Geographic variation in orangutan behavior and biology

Its functional interpretation and its mechanistic basis

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24.1 Introduction

Variation in the morphology, genetics, behavior and social organization among populations of a single species subject to distinct environmental pressures, or among a group of allopatric congeners descended from a recent common ancestor, is fascinating because different populations, subspecies or allopatric species can be seen as natural experiments. In these experiments the

effects of confounding variables (e.g., phylogeny) are minimized, permitting more fine-grained tests of hypotheses about how ecological factors shape morphology, behavior, and social organization. Such comparisons have been employed fruitfully to examine closely relationships emerging from broad correlational studies of multi-species data sets (Harvey *et al.* 1987; Nunn and van Schaik 2002). The order Primates is particularly well suited to these comparative approaches as field studies have provided data from multiple populations of many primate taxa.

Comparative primate studies have elucidated the effects of extrinsic factors on primate group size, stability, and composition. For example, predation risk has substantial effects. Where groups of colobines are more terrestrial or are within the geographic range of large raptors, they are more likely to contain multiple adult males (van Schaik and Hörstermann 1994). Likewise, on an oceanic island without feline predators, generally arboreal long-tailed macaques live in smaller groups that fission more and use the ground more often than their conspecifics on mainland Sumatra, where several species of feline predators are present (van Schaik and van Noordwijk 1985b). Plant productivity also has strong effects on primate behavioral ecology. For example, group size among baboons is positively correlated with rainfall, and therefore plant productivity (Dunbar 1992). On the other hand, the more frugivorous lowland gorillas live in smaller groups, less group cohesion and larger home ranges compared to the more folivorous mountain gorillas (Robbins and McNeilage 2003). This goes against the prevailing interspecific trend of larger group sizes among frugivores (Clutton-Brock and Harvey 1977), and therefore suggests this trend is spurious. Finally, some comparisons highlight the effect of population density on group composition. Among gibbons, polyandrous groups are common where densities are very high and thus opportunities for establishing territories or waiting in marginal habitats are low (U. Reichard *et al.*, personal communication).

More recent multivariate analyses have permitted the simultaneous examination of the effects of different extrinsic factors. For example, Kamilar (2006) performed a quantitative analysis of some

20 behavioral–ecological studies of baboons (*Papio*), and found that seasonality best predicted behavior, with the least seasonal habitats having the largest group sizes, the most resting time and a specialization on underground corms rather than fruits and seeds. A detailed comparison of all field studies of the genus *Pan* (chimpanzees and bonobos) by Doran *et al.* (2002b) revealed an interesting trend from east African to west African chimpanzees to bonobos (Central African, south of the Congo river) toward increasing mean party size, more lengthy periods of female sexual activity, and shorter inter-birth intervals, which were linked to decreasing seasonality in rainfall, and, presumably, a more constant availability of fruits. In both studies, rainfall seasonality was a strong environmental predictor of the behavioral variables, but neither study used direct measures of plant phenology, making it impossible to assess the role of differences in overall food abundance among sites. Thus, while resource availability appears to explain patterns of variation in socioecology, it is premature to conclude that temporal variation in food availability, rather than overall food availability, plays the more important role.

Orangutans have been the subjects of long-term field study at a number of different sites. During the 1980s and 1990s, these field studies began to reveal remarkable variation among orangutans on different islands, and even among sites on the same island. The challenge has been to systematically document this variability and to develop explanations for it.

This is the first book to focus explicitly on comparisons between orangutan populations, although we note that much remains to be done and that the comparisons and conclusions drawn herein are preliminary. In this chapter, we summarize the information presented in previous chapters, and develop and test some ideas to account for this variability. As data on social organization, behavioral ecology and habitat all comfortably map onto a single gradient, we propose that a simple, univariate framework may be sufficient to explain observed patterns of variation among orangutan populations.

Table 24.1 lists a number of characteristics that appear to differ systematically between Sumatran and Bornean orangutans. It also lists the sources

Table 24.1 Overview of observed differences between the well-studied orangutan taxa

	Sumatra _P. abelii_	Borneo _P. p. wurmbii_	Borneo _P. p. morio_	Source
Habitat				
Forest productivity	Higher	Lower	Lower	Chapter 7
Impact of masting	Less	More	Most?	Chapter 7
Tigers	Present	Absent	Absent	Chapter 3
Morphology				
Mandibles	Gracile	Robust	Very robust	Chapter 2
Tooth enamel	Thinner	Thicker	Thicker	T. Smith, personal communication
Average brain size (cc)	388	374	364	Taylor and van Schaik 2007
Behavioral ecology				
Variation in fruit intake	Low	Higher	Highest	Chapter 9
Reliance on non-fruit fallbacks	Very rare	Common	Commonest	Chapter 9
Female home range size	Larger	Intermediate	Smaller	Chapter 13
Female daily travel distance (m)	_c._ 820	_c._ 760	_c._ 230	Chapter 13
Ketone bodies in urine	Very rare	Rare	?	Knott 1998a; Wich _et al._ 2006a, unpublished data
Number of day nests built/day	_c._ 0.8	_c._ 0.4	_c._ 0.05	Chapter 19
Sensitivity to logging	High	Lower	Lowest	Chapter 6
Population density	Higher	Usually lower	Among lowest	Chapter 6
Terrestrial travel by flanged males	Very rare	Common	Common	Chapter 3
Social organization				
Sociability	Highest	Lower	Lower	Chapter 17
Male developmental arrest	Present	Absent?	Absent?	Chapter 16; van Schaik 2004
Duration of consortships	Very long	Shorter	Shorter	Chapter 16
Presence of forced matings	Rather low	High	High	Chapter 16
Susceptability to social stress	Lower	Higher	Higher	T. Weingrill, in preparation
Cultural repertoire	Large	Smaller	Small	Chapter 21
Presence of complex innovations	Multiple	Rare	Absent	Chapter 21
Life history				
Interbirth intervals (mean, years)	8.75	7.7	6.1	Chapter 5
Reduced association with mother	From _c._ 10 years	From _c._ 6 years	From _c._ 6 years	Chapter 12

of the conclusions; where possible we refer to previous chapters in this volume. Ideally, we would present a column for each orangutan subspecies, but there is as yet no field information on _P. p. pygmaeus_ of north-western Borneo, so it was excluded. There are good reasons to subdivide orangutans more finely than simply comparing Sumatran (_P. abelii_) and Bornean (_P. pygmaeus_) orangutans, however, because _P. p. wurmbii_ and _P. p. morio_ exhibit substantial differences for many of the variables listed. Indeed, the pattern in many entries is such that there is a gradient from _P. abelii_ in the north-west, through _P. p. wurmbii_ in western and central Borneo, to _P. p. morio_ in eastern Borneo.

24.2 Ecological variation among sites inhabited by orangutans

Differences in orangutan behavioral ecology among sites are almost certainly at least partly due to habitat differences, in particular the abundance and temporal variability of food, and perhaps also the abundance of predators. Marshall _et al._'s analyses of phenology data collected at

various orangutan study sites reported in Chapter 7 supported the hypothesis that Sumatran forests are generally better habitat for orangutans than Bornean forests. This is true in several respects. Mean rates of fruiting were higher in the Sumatran forests compared to Bornean forests matched for altitude and forest type. In addition, the Sumatran forests tended to have fewer months with very low fruit availability, although a strong habitat effect was also detected.

There are at least two major explanations for the observed differences in orangutan habitat quality between the two islands. First, Sumatra and Borneo have rather different geological histories (MacKinnon *et al.* 1996). Sumatra lies at the edge of a currently active subduction zone between two tectonic plates. The resulting recent and ongoing mountain building and volcanism lead to relatively intense erosion that provides continued mineral deposition in the lowland regions. In contrast, Borneo has an ancient core that dates back to at least the Paleozoic, to which material was added during the Mesozoic and early Cenozoic. These old rocks have become highly weathered; thus soil erosion and concomitant nutrient deposition in lowland forests is extremely limited. As a result, a much higher proportion of Sumatran soils are productive and suitable for agriculture. In general, then, Sumatra is the product of recent geological processes, whereas Borneo is very old and weathered, and therefore the soils of Sumatra tend to be higher in plant nutrients than those of Borneo.

The second explanation for differences in habitat quality is climatic variation. Although all forests in South East Asia exhibit seasonal changes in the production of flowers, fruit and leaves, these changes are overlaid by more severe climatic fluctuations that occur on longer time intervals. All forests in the region that are not secondary or seasonal swamps are subject to mast fruiting, a dramatic surge in flowering and fruiting of many tree species in the local forest community (van Schaik 1986; Ashton *et al.* 1988; Cannon *et al.* 2007). Its occurrence is linked to the approximately periodic occurrence of El Niño-Southern Oscillation events (ENSO) (Curran *et al.* 1999), variations in sea surface temperatures that originate in the eastern Pacific Ocean but affect rainfall patterns

through the tropics. ENSO's impact on the timing of masting is strongest in eastern Borneo and gradually wanes as one moves west (Ashton *et al.* 1988; Yasuda *et al.* 1999), and is stronger on Borneo than in northern Sumatra (Wich and van Schaik 2000). In addition to mediating the timing of mast fruiting episodes, ENSO events also exacerbate climatic variation among sites that may have important effects on orangutans. The most important of these is that the ENSO events, in interaction with a generally more seasonal climate (MacKinnon *et al.* 1996), tend to produce more damaging droughts in the eastern region of Borneo. Soil records indicate a long history of forest fires in this part of Malesia (Leighton and Wirawan 1986; Hoffmann *et al.* 1999; Siegert *et al.* 2001). During such long droughts and especially when forest fires erupt, the availability of edible foods becomes extremely low, and orangutans in eastern Borneo are forced to rely on inner bark of trees to a far greater extent than many other populations (see Table 8.2, Chapter 8). In habitat, then, the orangutans face a general west–east gradient of declining overall forest productivity, which at its eastern end is intensified by the effects of prolonged droughts and fires.

An additional factor of potential relevance in explaining variation in orangutan socioecology between Sumatra and Borneo is the absence of large predators on Borneo. Tigers are not currently found on Borneo, and probably have been absent from the island for a long time (Meijaard 1999), although tigers may have been temporarily present again after the last glaciation when the islands were connected via the dry land of the Sunda shelf. Where tigers are present, orangutans are more systematically arboreal (see Chapter 3), and terrestrial travel by flanged males on Borneo may affect social organization. In the next section, we will examine the mechanisms that link this ecological variation to the variation in orangutan behavioral ecology.

24.3 Behavioral variation among orangutan populations

24.3.1 Morphology, ecology, and life history

The entries in Table 24.1 are organized by topic: morphology, behavioral ecology, social

organization and life history. We expect that their variation is functionally linked, and discuss functional relationships along with the observed patterns. Morphologically, we see relative increases in mandibular robusticity and tooth enamel thickness along the west–east gradient. Mandibular robusticity indicates that eastern orangutans are faced with a mechanically more challenging diet, one that requires many more chewing motions each day (i.e. because eating leaves requires more chewing than eating the same amount of fruit), or more force to crush and open tougher and more resistant foods [see Chapter 2]). Relatively thicker enamel strengthens and protects the tooth crown from cracks and surface wear which is particularly important for orangutans that rely on very stiff foods like seeds (Vogel *et al.* 2008). In Borneo, there are indeed months in which fallback foods are relied on to a much higher degree than in Sumatra (see Chapter 8). Female home range sizes decrease from west to east, although forest type is an important contributor to variation as well. Similarly, the eastern orangutans have the shortest day journeys (see Chapter 13). This is not surprising, because folivores or others eating more abundantly available foods tend to have smaller home ranges than frugivores (Clutton-Brock and Harvey 1977). Moreover, from Sumatra to Borneo, we see an increase in the frequency with which ketone bodies are excreted in urine. Ketone excretion reflects metabolism of fat stores, thus indicating that a period of food scarcity has followed a period of food surplus, during which these fat stores were deposited (Knott 1998a; Wich *et al.* 2006a; see Chapter 11). It is tempting to speculate that the fact that fat stores are being mobilized indicates a greater tendency in *P. pygmaeus* to respond to food abundance by depositing large fat stores, i.e., to have so-called thrifty genotypes. Indeed, we have the impression that obesity in response to long-term food abundance is a phenomenon more commonly seen in zoos among Bornean orangutans than in Sumatran ones, but there has not yet been any formal study of this. We predict that *P. p. morio* is most susceptible to such obesity.

Another, more surprising, morphological difference is that cranial capacity, and therefore both absolute and relative brain size, decreases from west to east, with a particularly strong reduction in *P. p. morio* (Taylor and van Schaik 2007). This gradient is probably functionally linked to food as well, because a less frugivorous diet is often associated with relatively smaller brains (Harvey *et al.* 1987). The selective mechanisms are less clear, and the data to assess them are not available. It may be that there is a corresponding west–east trend toward increased gut size, in which case the explanation may lie in an evolutionary trade-off between investment in brains and guts, both metabolically costly tissues (Aiello and Wheeler 1995). Another possibility is that the relationship reflects a life history trade-off, with the eastern *P. p. morio* in particular having higher extrinsic mortality due to these periods of scarcity, and thus a faster-paced life history. At present, we lack the demographic information on other subspecies than the Sumatran one (Wich *et al.* 2004b; see Chapter 5) to evaluate this idea.

For the purpose of conservation, an important finding is that sensitivity to selective logging of the forests inhabited by orangutans decreases in the same direction, from west to east (Chapter 6). Given what we now know about diet and reliance on the type of fallback foods this is no longer surprising. Most folivores are better able to cope with selective logging than specialized frugivores (e.g., Meijaard *et al.* 2008), because logging may increase the availability of edible foliage from fast-growing pioneer plant species while reducing the availability of large fruit producing trees or important lianas and figs growing in timber trees (Johns and Skorupa 1987). Since the more western orangutans normally are not exposed to long periods of scarcity, and probably lack the evolved coping adaptations of the more eastern ones (larger guts or specialized gut flora and physiology, ability to deposit fat whenever times are good), they have greater difficulty coping with the effects of selective logging. One possibility is that eastern orangutans cope with scarcity by minimizing energy expenditure whenever inputs are low (see Chapter 8). If nest building is a costly activity, this would explain why there is a west–east gradient in the number of nests built per day (see Chapter 19), and why the variation in this feature within a subspecies, e.g., *P. p. wurmbii*, also follows habitat productivity, with those in

Tuanan being more active than those in Gunung Palung. Tuanan has higher mean fruit availability than Gunung Palung, and fewer periods of serious fruit scarcity.

All of this should add up to a difference in mean population density, and indeed it does. If we control for forest type, Sumatran orangutans live at higher densities than Bornean ones (see Chapter 6), and this downward trend appears to continue from *P. P. wurmbii* to *P. p. morio*, at least among the known study sites. There have been various attempts to predict orangutan density. Some significant relationships involved the percentage of fruit that contained soft pulp (van Schaik *et al*. 1995), the density of strangling fig trees (Wich *et al*. 2004a) or (negatively) of dipterocarp trees (Chapter 7). Less directly, orangutan density could be linked to soil pH in Sumatra (Wich *et al*. 2004a), probably because productivity in this region is linked to pH (van Schaik and Mirmanto 1985). However, all these relationships were tested only within a limited set of conditions and mostly on Sumatra only, and extrapolation has proved difficult (Johnson *et al*. 2005b; Marshall *et al*. 2006; Chapter 7). Perhaps the most important reason for this difficulty lies in the fact that the various orangutan populations are in fact different taxa, responding differently to the same environmental conditions. Moreover, in some cases, any possible effect of resource abundance is overwhelmed by the impact of hunting (Marshall *et al*. 2006), which is not surprising given the extremely slow life history of orangutans.

Besides these ecological and behavioral differences, we see differences in life history, at least with respect to the most easily measured variable, interbirth intervals. Their values again follow the west–east gradient, with the longest closed intervals found among the most frugivorous *P. abelii* and the shortest among the most folivorous *P. p. morio* (see Chapter 5). Sumatran infants develop only marginally more slowly than the Bornean ones, but after around age 6 Bornean infants at some sites quickly reduce their association with their mothers and become independent as a result of increased maternal intolerance. Thus, it seems that especially the final phase of the development process is compressed in Bornean orangutans (see Chapter 12). Although it makes sense to expect that Sumatrans

should show the highest adult survival, and thus the longest maximum lifespans, the quality of the data currently available to date do not permit any conclusion (see Chapter 5), even though some analyses of unedited captive data suggest there is no significant difference (Cocks 2007a; Anderson *et al*. 2008).

24.3.2 Social organization and cognition

We found no obvious and striking differences in social organization among the orangutan taxa. However, a variety of more subtle differences may in fact add up to substantial differences. First, Sumatran orangutans are more sociable, i.e., they more readily form parties in which movements are actively coordinated (see Chapter 17). Whereas orangutans everywhere form mixed-sex associations in the form of voluntary or enforced consortships (see Chapter 16), associations involving females and immatures are far more common at the Sumatran study sites (see Chapters 12 and 17). This is probably linked to another difference, namely in the size of female clusters. Female clusters contain females whose ranges overlap more than with others and whose associations are more than expected based on overlap alone (Singleton and van Schaik 2002; see Chapter 13). Although cluster analysis has only been carried out at Suaq, data from Gunung Palung (Knott *et al*. in press) suggest that these clusters are larger where ranges overlap more and probably also where density is higher.

Second, there is a clear difference between Sumatra and Borneo, with no known variation within Borneo, with respect to male sociosexual strategies and mating (see Chapter 16). Sumatran sites show a ratio biased almost 2:1 toward unflanged males, whereas the opposite is true for the known Bornean sites (Delgado and van Schaik 2000). Male Sumatran orangutans thus clearly show developmental arrest, in which unflanged males delay the acquisition of the fully developed secondary sexual characteristics, in particular the cheek flanges, the large throat pouch and the long hair on the arms and back. This delay may last for as long as 20 years or more (Utami *et al*. 2002). The lower ratio of unflanged males in Borneo suggests that this phenomenon is less pronounced in

P. pygmaeus. Perhaps related to this, long calls of flanged males in Sumatra tend to be composed of more pulses and be faster than those in Borneo (Delgado *et al*. Chapter 14). There may also be a tendency for males of *P. p. morio* to have a lower rate of emitting long calls, if early reports from Kutai (Rodman 1973b) and Sabah (Horr 1972) are included.

This difference in male developmental strategy may be linked to differences in sexual behavior. Consortships can be divided into voluntary and involuntary ones. The voluntary ones, in which the female and the male, usually the locally dominant flanged one, mutually coordinate their association, generally last longer in Sumatra. This island difference may be linked to productivity, because association is energetically costly for flanged males in particular (van Schaik 1999; Utami Atmoko 2000; Wich *et al*. 2006b) and the duration may be limited by mean energy supply in the habitat. Such long, voluntary consortships may lead to more reproductive monopolization than in Borneo, although the current data on paternity distributions across males are too few and confusing to be able to test this prediction (see Chapter 16). Greater monopolization by the dominant flanged male is consistent with the higher percentage of matings with non-dominant flanged males, and the greater proportion of forced copulation in Borneo, with either flanged or unflanged males (ibid.).

An explanation for greater male developmental arrest in Sumatra can therefore be formulated (van Schaik 2004). A Sumatran unflanged male faces the following dilemma. If he continues to mature he will become a fully flanged male, but the payoff in terms of matings may well be far less than his current siring rate as an unflanged male, unless he is able to become locally dominant. Flanged males that are not locally dominant acquire virtually no matings (van Schaik 2004). Unflanged males acquire matings in part by harassing other females before or after, and sometimes even during, consortships with the flanged males that are preferred by these females, and in part by having voluntary consortships with nulliparous females who are not attractive enough for the dominant flanged males. The latter strategy may in fact be rather successful for them (see Chapter 16). Unflanged males should

therefore be expected to break their developmental arrest when their prospects of becoming the locally dominant male are good. The assessment mechanisms used by males are not known, although we know that social stress does not play a role (Maggioncalda *et al*. 1999).

This hypothesis can account for the long periods of developmental arrest in areas where a dominant flanged male is well entrenched or others are ahead in the queue. If locally dominant flanged male Bornean orangutans are less able to monopolize paternities, because they are less able to sustain prolonged consortships, then developmental arrest may pay less, and below a certain level of paternity concentration in the dominant flanged male, may not be needed at all.

There may also be a difference in how flanged males compete, with the Sumatran ones seemingly having more stable dominance relations and a more clearly identified and stable dominant male, who is a full-time resident (see Chapter 16). Although quantitative data are lacking, the impression exists that flanged males in Borneo are more likely to engage in escalated fights instead of asymmetric avoidance, and carry the scars as witnesses, and may even have higher adult mortality because of it (Utami *et al*. Chapter 15). It is tempting to link this difference in competition style to the difference in productivity, as in Fig. 24.1, but it is also possible that flanged males on Borneo are much more mobile, since they can cover large distances through terrestrial travel. As a result, many more flanged males can converge at a sexually active female, and can switch between nearby females, which may make it impossible for one male to defend access to females for a long time.

Another difference that may be linked to the lower sociability of females is that, in captivity, Bornean orangutans tend to have higher cortisol values than Sumatran ones, indicative of social stress, when housed in groups, whereas values of animals housed alone have similar values (T. Weingrill, in preparation). Similarly, given the more active contest competition seen among males on Borneo, it may not be surprising that in captivity Bornean male orangutans tend to have higher testosterone values (T. Weingrill, in preparation). Similar analyses need to be conducted in the wild.
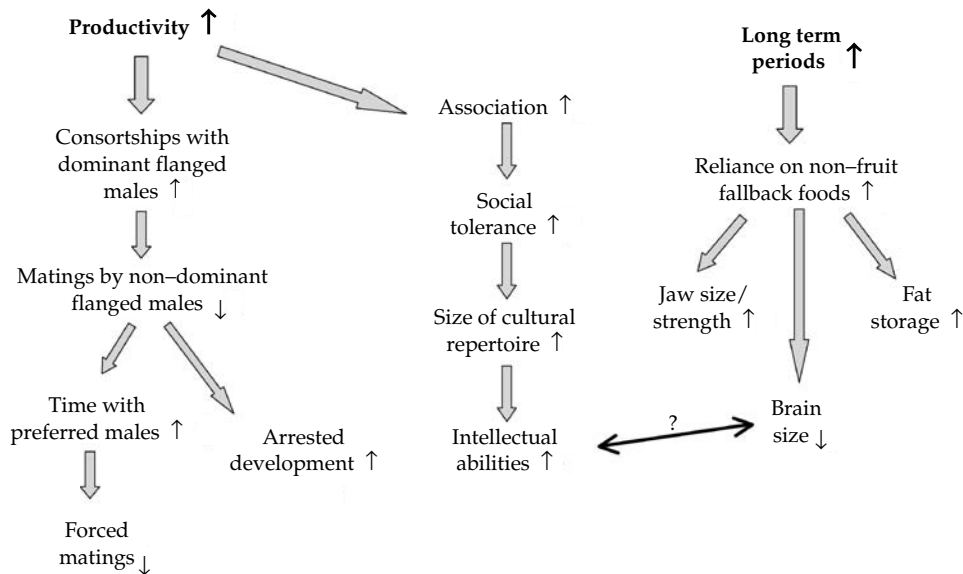
Figure 24.1 A hypothesis for the relationship between ecology and social organization of orangutans.

Finally, orangutans are known to use tools in several Sumatran populations (van Schaik 2004), whereas regular tool use that also involves tool manufacture is absent from Borneo. In general, Sumatra yields more evidence for the presence of cognitively complex innovations, defined by Whiten and van Schaik (2007) as innovations that can only arise through a process that involves insight. In the end, this difference may be due to differences in sociability, which affects the efficiency of social learning (van Schaik *et al.* 2003a; van Schaik 2006b, see Chapters 20 and 21), but the smaller brain size of east Bornean *P. p. morio* may also be related. There is no information on possible cognitive differences between the various *Pongo* taxa; it would obviously be very interesting to do systematic comparisons.

24.4 Mechanisms of orangutan variation

We can formulate three non-mutually exclusive major mechanisms for the observed geographic variability in characters (cf. Chapter 21). First,

variation in character values may reflect ontogenetic flexibility or plasticity, or what geneticists have called reaction norms (West Eberhard 2003). Much of the known variation is no doubt the result of such phenotypic plasticity. Thus, diet choice and seasonal changes in diet are to a large extent plastic responses to variation in availability of preferred food items. Likewise, home range sizes and the length of day journeys are largely responses to spatiotemporal variability in food availability. Finally, sociability may directly reflect food abundance and thus physical condition.

A second potential cause of regional variation in orangutan characteristics is that it reflects evolved local or regional adaptations. Thus, variation among populations may be due to differences in their genetic make-up. Many differences, however, may be due to a mix of genotypic and developmental differences. For example, consider differential responses to selective logging. Sumatran orangutans respond to the decline in fruit abundance in the same way as Borneans, i.e., by switching to a diet rich in inner bark of trees, foliage, and other vegetative matter (Rao and van Schaik 1997). The

fact that they cannot do so as effectively as the Borneans suggest they also have morphological or physiological differences, which in turn may either be due to long-term constitutional effects of early conditions (and thus still reflect plasticity) or the result of underlying genetic differences. Likewise, inter-island differences in orangutan jaw robusticity may reflect facultative remodeling of bone under different mechanical loads, evolved differences, or some combination thereof (Taylor 2002, 2006a). Finally, the reduced sociability of Bornean orangutans may be more than just a plastic response to variation in food supply and a lower average value of this variable. In captivity, they respond differently to being in permanent groups than Sumatran ones, showing a stress response whereas Sumatrans do not (Weingrill, in preparation), even though food is available more or less *ad libitum*.

Genetic differences are almost certainly involved in the geographic variation in interbirth intervals, although no differences have been found in captivity (Cocks 2007a; Anderson *et al.* 2008; Chapter 5), which might be the result of less than ideal survival in captivity during the early years of captive management (Chapter 5, Wich *et al.* unpublished data). If they were based on phenotypic plasticity we would have expected exactly the opposite responses: those with a more reliable energy supply, i.e. the western orangutans, would have the most rapid postnatal development and thus the shorter interbirth intervals, yet the opposite is the case (Wich *et al.* 2004b and Chapter 5). This suggests that different orangutan populations have genetically determined differences in the rate of growth and development, in the same way that gorillas develop more rapidly than chimpanzees (Leigh and Shea 1996; Wich *et al.* 2004b), or folivorous monkeys develop faster than frugivorous ones (Leigh 1994; Wich *et al.* 2007). However, the relatively small data sets from some sites warrant some caution, so it would be premature to dismiss other explanations for interbirth interval variation (see Knott *et al.* in Chapter 11).

The richly documented geographic variation in orangutan behavioral ecology provides a perspective on the known genetic variation across the four orangutan taxa (*P. abelii* and the three described subspecies of *P. pygmaeus*). It suggests that the genetic differences between these taxa are not (merely) the result of genetic drift, producing population units that are merely different due to the changes accumulated since they separated from a common ancestor, but instead differ in meaningful ways, leading to local and regional adaptations.

A third and final cause of geographic variation that is only applicable to behavior, but not, for instance to morphology, density and social organization, was discussed at length in Chapter 21. Individuals may invent novel behavioral variants that may be spread to others, and are thus maintained in a population, through social learning. Even nearby populations may become different in their cultural repertoires, if they are separated from others by a dispersal barrier, or perhaps merely a stretch of different habitat in which the innovation is not expressed. The potential for this is high because orangutan infants rely on their mothers to learn about their environment and their diet, as shown by direct observations (Jaeggi *et al.* 2008). The importance of social learning of basic skills is further highlighted by the finding that many orangutan mothers are unable to care for their infants if they are hand-reared (Cocks 2007b).

Cultural repertoires differ not just from site to site; after correcting for study duration and intensity, they are also larger at the Sumatran sites than the Bornean sites studied so far. Sociability plays an important role in maintaining cultural variants, and may in fact play a more important role in determining the equilibrium size of the cultural repertoire at a site than innovation rate does (van Schaik and Pradhan 2003). The higher sociability at Suaq and Ketambe is clearly linked to the larger cultural repertoires at these sites (van Schaik *et al.* 2003a), although it is not clear yet whether the larger repertoire there is due to greater social network size for infants or for immatures post weaning.

24.5 Discussion

24.5.1 Mechanisms underlying observed variation

The findings compiled in this book reveal a west–east gradient in habitat productivity and stability of food supply to which orangutan populations

have responded with an array of changes in density, diet, morphology, behavioral ecology, social behavior, developmental and sexual strategies, life history and even brain size. Although we can tentatively link all these biological changes to changes in productivity (Fig. 24.1), these hypotheses have not been tested properly, and much work is needed to do so.

Most of these differences in means are consistent with plastic responses, genetic differences, or a combination of the two. To the extent that genetic differences play a role, and species and subspecies have evolved adaptations to the average set of conditions they face, local populations of the same taxon experiencing rather different conditions may not exhibit much variation in responses (when compared with variation in response among distinct taxon). Whenever there is a genetic basis to a feature, there may be a limit to this flexibility due to gene flow from the 'average' habitat. It is well known that even moderate genetic exchange among populations is often enough to prevent local genetic differentiation (e.g., Futuyma 1998).

Disentangling the relative importance of genetic differences and phenotypic plasticity is important for conservation and for our understanding of the nature of intraspecific variation in general. Given that classic translocation experiments are impossible, we could learn much from comparisons of captive populations, provided they are conducted with individuals of clearly established provenance. Variation in captive orangutans is a curiously ignored source of information that is waiting to be tapped by future studies. For instance, if differences in jaw robusticity between Bornean and Sumatran orangutans are maintained in captivity, where the various taxa eat essentially similar diets, this would suggest that genetic differences at least contribute. Similarly, giving individuals of the different orangutan taxa the choice to join or leave others would help to establish an innate component to variation in gregariousness.

Parallel to captive studies, an interesting question for future research would be to see how Sumatran orangutans behave in habitats that have lower mean productivity or are more seasonal, or conversely, Bornean orangutans in highly productive habitats. The nature of these responses would reveal much about the nature of the mechanisms that bring about the differences in behavioral ecology and social organization. If these populations were found to behave just like the rest of their taxon, then this would imply that plasticity is relatively limited and genetic control of the various features rather rigid, suggesting that local adaptation is often imperfect due to swamping, as discussed above. If, in contrast, these populations were found to closely resemble those from the other island or subspecies inhabiting forests exhibiting similar ecological characteristics, this would imply that these local adaptations are largely brought about by broad reaction norms, including perhaps cultural processes. This is why studies in low-productivity and low-density habitats in Sumatra, such as the region near Batang Toru, or in dipterocarp forests subject to masting, such as the eastern lowlands in the northeastern part of the Sumatran orangutan distribution, might be very profitable.

If genetic differences do indeed play a key role in bringing about the phenotypic differences between the four orangutan taxa, this will confirm that the genetic differences found in many taxonomic studies (see Chapter 1) refer to functional variation rather than mere drift. Although, as argued above, further work is needed, there are enough indications of genetically based differences in life history, ecology and morphology, to conclude that the data compiled here argue in favor of the species designation of Sumatran versus Bornean orangutans, and in favor of at least the taxonomic separation between *P p. wurmbii* and *P. p. morio*. This finding has important implications for conservation, underscoring the need to keep taxa separate in reintroduction efforts.

24.5.2 Functional explanations

Food abundance features as a causal variable for the observed behavioral variation, but it is important to ask which aspects of food abundance play the major part. Marshall *et al.* (Chapter 7) found that a major difference between the Sumatran and Bornean study sites was in the occurrence of periods of very low fruit abundance, and also that orangutan densities across study sites were best predicted by fruit abundance during times of fruit scarcity. Thus, it

appears that the presence of periods of serious scarcity is a major predictor of the variation in orangutan behavioral ecology. Figure 24.1 suggests both factors may be important, hypothesizing that some features may be affected more strongly by mean productivity and others more by lean periods. A more quantitative analysis of this question would certainly be worthwhile, because it implies that changes in the ENSO phenomenon over time may have dramatic impacts on orangutan behavioral ecology and population densities.

It is interesting that other studies of geographic variation within a single primate taxon have found very similar patterns. Doran *et al.*'s (2002b) study of geographic variation in the genus *Pan* concluded that rainfall seasonality, which they equated with temporal variability in fruit abundance, was strongly correlated with the observed gradient in social organization. Although earlier analyses of primate communities indicated that seasonality did not play a major role in species distributions (van Schaik *et al.* 2005b), the results compiled here suggest that the presence of occasional periods of scarcity may play a larger role than hitherto assumed in the behavioral ecology of primate species. More detailed comparisons of orangutan populations may reveal the causal mechanisms underlying these correlations with temporal fluctuations in food availability.

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