured by selection. This is indeed observed [89]. Animals may achieve this increase in survival by staving off starvation, for example, by turning to extracted foods hidden inside an inedible matrix [92], or by becoming more effective at avoiding predation [93] or disease [94]. When larger brain size improves survival, this produces selection for a slower-paced life history via selection on a physiology that makes longer life possible [95], thus creating a direct link between

Table 3. Mechanisms of local adaptation: the gradient from canalized to plastic development.

	developmental canalization ←	→ developmental plasticity
body size	smaller	larger
life history	short-lived	long-lived
diet	specialist (incl. folivore)	generalist (incl. omnivore)
mobility	sessile	nomadic
brain	small	large

larger brains and slower life history. In effect, then, a cognitive improvement can only be favoured by natural selection if it actually improves survival (or reproduction, but empirical data suggest this is rare) by a broad enough margin to compensate for the cost to development and reproduction [49]. Many lineages may not encounter external conditions where this is the case.

Finally, maturing individuals acquire larger skill repertoires when social learning is possible, especially when more sophisticated forms of social learning can be deployed [75,80,96]. Where such efficient use of brain tissue is possible, selection on increased brain size should be easier. Indeed, brains turn out to be larger where opportunities for social learning are abundant, as where there is contact between generations and close social tolerance [49,80].

In the end, consideration of these limitations on brain size evolution may be more helpful in explaining variation in relative brain size among lineages than consideration of the cognitive benefits, as is traditionally done [97].

5. Discussion

(a) The flexibility gradient

The filters imposed by small body size, energetic quality and stability of the diet, unavoidable mortality and social contact may prevent animals that are small and short-lived from achieving the brain sizes needed to achieve optimum flexibility. Fortunately, these may also often be the very organisms that do not need it because they can achieve local adaptation through selection on genotypes that produce canalized phenotypes (table 3). Thus, the animals that cannot afford to evolve flexibility may not need it as much as others. On the other hand, animals able to evolve large brains are also those that can generate local adaptation through flexible and innovative behaviours, and are likely to have many opportunities for social learning through long parent–offspring association and strong social-learning abilities. In sum, rather than some kinds of organism achieving better local adaptation than others, there may be a gradient in the mechanisms to achieve the same fit between local conditions and behaviour: selection on specific genotypes versus selection on plasticity.

Obviously, there will be exceptions. Small organisms with fast-paced life history that frequently disperse long distances may not achieve adaptation to all habitat types they occupy, because genotypes in smaller populations may be swamped, and the flexibility route is not open to them. This is frequently reported [2]. Similarly, small organisms may be forced to

have a narrower diet or habitat selection than would be optimal given the limits on their behavioural plasticity.

(b) Large brains, slow life history and extinction risk

High developmental plasticity in behaviour should allow organisms to deal with changes in the environment, such as those in vegetation succession after occasional fires or droughts, or with the more gradual changes owing to human-induced trends in climate. Based on this reasoning, we should expect larger-brained organisms to be better able to cope with climate change. There is some evidence in favour of this notion. First, in some organisms, most of the adjustment to climate change so far is due to flexibility [8]. Second, among species introduced by people into new places, the larger-brained ones were more likely to establish themselves successfully, probably because they were most likely to deal with the many novel features in their new habitats [77].

On the other hand, the correlation between brain size and flexibility also places a serious limit on the ability to adapt to drastic change. Larger-brained species are demographically handicapped in that they have much lower population

growth rates [98], unless they show cooperative breeding. Thus, they should be more likely to go extinct once the critical rate of environmental change is exceeded, as a result of their long generation time, and low r_{\max} , a population's maximum growth rate under ideal conditions [45]. Large-brained and large-bodied organisms could therefore paradoxically be more vulnerable to extinction owing to climate change because they cannot reach genetically anchored adaptations via selection on canalized traits.

I thank Judith Burkart, Karin Isler, Michael Krützen, Maria van Noordwijk, Sri Suci Utami, Serge Wich and Erik Willems for discussion, two reviewers for helpful comments and all fellow orang-utan researchers for gathering the data that made the comparison possible. The orang-utan research reported here was supported by the A. H. Schultz Foundation and the Swiss National Fund. Permission to work in Indonesia and at the sites was kindly provided by the Indonesian State Ministry for Research and Technology (RisTek), the Director General Departemen Kehutanan (PHKA), Departemen Dalam Negeri, the local government in Central Kalimantan and the BKSDA Palangkaraya. I also thank our sponsor institutions: Fakultas Biologi Universitas Nasional (UNAS) in Jakarta, the Bornean Orangutan Survival Foundation (BOSF) and MAWAS in Palangkaraya and the Pusat Studi Satwa Primata of the Bogor Agricultural University (IPB).

References

- DeWitt TJ, Sih A, Wilson DS. 1998 Costs and limits of phenotypic plasticity. *Trends Ecol. Evol.* **13**, 77–81. (doi:10.1016/S0169-5347(97)01274-3)
- Foster SA. 1999 The geography of behaviour: an evolutionary perspective. *Trends Ecol. Evol.* **14**, 190–195. (doi:10.1016/S0169-5347(98)01577-8)
- Slatkin M. 1987 Gene flow and the geographic structure of natural populations. *Science* **236**, 787–793. (doi:10.1126/science.3576198)
- Potts R. 1998 Variability selection in hominid evolution. *Evol. Anthropol.* **7**, 81–96. (doi:10.1002/(SICI)1520-6505(1998)7:3<81::AID-EVAN3>3.0.CO;2-A)
- Stearns SC. 1989 The evolutionary significance of phenotypic plasticity. *BioScience* **39**, 436–445. (doi:10.2307/1311135)
- Pfennig DW, Wund MA, Snell-Rood EC, Cruickshank T, Schlichting CD, Moczek AP. 2010 Phenotypic plasticity's impacts on diversification and speciation. *Trends Ecol. Evol.* **25**, 459–467. (doi:10.1016/j.tree.2010.05.006)
- Van Buskirk J, Steiner UK. 2009 The fitness costs of developmental canalization and plasticity. *J. Evol. Biol.* **22**, 852–860. (doi:10.1111/j.1420-9101.2009.01685.x)
- Van Buskirk J. 2012 Behavioural plasticity and environmental change. In *Behavioural responses to a changing world: mechanisms and consequences* (eds U Candolin, BM Wong), pp. 145–158. Oxford, UK: Oxford University Press.
- Shettleworth SJ. 2010 *Cognition, evolution, and behavior*, 2nd edn. New York, NY: Oxford University Press.
- Byrne RW. 1995 *The thinking ape: evolutionary origins of intelligence*. Oxford, UK: University Press.
- Nisbett RE. 2009 *Intelligence and how to get it: why schools and cultures count*. New York, NY: W. W. Norton & Company.
- Deaner RO, Isler K, Burkart JM, van Schaik CP. 2007 Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain Behav. Evol.* **70**, 115–124. (doi:10.1159/000102973)
- Reader SM, Hager Y, Laland KN. 2011 The evolution of primate general intelligence. *Phil. Trans. R. Soc. B* **366**, 1017–1027. (doi:10.1098/rstb.2010.0342)
- Wich SA, Utami-Atmoko SS, Mitra Setia T, van Schaik CP (eds) 2009 *Orangutans: geographic variation in behavioral ecology and conservation*. Oxford, UK: Oxford University Press.
- van Schaik CP, Marshall AJ, Wich SA. 2009 Geographic variation in orangutan behavior and biology. In *Orangutans compared: geographic variation in behavioral ecology and conservation* (eds SA Wich, T Mitra Setia, SA Utami Atmoko, CP van Schaik), pp. 351–361. Oxford, UK: Oxford University Press.
- Wich SA, Vogel ER, Larsen MD, Fredriksson G, Leighton M, Yeager C, Brearly FQ, van Schaik CP, Marshall AJ. 2011 Forest fruit production is higher on Sumatra than on Borneo. *PLoS ONE* **6**, e21278. (doi:10.1371/journal.pone.0021278)
- Wich SA, Utami-Atmoko SS, Setia TM, Djoyosudharmo S, Geurts ML. 2006 Dietary and energetic responses of *Pongo abelii* to fruit availability fluctuations. *Int. J. Primatol.* **27**, 1535–1550. (doi:10.1007/s10764-006-9093-5)
- Hardus ME, Lameira AR, Zulfa A, Utami Atmoko SS, de Vries H, Wich SA. 2012 Behavioral, ecological, and evolutionary aspects of meat-eating by Sumatran orangutans (*Pongo abelii*). *Int. J. Primatol.* **33**, 287–304. (doi:10.1007/s10764-011-9574-z)
- Permana AG. In preparation. Cultural and cognitive aspects of nest building in orang-utans. PhD thesis, University of Zurich, Switzerland.
- van Noordwijk MA, Arora N, Willems EP, Dunkel LP, Amda RN, Mardianah N, Ackermann C, Krutzen M, van Schaik CP. 2012 Female philopatry and its social benefits among Bornean orangutans. *Behav. Ecol. Sociobiol.* **66**, 823–834. (doi:10.1007/s00265-012-1330-7)
- Weingrill T, Willems EP, Zimmermann N, Steinmetz H, Heistermann M. 2011 Species-specific patterns in fecal glucocorticoid and androgen levels in zoo-living orangutans (*Pongo* spp.). *Gen. Comp. Endocrinol.* **172**, 446–457. (doi:10.1016/j.ygcen.2011.04.008)
- Spillmann B, Dunkel LP, Van Noordwijk MA, Amda RNA, Lameira AR, Wich SA, van Schaik CP. 2010 Acoustic properties of long calls given by flanged male orang-utans (*Pongo pygmaeus wurmbii*) reflect both individual identity and context. *Ethology* **116**, 385–395. (doi:10.1111/j.1439-0310.2010.01744.x)
- Dunkel LP, Arora N, van Noordwijk MA, Utami Atmoko SS, Prathama Putra A, Krützen M, van Schaik CP. In press. Variation in developmental arrest among male orangutans: a comparison between a Sumatran and a Bornean population. *Front. Zool.*
- Krützen M, Willems EP, van Schaik CP. 2011 Culture and geographic variation in orangutan behavior. *Curr. Biol.* **21**, 1808–1812. (doi:10.1016/j.cub.2011.09.017)
- Utami SS, Goossens B, Bruford MW, de Ruiter JR, van Hooff JARAM. 2002 Male bimaturism and reproductive success in Sumatran orang-utans. *Behav. Ecol.* **13**, 643–652. (doi:10.1093/beheco/13.5.643)
- van Schaik CP. 1999 The socioecology of fission-fusion sociality in orangutans. *Primates* **40**, 73–90. (doi:10.1007/BF02557703)
- van Schaik CP. 2004 *Among orangutans: red apes and the rise of human culture*. Cambridge, MA: Harvard University Press (Belknap).

28. Knott CD, Beaudrot L, Snaith T, White S, Tschauner H, Planansky G. 2008 Female–female competition in Bornean orangutans. *Int. J. Primatol.* **29**, 975–997. (doi:10.1007/s10764-008-9278-1)
29. Dunkel L, van Schaik CP. In preparation. Flanged male mating strategies and the benefit of arrested development: a comparison between Sumatran and Bornean orang-utans.
30. Mitani JC. 1985 Sexual selection and adult male orangutan long calls. *Anim. Behav.* **33**, 272–283. (doi:10.1016/S0003-3472(85)80141-X)
31. Mitra Setia T, van Schaik CP. 2007 The response of adult orang-utans to flanged male long calls: inferences about their function. *Folia Primatol.* **78**, 215–226. (doi:10.1159/000102317)
32. Knott CD, Emery Thompson M, Stumpf RM, McIntyre MH. 2010 Female reproductive strategies in orangutans, evidence for female choice and counterstrategies to infanticide in a species with frequent sexual coercion. *Proc. R. Soc. B* **277**, 105–113. (doi:10.1098/rspb.2009.1552)
33. Mitani JC. 1985 Mating behaviour of male orangutans in the Kutai Game Reserve, Indonesia. *Anim. Behav.* **33**, 392–402. (doi:10.1016/S0003-3472(85)80063-4)
34. Pradhan GR, van Noordwijk MA, van Schaik CP. 2012 A model for the evolution of developmental arrest in male orangutans. *Am. J. Phys. Anthropol.* **149**, 18–25. (doi:10.1002/ajpa.22079)
35. Arora N *et al.* 2010 Effects of Pleistocene glaciations and rivers on the population structure of Bornean orangutans (*Pongo pygmaeus*). *Proc. Natl Acad. Sci. USA* **107**, 21 376–21 381. (doi:10.1073/pnas.0914051107)
36. Nater A. 2012 Processes underlying genetic differentiation and speciation in orangutans (*Pongo* spp.). PhD dissertation, Anthropological Institute and Museum, University of Zurich, Zurich, Switzerland.
37. Wich SA, Utami-Atmoko SS, Setia TM, Rijksen HD, Schurmann C, van Hooft JARAM, van Schaik CP. 2004 Life history of wild Sumatran orangutans (*Pongo abelii*). *J. Hum. Evol.* **47**, 385–398. (doi:10.1016/j.jhevol.2004.08.006)
38. Arora N *et al.* 2012 Parentage-based pedigree reconstruction reveals matrilineal clusters and male-biased dispersal in nongregarious Asian great apes, the Bornean orang-utans (*Pongo pygmaeus*). *Mol. Ecol.* **21**, 3352–3362. (doi:10.1111/j.1365-294X.2012.05608.x)
39. Nietlisbach P, Arora N, Nater A, Goossens B, van Schaik CP, Krutzen M. 2012 Heavily male-biased long-distance dispersal of orang-utans (genus: *Pongo*), as revealed by Y-chromosomal and mitochondrial genetic markers. *Mol. Ecol.* **21**, 3172–3186. (doi:10.1111/j.1365-294X.2012.05539.x)
40. Anholt RRH, Mackay TFC. 2010 *Principles of behavioral genetics*. Amsterdam, The Netherlands: Academic Press.
41. Latta RG. 1998 Differentiation of allelic frequencies at quantitative trait loci affecting locally adaptive traits. *Am. Nat.* **151**, 283–292. (doi:10.1086/286119)
42. Lande R. 1975 The maintenance of genetic variability by mutation in a polygenic character with linked loci. *Genet. Res.* **26**, 221–235. (doi:10.1017/S0016672300016037)
43. Wycherley J, Doran S, Beebee TJC. 2002 Frog calls echo microsatellite phylogeography in the European pool frog (*Rana lessonae*). *J. Zool.* **258**, 479–484. (doi:10.1017/S0952836902001632)
44. Eilers J, Slabbekoom H. 2003 Song divergence and male dispersal among bird populations: a spatially explicit model testing the role of vocal learning. *Anim. Behav.* **65**, 671–681. (doi:10.1006/anbe.2003.2081)
45. Chevin L-M, Lande R, Mace GM. 2010 Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biol.* **8**, e1000357. (doi:10.1371/journal.pbio.1000357)
46. Ramsey G, Bastian ML, van Schaik CP. 2007 Animal innovation defined and operationalized. *Behav. Brain Sci.* **30**, 393–437. (doi:10.1017/S0140525X07002373)
47. van Schaik CP, Knott CD. 2001 Geographic variation in tool use on *Neesia* fruits in orangutans. *Am. J. Phys. Anthropol.* **114**, 331–342. (doi:10.1002/ajpa.1045)
48. Tennie C, Call J, Tomasello M. 2009 Ratcheting up the ratchet: on the evolution of cumulative culture. *Phil. Trans. R. Soc. B* **364**, 2405–2415. (doi:10.1098/rsth.2009.0052)
49. van Schaik CP, Isler K, Burkart JM. 2012 Explaining brain size variation: from social to cultural brain. *Trends Cogn. Sci.* **16**, 277–284. (doi:10.1016/j.tics.2012.04.004)
50. Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C. 2001 Charting cultural variation in chimpanzees. *Behaviour* **138**, 1481–1516. (doi:10.1163/156853901317367717)
51. van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, Suzuki A, Utami SS, Merrill MY. 2003 Orangutan cultures and the evolution of material culture. *Science* **299**, 102–105. (doi:10.1126/science.1078004)
52. Russon A, Galdikas B. 1993 Imitation in ex-captive orangutans. *J. Comp. Psychol.* **107**, 147–161. (doi:10.1037/0735-7036.107.2.147)
53. Dindo M, Stoinski T, Whiten A. 2011 Observational learning in orangutan cultural transmission chains. *Biol. Lett.* **7**, 181–183. (doi:10.1098/rsbl.2010.0637)
54. Jaeggi AV, Dunkel L, van Noordwijk MA, Wich SA, Sura AAL, van Schaik CP. 2010 Social learning of diet and foraging skills by wild immature Bornean orangutans: implications for culture. *Am. J. Primatol.* **72**, 62–71. (doi:10.1002/ajp.20752)
55. Forss SIF, van Schaik CP. In preparation. From conservative to curious: response to novelty and the captivity effect in orang-utans.
56. Rijksen HD. 1978 *A fieldstudy on Sumatran orang-utans* (*Pongo pygmaeus abelii* Lesson 1827). Wageningen, The Netherlands: H. Veenman & Zonen, BV.
57. Greenberg R. 2003 The role of neophobia and neophilia in the development of innovative behaviour of birds. In *Animal innovation* (eds SM Reader, KN Laland). Oxford, UK: University Press.
58. Bastian ML, Zweifel N, Vogel E, Wich SA, van Schaik CP. 2010 Diet traditions in wild orangutans. *Am. J. Phys. Anthropol.* **143**, 175–187. (doi:10.1002/ajpa.21304)
59. Glander KE. 1982 The impact of plant secondary compounds on primate feeding behavior. *Yearb. Phys. Anthropol.* **25**, 1–18. (doi:10.1002/ajpa.1330250503)
60. Galef BG, Dudley KE, Whiskin EE. 2008 Social learning of food preferences in ‘dissatisfied’ and ‘uncertain’ Norway rats. *Anim. Behav.* **75**, 631–637. (doi:10.1016/j.anbehav.2007.06.024)
61. Doran DM, Jungers WL, Sugiyama Y, Fleagle JG, Heesy CP. 2002 Multivariate and phylogenetic approaches to understanding chimpanzee and bonobo behavioral diversity. In *Behavioural diversity in chimpanzees and bonobos* (eds C Boesch, G Hohmann, LF Marchant), pp. 14–34. Cambridge, UK: Cambridge University Press.
62. Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C. 1999 Cultures in chimpanzees. *Nature* **399**, 682–685. (doi:10.1038/21415)
63. McGrew WC. 2004 *The cultured chimpanzee: reflections on cultural primatology*. Cambridge, UK: Cambridge University Press.
64. van Schaik CP, van Noordwijk MA, Wich SA. 2006 Innovation in wild Bornean orangutans (*Pongo pygmaeus wurmbii*). *Behaviour* **143**, 839–876. (doi:10.1163/156853906778017944)
65. Langergraber KE *et al.* 2011 Genetic and ‘cultural’ similarity in wild chimpanzees. *Proc. R. Soc. B* **278**, 408–416. (doi:10.1098/rspb.2010.1112)
66. Lycett SJ, Collard M, McGrew WC. 2009 Cladistic analyses of behavioural variation in wild *Pan troglodytes*: exploring the chimpanzee culture hypothesis. *J. Hum. Evol.* **57**, 337–349. (doi:10.1016/j.jhevol.2009.05.015)
67. Kamilar JM. 2006 Geographic variation in savanna baboon (*Papio*) ecology and its taxonomic and evolutionary implications. In *Primate biogeography* (eds SM Lehman, JG Fleagle), pp. 169–200. New York, NY: Springer.
68. Vasey N. 2000 Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*: I. Interspecific patterns. *Am. J. Phys. Anthropol.* **112**, 411–431. (doi:10.1002/1096-8644(200007)112:3<411::AID-AJPA10>3.0.CO;2-R)
69. Stambach E. 1987 Desert, forest, and montane baboons: multilevel societies. In *Primate societies* (eds BB Smuts, DL Cheney, RM Seyfarth, RW Wrangham, TT Struhsaker), pp. 112–120. Chicago, IL: University of Chicago Press.
70. Ossi K, Kamilar JM. 2006 Environmental and phylogenetic correlates of *Eulemur* behavior and ecology (Primates: Lemnidae). *Behav. Ecol. Sociobiol.* **61**, 53–64. (doi:10.1007/s00265-006-0236-7)
71. Peck DR, Congdon BC. 2005 Colony-specific foraging behaviour and co-ordinated divergence of chick development in the wedge-tailed shearwater

- Puffinus pacificus*. *Mar. Ecol. Prog. Ser.* **299**, 289–296. (doi:10.3354/meps299289)
72. Frynta D, Slabova M, Vachova H, Volfova R, Munclinger P. 2005 Aggression and commensalism in house mouse: a comparative study across Europe and the Near East. *Aggress. Behav.* **31**, 283–293. (doi:10.1002/ab.15555)
73. Rendell L, Whitehead H. 2001 Cultures in whales and dolphins. *Behav. Brain Sci.* **24**, 309–382. (doi:10.1017/S0140525X0100396X)
74. Hunt GR, Gray RD. 2003 Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proc. R. Soc. Lond. B* **270**, 867–874. (doi:10.1098/rspb.2002.2302)
75. Reader SM, Laland KN. 2002 Social intelligence, innovation and enhanced brain size in primates. *Proc. Natl Acad. Sci. USA* **99**, 4436–4441. (doi:10.1073/pnas.062041299)
76. Lefebvre L, Reader SM, Sol D. 2004 Brains, innovations and evolution in birds and primates. *Brain Behav. Evol.* **63**, 233–246. (doi:10.1159/000076784)
77. Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L. 2005 Big brains, enhanced cognition, and response of birds to novel environments. *Proc. Natl Acad. Sci. USA* **102**, 5460–5465. (doi:10.1073/pnas.0408145102)
78. Overington SE, Morand-Ferron J, Boogert NJ, Lefebvre L. 2009 Technical innovations drive the relationship between innovativeness and residual brain size in birds. *Anim. Behav.* **78**, 1001–1010. (doi:10.1016/j.anbehav.2009.06.033)
79. Custance DM, Whiten A, Fredman T. 2002 Social learning and primate reintroduction. *Int. J. Primatol.* **23**, 479–499. (doi:10.1023/A:1014961415219)
80. van Schaik CP, Burkart JM. 2011 Social learning and evolution: the cultural intelligence hypothesis. *Phil. Trans. R. Soc. B* **366**, 1008–1016. (doi:10.1098/rstb.2010.0304)
81. Rolfe DFS, Brown GC. 1997 Cellular energy utilization and molecular origin of standard metabolic rate in mammals. *Physiol. Rev.* **77**, 731–758.
82. Laughlin SB, de Ruyter van Steveninck RR, Anderson JC. 1998 The metabolic cost of neural information. *Nat. Neurosci.* **1**, 36–41. (doi:10.1038/236)
83. Kennedy C, Sokoloff L. 1957 An adaptation of the nitrous oxide method to the study of cerebral circulation in children: normal values for cerebral blood flow and cerebral metabolic rate in childhood. *J. Clin. Invest.* **36**, 1130–1137. (doi:10.1172/JCI103509)
84. Bauchinger U, Wohlmann A, Biebach H. 2005 Flexible remodeling of organ size during spring migration of the garden warbler (*Sylvia borin*). *Zoology* **108**, 97–106. (doi:10.1016/j.zool.2005.03.003)
85. Allman JM. 1999 *Evolving brains*. New York, NY: Scientific American Library.
86. Striedter GF. 2005 *Principles of brain evolution*. Sunderland, MA: Sinauer Associates.
87. Navarrete A, van Schaik CP, Isler K. 2011 Energetics and the evolution of human brain size. *Nature* **480**, 91–93. (doi:10.1038/nature10629)
88. van Woerden JT, van Schaik CP, Isler K. 2010 Effects of seasonality on brain size evolution: evidence from strepsirrhine primates. *Am. Nat.* **176**, 758–767. (doi:10.1086/657045)
89. Isler K, van Schaik CP. 2009 The expensive brain: a framework for explaining evolutionary changes in brain size. *J. Hum. Evol.* **57**, 392–400. (doi:10.1016/j.jhevool.2009.04.009)
90. Barton RA, Capellini I. 2011 Maternal investment, life histories, and the costs of brain growth in mammals. *Proc. Natl Acad. Sci. USA* **108**, 6169–6174. (doi:10.1073/pnas.1019140108)
91. Barton RA. 1999 The evolutionary ecology of the primate brain. In *Comparative primate socioecology* (ed. PC Lee), pp. 167–203. Cambridge, UK: Cambridge University Press.
92. Byrne RW. 1997 Machiavellian intelligence. *Evol. Anthropol.* **5**, 172–180. (doi:10.1002/(SICI)1520-6505(1996)5:5<172::AID-EVAN6>3.0.CO;2-H)
93. Zuberbühler K, Byrne RW. 2006 Social cognition. *Curr. Biol.* **16**, R786–R790. (doi:10.1016/j.cub.2006.08.046)
94. Nunn CL, Altizer S. 2006 *Infectious diseases in primates: behavior ecology and evolution*. New York, NY: Oxford University Press.
95. Stearns SC, Ackermann M, Doebeli M, Kaiser M. 2000 Experimental evolution of aging, growth, and reproduction in fruitflies. *Proc. Natl Acad. Sci. USA* **97**, 3309–3313. (doi:10.1073/pnas.97.7.3309)
96. Whiten A, van Schaik CP. 2007 The evolution of animal 'cultures' and social intelligence. *Phil. Trans. R. Soc. B* **362**, 603–620. (doi:10.1098/rstb.2006.1998)
97. Dunbar RIM. 2003 The social brain: mind, language, and society in evolutionary perspective. *Annu. Rev. Anthropol.* **32**, 163–181. (doi:10.1146/annurev.anthro.32.061002.093158)
98. Isler K, van Schaik CP. 2009 Why are there so few smart mammals (but so many smart birds)? *Biol. Lett.* **5**, 125–129. (doi:10.1098/rsbl.2008.0469)