Preface

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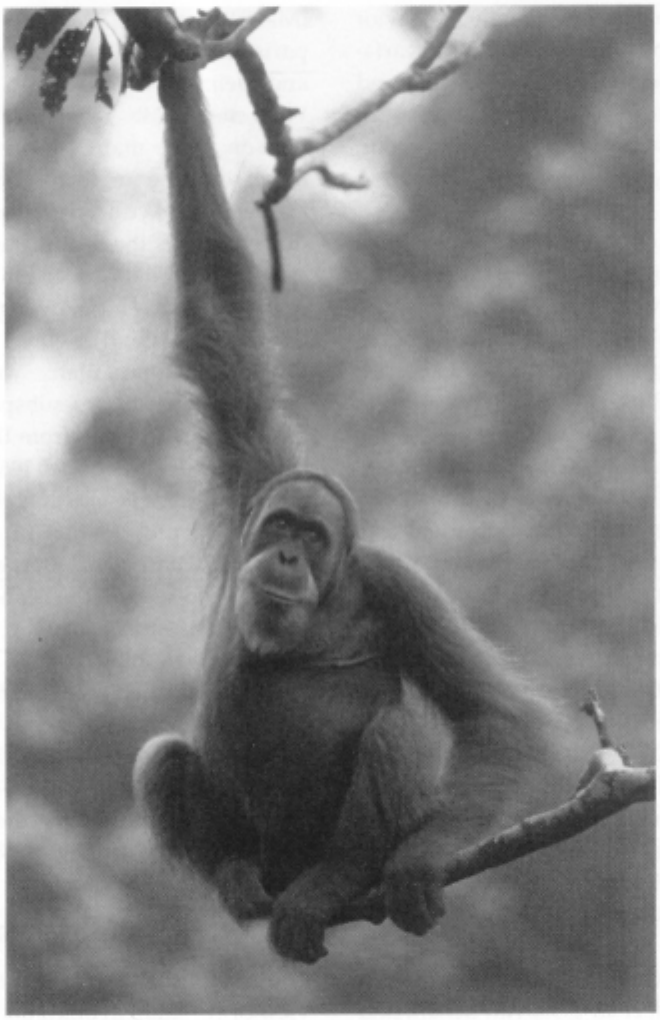

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Geographic variation

One of the central aims of biology is to understand variation in biological traits in an adaptive framework. Studies that examine such variation within species or between allopatric species are of high importance to enlarge our understanding of the sources of variation. Such studies can complement

interspecific comparisons for two main reasons (Harvey and Pagel 1991). First, within-species populations or allopatric species have mostly been separated for a shorter duration than other species, and secondly they are more likely to still inhabit the same locations in which adaptive changes were selected for (Foster *et al.* 1992). Further, examining variation within species or between allopatric species can also elucidate the speciation process itself, especially when variation occurs at the genetic level or that of reproductive behavior (Foster 1999; Foster and Endler 1999). Such variation has been documented in many species and concerns among others, feeding behavior; social behavior; reproductive behavior; vocal behavior; life history; morphology; and genetics (Foster and Endler 1999).

Because primates are a relatively well-studied lineage, there have been quite a few studies examining variation within species and between allopatric species. These studies have covered a wide range of topics: genetics (e.g. Jones *et al.* 1973; Goldberg and Ruvolo 1997a, b; Fausser *et al.* 2000); morphology (e.g. Groves 1967; Cheverud and Moore 1990; Groves 2001; Johnson *et al.* 2005a); diet and foraging behavior (e.g. Nishida *et al.* 1983, Chapman and Fedigan 1990; Panger *et al.* 2002); vocalizations (e.g. Marshall *et al.* 1999; Mitani *et al.* 1999; Delgado 2007; Wich *et al.* 2008); stress response (e.g. Boinski 1999); social behavior (e.g. McGrew and Tutin 1978); time budgets (e.g. Singh and Vinathe 1990); positional behavior (e.g. Sugardjito and Cant 1994); group size (e.g. Dunbar 1993); density (e.g. van Schaik *et al.* 1995; Balcomb *et al.* 2000; Wich *et al.* 2004a), life history (e.g. Wich *et al.* 2004b) and foraging behavior (e.g. van Schaik and Knott 2001).

In addition to studies that were mainly focused on one aspect of variation there have recently been several studies that examined behavioral variation in a few well studied species to examine specifically the possible importance of social learning in such variation (Whiten *et al.* 1999, van Schaik and Knott 2001; Perry *et al.* 2003, van Schaik *et al.* 2003a, 2006a).

Together, these studies have increased the appreciation of the variation within species and among allopatric congeneric species that primate species exhibit, and several books on great apes have begun to explore such variation. For a general text see Fragaszy and Perry (2003); for chimpanzees and bonobos Boesch *et al.* (2002), and for gorillas Taylor and Goldsmith (2003).

Orangutan research

Although researchers began to suspect the existence of geographic variation in orangutans very soon after the first field studies had been conducted (MacKinnon 1974, Rijksen 1978), systematic comparisons have only recently been made (Rijksen and Meijaard 1999, Delgado and van Schaik 2000, Wich *et al.* 2004b, Taylor 2006a). These recent comparisons have mainly been made possible by an increase in the number of sites where orangutans are being or have been studied, the increased duration of some of these studies, as well as the usage of standardized data-collection methods (see: http://www.aim.unizh.ch/orangutannetwork.html) (Figure 1 and Box 1).

Although orangutans were once considered one species with two subspecies, the last decade has seen a shift away from the idea of having two subspecies (van Bemmel 1968, Jones 1969), one on Sumatra (*Pongo pygmaeus abelii*) and one on Borneo (*P. p. pygmaeus*) to that of two separate species (Sumatra: *Pongo abelii*; Borneo: *P. pygmaeus*), with three subspecies on the island of Borneo (*P. p. pygmaeus, P. p. wurmbii and P. p. morio*: Zhi *et al.* 1996; Warren *et al.* 2001; Steiper 2006). Since we will examine variation with and between the Sumatran and Bornean orangutan this book deals with both intra-specific and allopatric species variation. That the two orangutan species are closely related is expressed by the fact that the two species have the ability to interbreed and produce fertile offspring.

An overview of this book

The aim of this book is to provide a coherent overview of variation in orangutans at several levels. To achieve this aim, the book is divided into several sections that have topic-oriented chapters presenting data from the orangutan populations for which data were available. A prerequisite for this approach was that researchers were willing to share unpublished data on topics that they themselves did not

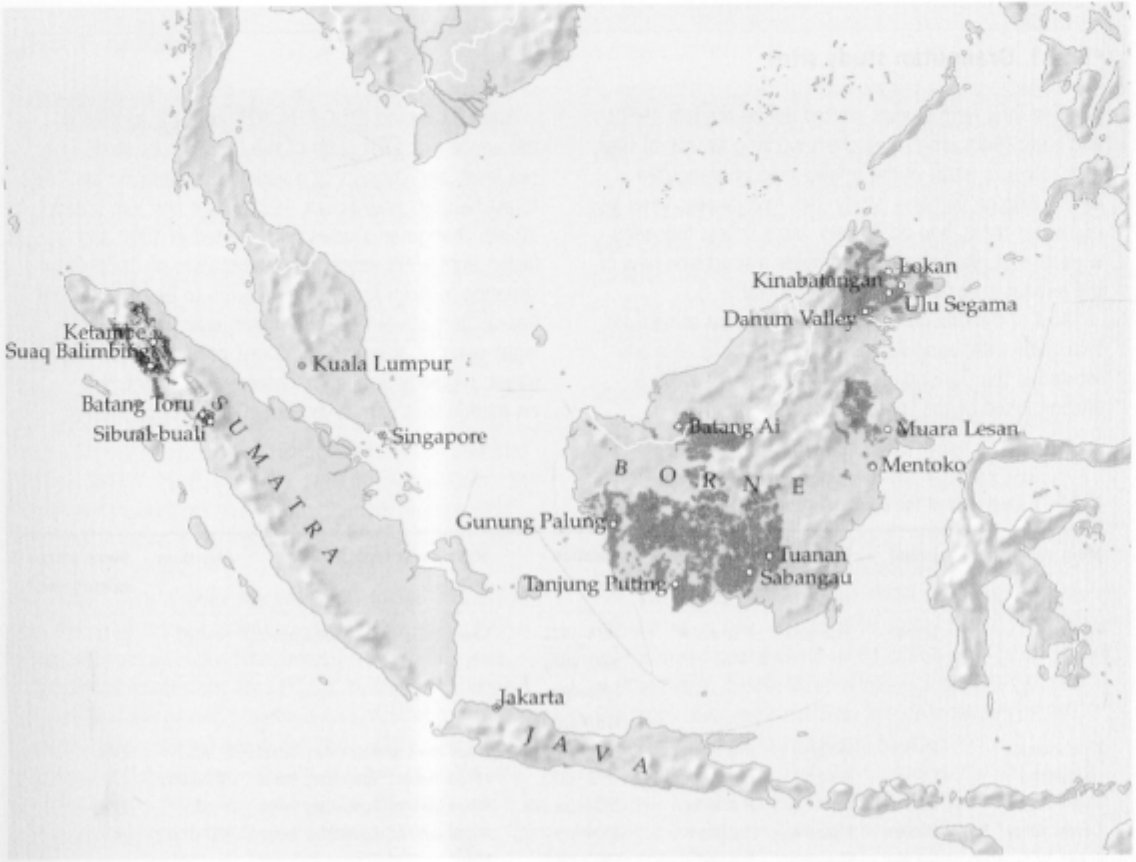

Figure 1 Map with the locations of the orangutan research sites. Dark shaded areas indicate orangutan distribution. (map copyright Perry van Duijnhoven)

publish on for their particular site. When we suggested this approach to our orangutan research colleagues, many were enthusiastic about the idea and freely started to share data with each other. As a consequence of this approach, most chapters contain a long list of authors that generously shared data and ideas.

The first section of the book covers general features of orangutans (Chapters 1–6), and commences with an overview of orangutan genetics and taxonomy (Chapter 1). In this chapter Goossens *et al.* outline the basis for the traditional classification of orangutans into one species and two subspecies (*Pongo pygmaeus pygmaeus* in Borneo and *P. p. abelii* in Sumatra) and how this classification has recently been challenged by molecular data. The current classification instead suggests two separate species *P. pygmaeus* in Borneo and *P. abelii* in Sumatra. Moreover, three subspecies have been described on Borneo: *P. p. pygmaeus* in Sarawak and Northwest Kalimantan, *P. p. morio* in Sabah and East Kalimantan and *P. p. wurmbii* in West, Central and South Kalimantan. Despite the huge progress in the molecular field the authors sketch the challenges for the future and which questions remain to be addressed.

In the second chapter Taylor uses an ecogeographic model based on her work on the African apes to examine variation in jaw morphology in orangutans. She shows that the two species and subspecies differ in their jaw morphology and that these differences can be related to variation in their diet. Her analyses indicate that *Pongo p. morio*, which is characterized by the longest lean

Box 1 Orangutan study sites

The first long term studies started during the late 1960s and early 1970s with researchers working at several sites. Probably as a result of the smaller area of orangutan distribution on Sumatra, study sites have always been less numerous there than on Borneo. More or less following a west–east gradient we will provide a short overview of the habitat in each of the study sites (Table 1).

Most of the orangutan data from Sumatra come from two study sites: Suaq Balimbing and Ketambe that are located in the Gunung Leuser National Park, which is encompassed by the Leuser Ecosystem.

Suaq Balimbing (3° 04′ N, 97° 26′ E) is located in the western coastal plain of the Leuser Ecosystem, near sea level, and consists of a variety of floodplain and hill forest habitats (van Schaik 1999; Wich and van Schaik 2000). Orangutan studies here started in 1992 and lasted until 1999 when the deterioration of the political situation in Aceh forced the research to be discontinued. Researchers started to work there again in 2007 after eight years of absence. The forest consists of tall riverine forest; regularly flooded backswamps near the river on muddy soils with a very irregular and open forest;

Table 1 Overview of the orangutan study sites

Main study sites	Island	Country	(Sub)species	Duration (year–year)	Main forest type(s)	Elevation	Mean annual rainfall (mm)
Mentoko[1–6]	Borneo	Indonesia	*P. p. morio*	1970–1971, 1977–1979, 1981–1982, 1987–present	Mixed lowland dipterocarp forest	30–320	2177
Kinabatangan[7]	Borneo	Malaysia	*P. p. morio*	1999–present	Mixed lowland dipterocarp forest	0–50	2990
Ulu Segama[8]	Borneo	Malaysia	*P. p. morio*	1968–1970	Mixed lowland dipterocarp forest	245–500	
Muara Lesan[9, 10]	Borneo	Indonesia	*P. p. morio*	2004–present	Mixed lowland dipterocarp forest	0–400	2000
Danum Valley[11, 12]	Borneo	Malaysia	*P. p. morio*	2004–present	Mixed lowland dipterocarp forest	160–300	2670
Lokan[13–15]	Borneo	Malaysia	*P. p. morio*	1967–1969	Mixed lowland dipterocarp forest	15–150	
Batang Ai[16, 17]	Borneo	Malaysia	*P. p. pygmaeus*	2006–present	Mixed lowland/hill dipterocarp forest	100–975	3500
Tanjung Puting[18]	Borneo	Indonesia	*P. p. wurmbii*	1971–1975	Dry lowland dipterocarp, peat and freshwater swamp	10–40	3026
Gunung Palung[19, 20]	Borneo	Indonesia	*P. p. wurmbii*	1986–2003, 2007–present	Dry lowand and hill dipterocarp, peat swamp	5–1000	4300
Sabangau[21, 22]	Borneo	Indonesia	*P. p. wurmbii*	2003–present	Peat swamp	0–50	2790
Tuanan[23, 24]	Borneo	Indonesia	*P. p. wurmbii*	2003–present	Peat swamp	2	3010
Suaq Balimbing[25, 26]	Sumatra	Indonesia	*P. abelii*	1992–1999, 2007–present	Peat swamp, freshwater swamp, hill dipterocarp	5–150	3362
Ketambe[27–29]	Sumatra	Indonesia	*P. abelii*	1971–present	Dry lowland, alluvial, submontane	350–1000	3288
Sibual-buali[30, 31]	Sumatra	Indonesia	*P. abelii*	2001–2003	Lower montane, hill dipterocarp	1000	
Batang Toru[32]	Sumatra	Indonesia	*P. abelii*	2006–present	Submontane, hill dipterocarp, high altitude peat swamp	600–1150	4000

Elevation in meters as range.

1–6 1, Rodman 1973a; 2, 1977; 3, Mitani 1985a; 4 ,Mitani 1985b; 5, Leighton and Leighton 1983; 6, Suzuki 1992; 7, Ancrenaz *et al.* 2004a; 8, MacKinnon 1974; 9, Yijun and Hussin 2003; 10, Marshall *et al.* 2006; 11, Walsh and Newberry 1999; 12, Kanamori *et al.* 2006; 13, Horr 1972; 14, Horr 1975; 15, Horr 1977; 16, M. Gumal Personal communication; 17, UNESCO 2004; 18, Galdikas 1978; 19, Knott 1998a; 20, Marshall 2004; 21, Page *et al.* 2004; 22, S. Husson personal communication; 23, van Schaik *et al.* 2005a; 24, van Schaik unpublished data; 25, van Schaik 1999; 26, van Schaik unpublished data.; 27, Rijksen 1978; 28, van Schaik and Mirmanto 1985; 29, Wich and van Schaik 2000; 30, R. Djojoasmoro personal communication; 31, Wich and Geurts unpublished data.; 32, G. Fredriksson personal communication.

continues

Box 1 ***continued***

structurally simple, but generally closed canopy peat swamp forest whose peat layer increases in thickness away from the river; and mixed dipterocarp hill forest. As is usual for the region the site experiences two wetter and two drier periods; annual rainfall is approximately 3400 mm.

More to the northeast in the Leuser Ecosystem in the upper parts of the Alas River valley lies the Ketambe research area (3° 41′ N, 97° 39′ E), at an altitude of 320 m and up. Orangutan research at this site started in 1971 and continues until today. This study area mainly consists of primary mixed dryland rain forest and some alluvial forests poor in dipterocarps along the Ketambe and Alas rivers (Rijksen 1978; van Schaik and Mirmanto 1985). The site also experiences two wetter and two drier periods and has a mean annual rainfall of 3288 mm (Wich and van Schaik 2000).

After a recent rediscovery of an orangutan population to the south of the Leuser Ecosystem (Wich *et al.* 2003a), two research locations have been opened in that area. The Sibuali-buali study area (1° 33′ N, 99° 12′ E) is part of the similarly named protected area. A brief orangutan study was conducted here from 2001–2003. The orangutan habitat there consists of submontane forests. Although no rainfall data are available from this area it is likely to be close to the rainfall in Batang Toru due to its vicinity to that site.

The other site in the area is Batang Toru (1° 41′ N, 98° 59′ E). Orangutan research at this remote site started in 2006. The study area consists of hill dipterocarp and submontane forest with small patches of highland peat. This is the only high elevation orangutan study site that is currently operating: it has an annual rainfall of 4000 mm (G. Fredriksson personal communication).

Orangutan study sites are more numerous on Borneo. The most western study site on Borneo is Gunung Palung. The Cabang Panti research site (1° 13′ S, 110° 07′ E) in Gunung Palung is located in the Gunung Palung National Park, West Kalimantan. Studies on orangutans at Cabang Panti started in 1986 and continued until 2003 when the station was temporarily closed. Work resumed again in 2007 and is ongoing. The forest here is a mosaic of several forest types: peat swamp; riverine forest; freshwater swamp; alluvial bench; lowland sandstone and lowland granite. General descriptions and detailed data on the plant composition of each habitat are provided in Webb (1997), Cannon and Leighton (2004), Marshall (2004), and Cannon *et al.* (2007, 2008). Annual rainfall at Cabang Panti is 4300 mm (Table 1).

Tanjung Puting (2° 45′ S, 111° 57′ E) is located in Tanjung Puting National Park in the province of Central Kalimantan. Orangutan research at this site started in 1971 and most data that have been published are from the 1971–1975 period. The forest is a mixture of lowland dipterocarp forest and periodically flooded peat swamps (Galdikas 1978). The site receives a mean annual rainfall of 3026 without any clear discernable dry period (Galidkas 1978).

The Batang Ai study area (1° 14′ N, 112° 03′ E) is situated in the Batang Ai National Park in Sarawak, Malaysia. The main forest type here is mixed lowland and hilly dipterocarp. Annual rainfall in the area is approximately 3500 mm per year (M. Gumal personal communication, UNESCO 2004).

Sabangau (2° 19′ S, 114° 00′ E) is located in Central Kalimantan within the Natural Laboratory for the Study of Peat Swamp Forest. The study of the orangutans at this site started in 2003 and continues until today. The habitat type is mixed peat-swamp forest with a peat depth of 1–4 m (Page *et al.* 1999). Mean annual rainfall is 2790 mm. The study area was selectively logged from 1991–1997, followed by illegal logging until March 2004.

Tuanan (2° 09′ S, 114° 26′ E) is located in the Mawas Reserve, Central Kalimantan. Similar to Sabangau, orangutan research started here in 2003 and continues until today. The site consists of peat swamp on shallow peat (≤2 m deep), not far from the Kapuas Murung river and therefore subject to some seasonal flooding. It is near sea-level. The site is disturbed, having been subject to selective commercial logging in the early 1990s, followed by opportunistic logging until the end of 2002 (van Schaik *et al.* 2005a).

Mentoko (0° 24′ N, 117° 16′ E) is located in Kutai National Park in East Kalimantan. This site has been the location of intermittent orangutan studies. The first one started in 1970 and lasted until 1971 (Rodman 1977). The second one started in 1977 and lasted until 1979 (Leighton 1993), the third study lasted from 1981–1982 (Mitani 1985a, b), and other phase, in a nearby study area, began in 1987 (Suzuki 1992). The area consists of alluvial forest and dry lowland dipterocarp (Rodman 1977; Leighton and Leighton 1983; Leighton 1993). Mean annual rainfall in the area is 2177 mm.

Muara Lesan (1°42′ N, 117°10′ E) lies in Berau, East Kalimantan. Orangutan studies at this site started in 2004 and continue until today. The dominant geological features in the study area are the Gie River and the Gajah mountains. The forest in this area is comprised

continues

Box 1 ***continued***

of predominantly lowland and hill dipterocarp forest at a range of elevations. Small areas of freshwater and peat swamp habitats also occur in the area. Between 1999 and 2001 selective logging occurred in parts of the area. Annual rainfall is *c.* 2000 mm, without any real dry months but with a somewhat drier period in June (Walsh and Newbery 1999; Yijun and Hussin 2003).

Danum Valley (5° 01′ N, 117° 44′ E) is located in Sabah. Research at this site has recently started in 2004 and is ongoing. The site mainly consists of lowland and hilly dipterocarp forest. The area basically has no months that are dry (<100 mm), but less rain generally falls in March and April with a total annual rainfall of 2670 (Walsh and Newbery 1999).

Kinabatangan (5° 32′ N, 118° 18′ E) is located in Sabah along the Kinabatangan River. Studies on orangutans here started in 1999 and are ongoing. A large portion of the study area is flat and low (10–20 m above sea level [asl]), with the remainder covered in low mudstone hill peaks of ~50 m asl. Most of the area is poorly drained and subject to periodic flooding. Before extensive human disturbance of the area, the main climax formation in the Kinabatangan floodplain were lowland dipterocarp forests in better drained areas, seasonal fresh water swamp and swamp forests in poorly drained areas, riparian forests in flood-free terraces along the rivers, mangrove forests, limestone forests, and heath forests (Fox 1978). Today, they are at various stages of degradation and successional regeneration. They are also highly fragmented and surrounded by industrial oil-palm plantations. Total annual rainfall for Kinabatangan is 2990 mm (Ancrenaz *et al.* 2004a).

As the two previous sites, the Lokan, study area is also situated in Sabah along the Lokan River (Horr 1977). The site consists of lowland dipterocarp forest, but also contains riverine forest that is seasonally or permanently inundated. This was the first site in Borneo were orangutan research occurred. Studies here were conducted from 1967–1969 (Horr 1972, 1975).

Ulu Segama (5° 04′ N, 117° 48′ E). The forest in the Ulu Segama study area is mixed dipterocarp forest on hilly terrain with many valleys and ridges. As with Lokan this site was one of the first to have an orangutan study: 1968–1970 (MacKinnon 1974). Although for both Lokan and Ulu Segama there are no rainfall data, the vicinity to Kinabatangan and Danum Valley indicates a similar rainfall to those sites.

fruiting periods and as a result relies to the greatest extent on resistant and hard foods, exhibits the relatively most robust mandible, and thus displays the relatively greatest capacity to counter large and repetitive jaw loads. *Pongo abelii*, which maintains a fruit-dominated diet even in times of fruit scarcity, displays the relatively least robust mandible. Orangutans are further shown to display a relationship between variance in energy intake, feeding efficiency, and relative brain size, suggesting a link among morphological divergence, behavioral ecology, and life history.

Orangutans live in a complex three-dimensional world where they need to cope with locomotion despite their large body size. In Chapter 3, Thorpe and Crompton compile the current available data on locomotion in orangutans and examine positional behavior. Despite methodological differences between studies, results imply that, while *P. abelii* and *P. p. morio* have the capacity to perform the same gross range of positional behaviors, they actually exhibit quantitatively different positional behavior repertoires and show distinct patterns of association between positional behavior and support use. It is not yet clear, however, whether these differences can be ascribed to species-specific variation or whether habitat variation is responsible for this.

Although orangutans are by no means as vocal as chimpanzees or bonobos, their vocal and sound production has been greatly understudied. In Chapter 4, Hardus *et al.* show that orangutans at least have 32 different sounds and vocalizations that can be distinguished. These range from soft mother–infant retrieval sounds to the long distance long call vocalization made by flanged males. Interestingly, not all of these are produced by all individuals in all populations and several occur only in certain populations, but not in others. These preliminary findings indicate that there might be

socially learned variation in orangutan sounds and vocalizations and that the cultural domain includes these. This opens the way for exciting new studies that could examine the role of social learning on vocalizations and sounds in orangutans.

Being large-bodied great apes, orangutans have a slow life history and indeed the slowest for any great ape (Knott 2001; Wich *et al.* 2004b). Wich *et al.* summarize the current data and show that one feature of life history, the duration of interbirth intervals, shows variation between the (sub)species, with the Sumatran orangutans having the longest interbirth intervals and the Bornean orangutans in the eastern part (*P. p. morio*) the shortest. Wich *et al.* argue that such variation could be the result of variation in mortality regimes on the two islands, with mortality on Borneo suggested to be higher due to lower fruit availability compared to Sumatra (Chapter 7). Data from captive orangutans do not support such mortality differences but are influenced by a host of management issues that perhaps cloud such differences. Only more data on mortality from wild populations can answer this question.

Chapter 6 by Husson *et al.* examines variation in orangutan distribution and density. They show that orangutan distribution is becoming increasingly narrow, fragmented and disturbed. As a result the Sumatran orangutan is classified as critically endangered with a total wild population size of at most 6700 individuals distributed over only three populations larger than 1000 individuals and many smaller ones. The Bornean orangutan is endangered and a total of approximately 54,000 individuals survive in the wild, with 17 populations containing more than 1000 individuals. Trends on Borneo are, however, similar to those on Sumatra and orangutans mostly live in relatively small and isolated forest fragments. Using a large dataset they show that orangutan density on Sumatra is higher than in Borneo, but that there are no considerable differences between the subspecies in Borneo. In addition, they find support for the hypothesis that orangutan densities are higher in sites with less extreme periods of food shortage and that heavy logging has a large negative impact on densities for both Sumatra and Borneo. On Borneo there are indications that well-managed selective logging operations appear to have little effect on orangutan density, but for these findings cannot be generalized to all orangutan taxa and Sumatran orangutans particularly are thought to be very susceptible to logging.

The second section (Chapters 7–10) of the book is focused on orangutan ecology and starts with Marshall *et al.* who carefully examine the common assumption that Sumatran forests are of higher quality for orangutans than Bornean forests, and that this is both the proximate and ultimate cause of many of the differences in socio-ecology between the two orangutan species. The comparison indicates that in general Sumatran forests have both a higher mean fruit availability, and less variability in it, than forests on Borneo. This difference provides the ecological framework in which to interpret the various differences in orangutan behavioral ecology outlined in subsequent chapters.

As food production may influence activity and diet, Chapter 8 by Morrogh-Bernard *et al.* examines whether there is variation in orangutans' activity budget and diet. They find that activity budgets in orangutans differ and can be broadly differentiated into two strategies: (1) *'sit and wait'*, in which orangutans aim to minimize their energy expenditure by spending long periods of time resting and relatively short periods feeding and traveling; or (2) *'search and find'* in which orangutans aim to maximize their energy intake by resting little and mainly feeding or moving in search of food. Orangutans adopt the first strategy in mixed-dipterocarp forests characterized by mast-fruiting events and irregular fruit availability; and adopt the second strategy in swamp forests with a regular supply of fruit, or in dryland forests with high strangling-fig density, as well as during short-term glut in fruit abundance in the other habitats. Geographic variation in diet is most pronounced for inner bark, invertebrate and fruit feeding, with orangutans on Sumatra feeding less on inner bark and more on invertebrates and showing a more stable proportion of fruit and leaves in their diet compared to orangutans on Borneo.

As a result of the productivity variation between the islands it could be that there is variation in the number of food items and species orangutans include in their diet. Russon *et al.* examine this issue in Chapter 9 by compiling such data from a

large number of sites that represent both islands, multiple habitat types, varied degrees of degradation, and wild and rehabilitant populations. The data indicate that as habitat productivity declines, the total plant taxa eaten at a site increases. They also report an increase in both the intensity at which individual food taxa are used and the proportion of plant food species from which important food types are eaten. Further explorative analyses suggest medical plant use, cultural influences on food knowledge, and the relationship between orangutan and other great ape diets.

The possibility of medical usage of food items is further explored by Foitová *et al.* (Chapter 10), who provide an overview of the parasite data that are available on orangutans. Although much work is still to be done and no clear geographical variation can yet be determined, the overview provides suggestions for future research based on a thorough compilation of current knowledge.

The third section of the book (Chapters 11 and 12) focuses on orangutan reproduction and development. The fact that this section is short illustrates our relative lack of knowledge on these topics, which should be no surprise for a species with such slow life history. Chapter 11 by Knott *et al.* examines the potential paradox provided by the life history differences that have been reported in orangutans (Chapter 5). These data might present a paradox because physiological models of reproductive ecology suggest that the higher habitat quality of Sumatra should lead to shorter interbirth intervals. In this chapter the intriguing difference between Sumatran and Bornean orangutans is evaluated in light of models that specify how energetics influence reproduction in apes and humans. From this review, the authors derive a set of recommendations for future research that will lead to a more thorough understanding of orangutan reproductive ecology.

If orangutans on Sumatra do indeed have a slower life-history pace than those on Borneo, it should be reflected in their development. The compilation of data by van Noordwijk *et al.* (Chapter 12) on wild Sumatran and Bornean orangutans reveals a similar development of essential survival skills up to *c.* 5 years of age, but earlier complete weaning and start of independent ranging through cessation of the association between mother and offspring among Bornean orangutans, despite reported higher food availability in Sumatra. It is suggested that this difference is related to the difference in the hypothesized main cause of mortality: starvation during irregular periods of widespread drought in Borneo vs predation in Sumatra. The benefits of association to both mother and offspring are likely to be different under these different selection pressures. To fully understand the differences between and variation among Bornean and Sumatran orangutans more high quality long-term demographic data on several populations are needed.

The fourth section deals with the social system of orangutans (Chapters 13–18). In Chapter 13, Singleton *et al.* address the large geographic variation in home range estimates of orangutan females. They find that this variation has two major components, one due to the 'grain' of habitat heterogeneity and another due to taxonomic affiliation. First, in habitats in which animals can move easily between different parts of their range with very different food abundance, orangutans have larger ranges than in habitats where this is not possible; in such areas, they will have to switch more often to fallback foods. Second, controlling for this effect, we see an east–west gradient of increasing home range size, linked to the increase in continuous reliance on frugivory.

One of the most important orangutan vocalizations for the social organization is the flanged male's booming vocalization, called the long call. In Chapter 14, Delgado *et al.* examine geographic variation in long call characteristics. Documenting and explaining such variation is important as it can be used to infer phylogenetic relationships and can provide insights into social organization. The results of this chapter indicate that there are several acoustic characteristics that show variation between individuals, populations and orangutan taxa. The authors then discuss the potential influence of ecological, genetic, and social factors on long call variation. They conclude that the patterns of observed differences among orangutan populations are probably best explained by differences in either genetic characteristics and/or forest structure, but these hypotheses remain to be tested more rigorously.

Long calls play an important role in both male–male and male–female relationships and in Chapter 15 Utami Atmoko *et al.* examine the nature of male–male relationships and investigate the role of long calls in these relationships. They show that long calls function in flanged male spacing, with the local dominant flanged male approaching long calls and other flanged males avoiding them. Relationships between flanged males are invariably antagonistic and they form dominance relationships that are not always transitive and hence hierarchies that are non-linear. Although flanged males are more tolerant toward unflanged males, they often chase unflanged males when in consortship, but as a result of their lower maximum speed never actually catch them. In stark contrast to relationships between flanged males, those between unflanged males are often tolerant and on occasion they form travel associations. Nevertheless, antagonistic behavior between unflanged males also occurs.

Chapter 16 by Utami Atmoko *et al.* explores orangutan mating behavior and strategies in relation to the pronounced sexual dimorphism and male bimaturism that characterizes orangutans. The data reviewed by Utami Atmoko *et al.* show that male–male competition is highly affected by the reproductive condition of the females and female preference for associating with particular males. Dominant flanged adult males cannot easily exert permanent control over access to reproductive females as a result of the wide dispersion of potentially reproductive females in both space and time. Accodingly, paternity data from both islands show that both unflanged males and flanged males father offspring.

In Chapter 17, Mitra Setia *et al.* review the data on associations and male–female relationships, and build a synthetic picture of orangutan social organization. At least for Sumatra, they suggest that orangutans form loose communities, organized around clusters of related females who have highly overlapping home ranges and above-average mutual tolerance, and a dominant flanged male, who is preferred by these females as mate and with whom they tend to coordinate their ranging, in the form of earshot associations. It is not clear whether the same picture also applies to all Bornean populations.

In Chapter 18 van Schaik *et al.* examine two main factors that can influence ecological sex differences in wild orangutans. Males and females might differ as the result of differing needs due to reproduction and body size, especially pronounced in the highly sexually dimorphic orangutan. Variation can also be the result of differences in sociosexual strategies, usually because males are forced to travel more widely or minimize feeding time relative to females. Van Schaik *et al.* find that both hypotheses are important. The effect of reproductive needs by females results in higher total feeding time per day, more time foraging on insects, and less time resting. However, differences in sociosexual strategy probably explain why unflanged males moved more and traveled faster than flanged males, and have shorter feeding bouts. The authors also examined the potential influence of body size on time budgets, diet and the toughness and elasticity of food items, but found that body size exerts little influence on those variables.

The fifth section deals with orangutan cognition (19–21) and starts with a chapter on orangutan nest building. Orangutans build nests virtually every day, and they learn this gradually as infants. In Chapter 19, Prasetyo *et al.* show that orangutans are highly selective in the choice of tree species for nests, especially for night nests. They also found that many aspects of nest building vary geographically, especially between Sumatra and Borneo, but also within Borneo, including the proportion of nests that are built from scratch rather than being reused and rebuilt, the tendency to build nests during daytime resting bouts, and the position within the trees in which the nests are built. Some aspects of nest building clearly show cultural variation.

Chapter 20 (Russon *et al.*) examines spontaneous innovation in orangutans and compares rehabilitant and wild orangutans. The chapter provides an overview of rehabilitant and wild orangutan innovations, aims to validate the wild orangutan innovations and to determine the innovative processes involved. The validation suggested by Russon *et al.* using rehabilitant data suggests dropping some entries, adding others, and lumping or splitting others. They approximated what was innovated by comparing potential wild innovations with similar species-typical and rehabilitant variants. These

comparisons suggest that orangutans innovate by making small extensions to existing skills: combining old skills in new ways, adding a tool, applying old skills to new functions, and changing the items used.

In Chapter 21, van Schaik *et al.* review what is known of geographic variation in behavior that can be said to be cultural in nature, i.e. consist of socially transmitted innovations. At this stage, there is evidence for 26–35 such cultural variants, depending on the confidence in the basic data.

The final section of the book, Chapters 22 and 23, deals with conservation. As was shown in Chapter 6, by Husson *et al.*, orangutan numbers in the wild are low and populations for the most part live in relatively small and isolated forest fragments that are increasingly also disturbed by timber extraction or other human activities. To maximize conservation strategies it is important to evaluate the potential future scenarios for orangutan populations under different circumstances. Marshall *et al.* (Chapter 22) use a Population Viability Analysis (PVA) to consider the conservation implications of orangutan life history and population biology. The analyses by Marshall *et al.* indicate that orangutan populations of 250 individuals and larger are necessary to ensure good demographic and genetic stability. Given this number and typical densities approximately 500–1000 km^2 of habitat is required to maintain a demographically and genetically healthy population of Bornean orangutans. As some Sumatran forests appear to support higher orangutan densities, a slightly smaller area may be sufficient on Sumatra. Regardless, relatively few protected areas contain 500 km^2 of good orangutan habitat. This means that protection and management of orangutans outside formally protected areas is required to maintain viable populations. Because orangutans have such slow life history (Chapter 5) populations under no external threats can grow at a maximum of 2% annually and it is likely that very few wild populations achieve this rate. Consequently, the loss of only a few individuals per year due to hunting or other factors can be the difference between persistence and extinction. Marshall *et al.* also argue that because of the orangutan's slow life history and unusual population biology there are long time lags between insults and detectable reduction in population size. Thus, once it is detected that a population is in decline, it may already be too late to save it. A precautionary approach is therefore necessary to avert the extinction of orangutan populations.

As a result of the continuing reduction of orangutan habitat there are more and more orangutans coming into to centers that aim to rehabilitate orangutans into the wild. In Chapter 23, Russon reviews the history of orangutan rehabilitation efforts, including its priorities, politics, and practicalities relative to conservation. Russon suggests that despite its complexities and challenges orangutan rehabilitation success rates that are available are within the range reported for other primate reintroductions. She also shows how orangutan rehabilitation has also improved its practices over time and how it contributes to conservation in multiple ways. Russon argues that especially for law enforcement orangutan confiscation and rehabilitation remain essential. She also describes the enormous challenges that rehabilitation projects face, the major one of which is to identify suitable habitat for the surge of orangutans coming into these centers, especially on Borneo.

In Chapter 24 van Schaik *et al.* synthesize the main results from the book.