CHAPTER 9

Geographic variation in orangutan diets

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9.1 Introduction

This chapter compares orangutan diets, both across orangutan sites and relative to other great apes, based on current food lists. Orangutan diets are typically represented in terms of the allocation of feeding time to different food types such as fruit, vegetable matter, bark, insects, and other items (e.g. Fox *et al.* 2004; Wich *et al.* 2006a; Chapter 8 this volume). Understanding a species' diet, however, also requires a comprehensive list of the food items eaten (Tutin *et al.* 1994; Rodman 2002).

Rodman (2000, 2002) used food lists to characterize and compare the diets of each of the great apes. His orangutan diet was based on food lists for six populations, five in Borneo and one in Sumatra, including one Bornean population of rehabilitants. Orangutan food lists have since been expanded for several of the sites that Rodman included and new lists have been developed for nine others (six wild, three rehabilitant). We updated and extended the compiled orangutan food list to include all 15 sites, representing 11 populations in Borneo (eight wild, three rehabilitant) and four in Sumatra (three wild, one rehabilitant; see Box 9.1). Aims in this chapter are to explore the potential of such food lists for characterizing orangutan diets, assessing factors that affect their variation, and suggesting other possible uses.

9.2 Background

There are many reasons to study the diets of orangutans and other living great apes. Understanding orangutan diets is important in comprehending their biological adaptation, including how ecological conditions affect their distribution and behavior. Other issues currently being explored are whether orangutans generate food cultures or gain medicinal benefits from items they ingest (see Chapter 10). All three topics have important implications for conservation. More broadly, the extent to which orangutan and African great ape diets are comparable has implications for whether the earliest *Hominidae* diets derive from African hominoid diets or large hominoid diets in general (Rodman 2002). Food lists offer a relatively little used perspective on orangutan diets, and knowledge of the range and distribution of orangutan foods across their current range should contribute to all these issues.

Food lists offer an alternative to differential feeding time as a basis for detecting interpopulation commonalities and differences in orangutan diets. Orangutan diets are known to vary with ecological factors, including habitat differences in species composition, productivity, and annual or supra-annual seasonality, which create temporal variability in food availability. Fruit abundance is recognized as the best ecological predictor of orangutan densities in undisturbed habitats, so habitat productivity is probably the key ecological factor underlying variation in orangutan diets (for overviews see Rodman 1988; van Schaik *et al.* 1995; Rijksen and Meijaard 1999). We considered three major habitat factors: island (Borneo, Sumatra), habitat type (e.g., swamp, hill, lowland), and habitat quality (e.g., secondary, logged, pristine).

Borneo and Sumatra differ in habitat productivity, which probably contributes to inter-island differences in orangutan diets. Sumatran forests are the more productive in orangutan foods (van Schaik *et al.* 1995; van Schaik 1996; Knott 1998a; Marshall *et al.* 2006; Wich *et al.* 2006a, b). Both islands experience seasonal fluctuations in fruit availability, the most extreme being El Niño Southern Oscillation-linked mast fruiting and severe food scarcities that occur at 2–10 year intervals (Wich and van Schaik 2000). Masting is a supra-annual event involving synchronous fruiting of many tree genera (Ashton *et al.* 1988). It affects orangutan food availability everywhere but its effects may be less severe on Sumatra than Borneo (Knott 1998a; Delgado and van Schaik 2000). Inter-island differences in productivity are reflected in orangutan densities and feeding behavior. Sumatra supports orangutans at higher densities than Borneo in comparable habitats (Rijksen and Meijaard 1999; van Schaik 1999; Delgado and van Schaik 2000). Sumatran orangutans may spend a slightly higher percentage of their feeding time on high quality foods (fruit, insects) and a lower percentage on low quality foods (bark, vegetation) than Borneans, may maintain a higher percentage of figs and fruit in their diet year round, and may not have to shift to fallback foods during fruit scarcities (Rodman 1988; Rijksen and Meijaard 1999; Knott 2005; Marshall and Wrangham 2007; Wich *et al.* 2006b). Borneans fall back on cambium and leaves (Knott 1998a); they also have more robust jaws, consistent with their greater reliance on bark and other potentially tough tissues (Taylor 2006a).

Different types of habitat may support orangutans at different densities. Lower orangutan densities have been found in swamp or lowland/dry (hill) versus lowland/alluvial (riverine) habitats (Delgado and van Schaik 2000). The best orangutan habitat may be in large alluvial areas, including swamps, where flooding and run-off from adjacent slopes provide permanent water and regular fresh nutrient supply (Rijksen and Meijaard 1999). These conditions are probably what afford regular, multi-seasonal production of large quantities of fruits in a number of tree species. In Bornean dryland forest, most fruit tree species tend to fruit synchronously inter- and intra-specifically, which results in seasonal peaks and lengthy scarcities in fruit supply (Leighton and Leighton 1983; Rijksen and Meijaard 1999). Alluvial and swamp forests are also less affected by masting than dryland forests because they tend to have relatively lower proportions of mast-fruiting species (van Schaik 1996).

Orangutans should be particularly vulnerable to habitat quality, given their needs. For a given habitat type, orangutan densities have been shown to be considerably lower in secondary or recently logged versus pristine or old logged forests, with drops as high as 50–100% immediately after logging (Rijksen 1978; Aveling and Aveling 1979; Davies 1986; van Schaik *et al.* 1995; Rao and van Schaik 1997; Felton *et al.* 2003; Ancrenaz *et al.* 2004b). Rao and van Schaik (1997) argued that feeding efficiency is markedly reduced in logged forest because orangutan behavior differs in logged versus untouched forest: less resting, much shorter feeding bouts, and more travel are seen in logged forests. Secondary effects of logging, in the form of altered soil productivity, damage to surrounding forest beyond the timber removed, and increased exposure to predator risk, may further affect orangutans (Rijksen and Meijaard 1999; Felton *et al.* 2003). Logging effects on orangutans may vary between sites because logging practices differ between areas and habitat types and logged habitat may recover over time (Rijksen and Meijaard 1999; Morrogh-Bernard *et al.* 2003; Knop *et al.* 2004).

Internal factors also affect diet, including species-typical food preferences and responses to seasonal fluctuations in food availability, species parameters like adult body size, and within-species differences. Orangutans, like other great apes, show strong preferences for fruits along with broad variety in their diets (Yamagiwa 2004), so they qualify as frugivores and generalists. Their foraging strategies show correspondingly flexible responses to fluctuating fruit availability that may be characterized as 'selective but eclectic' (Rogers *et al.* 2004). Orangutans may alter time feeding, diet composition, food selectivity, ranging patterns, and energy expenditure (Leighton and Leighton 1983; Buij *et al.* 2002; see Knott 2005 for an overview). They alter diet composition by feeding exclusively on fruit when it is abundant, increasing reliance on insects or vegetation when fruit is scarce, and switching to keystone or fallback foods during food scarcities (Galdikas 1988; Leighton 1993; Knott 1998a; Rijksen and Meijaard 1999). They also alter ranging patterns within the limits of staying primarily within large home ranges (Singleton 2000, Singleton and van Schaik 2001). The result is contingent use of the two strategies—pursuing fruit within their range where possible but shifting to the less preferred foods available in their range when fruit scarcities become extreme (Singleton 2000)—which should moderate ecological influences.

Individual differences that can affect diet include age, sex, female reproductive state, and learning. Learning is particularly important as the basis for orangutan food knowledge (van Noordwijk and van Schaik 2005) and food lists may shed light on several learning-related issues. There is a good possibility that orangutans eat items with medicinal value (Kissler 2003; Foitova *et al.* 2006, Chapter 10 this volume). Social learning of foods is currently of interest given evidence of cultural influences on orangutan foraging skills (van Schaik and Knott 2001; Russon 2003a; van Schaik *et al.* 2003a; Fox *et al.* 2004). Orangutans may try novel foods, for instance, only after watching companions eat them (Rijksen 1978; Galdikas and Vasey 1992; Peters 1995; Russon 2002). Rehabilitants are also interesting because of their atypical learning histories and communities (see Chapter 23). Available evidence suggests their diets may approach wild patterns within a year or two of resuming forest life, even when supplemental provisions are provided, although idiosyncracies have been detected: they eat items that wild orangutans ignore, for instance, notably non-standard items like gingers and grasses (see Chapter 23).

9.3 The present study

This chapter presents the current orangutan food list and findings on the relationships it suggests between the foods eaten at a site, indices of habitat productivity, and wild–rehabilitant status. The governing hypothesis is that more versus less productive habitat allows orangutans to feed on fewer taxa and to use them less intensively. Accordingly, we predicted that orangutans ranging in less versus more productive habitat (Borneo vs Sumatra, swamp vs hill vs riverine areas, logged vs unlogged) would feed on a larger number of plant taxa, use a larger proportion of their plant food taxa for each food type, and use a smaller proportion of their plant food taxa for fruit and a larger proportion for non-preferred foods (e.g., bark, leaves). We did not predict overall differences between rehabilitant and wild diets because rehabilitant food lists represent forest-experienced individuals but did predict unusual items in rehabilitant diets. We also considered the potential of food lists for exploring use of medicinal items and cultural influences on diet. Finally, we revisited Rodman's (2002) comparison of great ape diets.

9.4 Results

9.4.1 Orangutan foods, diets, habitat, and status

We compiled and updated the orangutan food list based on food lists for 15 field research sites (Box 9.1, Table 9.1; see http://www.yorku.ca/arusson for the complete food list). We used the food list for each site, i.e., the set of foods eaten, to represent the local diet. We assessed the influences of three ecological factors (island, habitat type, habitat quality; see Box 9.2) and orangutan status (wild, rehabilitant) on orangutan diets. See Box 9.3 for a discussion of limitations associated with these data and this approach.

9.4.2 Dietary breadth

The original form of the updated orangutan food list includes 1693 species (1666 plant, 16 invertebrate, 4 vertebrate, 7 other). Plant food species represent 453 genera and 131 families. Invertebrate foods include ants (4 species), termites (4 species), caterpillars (2 species), leeches, bee larvae, wasps, maggots, crickets, ticks, and other insects (1 species). Vertebrates are gray tree rat, slow loris, gibbon, eggs (probably birds'), and perhaps young birds. Other items are honey, various fungi, moss, urine, soil, and water. Tables 9.2–9.4 show the diversity and distribution of plant foods and plant food items in terms of both comparable and formally identified taxa; Rodman's (2002) values are included in Tables 9.2 and 9.3 for comparison.

The most obvious pattern overall is dietary variability between sites (Table 9.2, 12–84 families, 21–221 genera, 25–379 species; Table 9.4 for studies over 1 year long and reporting non-fruit plant foods systematically: percentage of species used for fruit [34–92], flowers [0–28], leaves [4–69], pith [0–23], bark [3–35], other vegetation [0–31]). The interpopulation variation probably has an important debt to ecological factors but also to differences in study time span. We assessed the relationship between each of these factors and dietary range.

9.4.3 Sources of interpopulation variation in orangutan diets

9.4.3.1 Time spanned by study

Length of study has well known effects on the range of foods consumed (Knott 1998a; Chapman *et al.* 2002; Rogers *et al.* 2004). Short-term studies are unlikely to sample extremes of food abundance, for instance, so they are not likely to record responses to scarcities or rarely available foods. We assessed this effect by correlating study time span (in years) with the range of foods in the diet (comparative food list, Pearson r, n = 15 sites). Correlations were significant for number of food taxa (family: r = 0.75, p = 0.001; genus: r = 0.87, p <0.0001, species: r = 0.87, P <0.0001) and total plant food items (r = 0.81, p = 0.0003); they were not significant for average number of items eaten per species (r = 0.09, p = 0.74) or proportions of plant species in the diet exploited per food type (Pearson r's –0.09 to 0.16, p >0.5 for all types). Ketambe influenced analyses heavily because research spanned 33 years; the next longest studies were at Gunung Palung and Kinabatangan, at 8 years each. Without Ketambe, correlations for number of food taxa were statistically identical; the correlation for bark reached significance (r = 0.54, p = 0.05; and correlations for 'other' plant parts (r = 0.47, P = 0.09) and fruit

Table 9.1 Orangutan sites contributing food lists

Site	Region	Location and elevation	Habitat types[1]	Habitat quality[2]	Taxon	Wild rehab	Timespan	Sources
Lower Kinabatangan River	Sabah, Malaysia	05° 35′ N 118° 05′ E 0–50 m	**Semi-inundated mixed lowland dipterocarp**, seasonal freshwater swamp, secondary	Logged	*P. pygmaeus morio*	W	1998–2006	Ancrenaz *et al.* 2004a, 2005
Ulu Segama	Sabah, Malaysia	05° 04′ N 117° 48′ E 150–600 m	**Dry lowland dipterocarp**, lower montane	Not logged	*P. pygmaeus morio*	W	1968–1970	MacKinnon 1974
Danum Valley	Sabah, Malaysia	05° 01′ N 117° 44′ E 160–300 m	**Dry lowland dipterocarp**, mixed lowland dipterocarp, riverside	Not logged	*P. pygmaeus morio*	W	2004–2005	Kanamori and Kuze unpub; Kuze *et al.* 2006; Ancrenaz *et al.* 2005
Mentoko, Kutai NP	East Kalimantan	0° 24′ N 117° 16′ E 30–320 m	**Dry lowland**, mixed lowland dipterocarp, seasonally flooded alluvial bench forest	Not logged	*P. pygmaeus morio*	W	1970–1972 1977–1979	Rodman 1973b, unpublished; personal communication; Leighton 1993
Sungai Wain	East Kalimantan	01° 06′ S 116° 49′ N 20–100 m	**Dry lowland dipterocarp**, swamp	Not logged	*P. pygmaeus*	R	1994–2000	Russon *et al.* 2000; Peters 1995
Beratus (or Meratus)	East Kalimantan	00° 58′ S 116° 19′ E 100–1000 m	**Lowland-hill dipterocarp**, some swamp	Logged (to 1993)	*P. pygmaeus*	R	1999–2003	Russon *et al.* 2003
Tuanan	Central Kalimantan	02 ° 09′ S 114° 26′ E 2 m	**Peat swamp**	Logged	*P. pygmaeus wurmbii*	W	2003–2005	Tuanan orangutan project Universitas Nasional Jakarta—University of Zürich, Switzerland
Sabangau	Central Kalimantan	02° 03′ S 113° 54′ E 5–10 m	**Peat swamp**	Logged	*P. pygmaeus wurmbii*	W	2003–2005 (1.5 years)	Morrogh-Bernard and Husson unpublished
Tanjung Puting NP	Central Kalimantan	02° 45′ S 111° 57′ E 10–40 m	**Dry lowland**, heath, peat swamp, freshwater swamp	Not logged	*P. pygmaeus wurmbii*	W	1971–1975	Galdikas 1978

Table 9.1 (*cont.*)

Site	Region	Location and elevation	Habitat types[1]	Habitat quality[2]	Taxon	Wild rehab	Timespan	Sources
Sungai Rayu, Matang Wildlife Centre	Kubah NP, Sarawak	01° 36′ N 110° 09′ E 20–120 m	**Lowland mixed dipterocarp**, *kerangas*		*P. pygmaeus*	R	1999–2001	Ramlee 2005
Gunung Palung	West Kalimantan	01° 13′ S 110° 07′ E 5–1000 m	Montane, granite, alluvial terrace, freshwater and peat swamp	Not logged	*P. pygmaeus wurmbii*	W	1994–2001, 2005	Knott 1998a, unpub.
Bukit Tigapuluh	Riau Sumatra	0° 40′–1° 25′ S 102° 10′–50′ E 60–843 m	**Lowland dipterocarp**	**Logged**	*P. abelii*	R	2002–2004	Pratje unpublished; Riedler 2007; Whitmore and Samsoedin 1991
Ranun, Langkat	N Sumatra		Alluvial lowland, montane	Not logged	*P. abelii*	W	1971 (8 months)	MacKinnon 1974
Ketambe	N Sumatra	03° 41′ N 97° 39′ E 350–1000 m	**Dry lowland**, subcolline	Not logged	*P. abelii*	W	1971–2004	Rijksen 1978; Ketambe orangutan project Universitas Nasional Jakarta—Utrecht University Netherlands—SOCP[3]
Suaq Balimbing	N Sumatra	03° 42′ N 97° 26′ E 5–150 m	Coastal **peat swamp**, transitional swamp, back swamp, riverine, hill	Not logged	*P. abelii*	W	1994–1999	Suaq Balimbing orangutan project Universitas Indonesia Jakarta—Duke University USA

[1] Habitat type where most orangutan data have been collected is **bold**.

[2] Not logged vs logged (prior to/during data collection).

[3] Sumatran Orangutan Conservation Programme.

Box 9.1 Orangutan food list compilation

We obtained food lists from 15 orangutan field research sites, the 6 that Rodman included (Ketambe, Gunung Palung, Tanjung Puting, Sungai Wain, Mentoko, Ulu Segama) plus nine more (Suaq Balimbing, Ranun Langkat, Bukit Tigapuluh, Sungai Rayu, Sabangau, Tuanan, Beratus, Danum Valley, Kinabatangan) (Table 9.1, Fig. 1 in the Preface). We used published lists for Tanjung Puting (Galdikas 1978), Mentoko (Rodman 1973a, 1988 per Rodman 2002; Leighton 1993), Sungai Wain and Beratus (Russon *et al.* 2000, 2003), and Ulu Segama and Ranun-Langkat (MacKinnon 1974). We obtained updates to Rijksen's (1978) Ketambe food list from Wich and unpublished lists for other sites directly from researchers: Gunung Palung (Knott), Tuanan (van Schaik, Wich), Sabangau (Husson, Morrogh-Bernard), Suaq Balimbing (van Schaik, Singleton), Bukit Tigapuluh (Pratje), Kinabatangan (Ancrenaz), Danum Valley (Kuze, Kanamori), and Sungai Rayu (Hatta). We combined all site lists into a single list showing all taxa eaten, the parts of each taxon eaten, and the sites at which each taxon and taxon part are eaten.

Standardization: food identification and naming

At all sites and in all studies, food items were identified primarily by direct behavioral observation, i.e., orangutans were observed selecting and eating them. MacKinnon (1974) reported identifying a few items from feces. At wild sites, food data were collected during focal nest-to-nest follows. Data collection procedures differed to some degree within sites, partly due to changing conditions over time, as well as between sites. Known limitations include:

1. data from partial day follows were typically included in food lists;
2. percentages of unidentified taxa are high at most sites (average 44%, range 12–78%: see Table 9.2);
3. the Suaq Balimbing food list is incomplete for plant parts eaten per taxon;
4. the Bukit Tigapuluh food list includes a very high percentage of plant food taxa identified by local name only (55%; average/SD across all sites 11%/14.9%);
5. only studies at Gunung Palung, Danum Valley, Kinabatangan, and Ketambe spanned mast fruiting events.

Taxonomy

Compilation involved reconciling and standardizing taxonomic information in site food lists and correcting errors detected. We followed Rodman's error correction procedures and conventions (see Rodman 2002 for details): Briefly, we corrected obvious mechanical errors directly, accepted researchers' original identifications as accurate, referred inconsistencies to contributors for resolution, and incorporated changes only after verification by contributors. For all analyses but one (assessments of dietary breadth at each site), we dropped species that were identified by local name only because local to scientific name conversions are unreliable.

Nomenclature

Nomenclature varied across contributors. For plant foods, we standardized to Index Kewensis, per the International Plant Names Index (IPNI, Internet version, 08/2006). Where IPNI did not resolve naming anomalies, we consulted contributors then other publications, e.g., Mabberley (1997), the Plants database, the Integrated Taxonomic Information System (http://www.itis.usda.gov), World Agroforestry Centre—SE Asia (http://www.worldagroforestry.org/sea), and botanical experts at relevant herbaria (e.g., Wanariset, Leiden, CIMTROP). Where these methods failed to resolve names, we listed the item as unidentified at the unresolved level and noted the original name in comments.

Food types

We classified food types using Rodman's system (2002) with two modifications: we collapsed fruit parts into a single class that included ingested seeds (few if any studies confirmed non-digestion via feces, and few studies distinguished the fruit parts consumed) and added an animal food class (invertebrates, vertebrates). Finer distinctions were recorded at many sites but distinctions varied between sites, so comparisons were possible only after collapsing into the following broad types: *fruit* (any parts of a plant's fruiting body—whole fruit, pulp, aril, seed, skin, seed), *flower* (any parts of a plant's sexual reproductive structures—carpel, stamen, calyx, corolla, main supporting stem), *leaf* (all leaves—young and mature, shoots), *pith* (all material within plant stems, e.g., in leaf stems, petioles; parenchyma, meristem), *bark* (all bark-related material, i.e., bark itself, cambium or phloem), *other vegetation* (plant items not in other plant classes, e.g., roots, orchid bulbs, unidentified plant parts), *animal* (invertebrate and vertebrate matter, e.g., ants,

continues

Box 9.1 *continued*

termites, small mammals, bird eggs), *other* (non-plant non-animal items, e.g., fungi, honey, water, soil).

Diet measures

Specific diet measures included taxonomic breadth (number of families, genera, and species fed upon), average number of items eaten per plant species, and the proportion of plant food species from which each food type (fruit, flowers, leaves, pith, cambium) was taken.

Interpopulation comparisons used one of three forms of the combined food list: *original*, *comparative*, and *identified*. The *original* list includes all taxa listed by site researchers, including all locally and unidentified ones. The *comparative* list includes only taxa comparable across sites; per Rodman (2002), for each site we collapsed genera and species that were unidentified or only locally identified into a single unidentified genus per family or species per genus, respectively. The *identified* list includes formally identified taxa only.

Box 9.2 Habitat measures

The habitat represented by each site was classified for *island* (Borneo, Sumatra), *habitat type* (dominant forest type), *habitat quality* (logged, unlogged).

We treated sites on Borneo and Sumatra as different in habitat because of recognized differences in forest productivity between the two islands.

Characterizing a site's habitat type is not straightforward because orangutan research sites typically include a mosaic of habitat types (see Table 9.1). Food lists represent all items eaten at a given site, so they typically include items from multiple habitat types. The information provided in food lists did not link food taxa to habitat type, so we classified sites by the habitat type that appears to dominate: lowland/riverine (Ketambe, Sungai Rayu, Mentoko, Danum Valley), lowland/hill (Gunung Palung, Beratus, Ranun Langkat, Ulu Segama, Bukit Tigapuluh, Sungai Wain), and swamp (Kinabatangan, Sabangau, Suaq Balimbing, Tanjung Puting, Tuanan). This classification reflects the view that the best functional separation within lowland forests is probably dryland (i.e., hills) versus extensive floodplains or terraces. The former but not the latter tend to be covered by dense dipterocarp forest. This classification clearly ignores variation between the sites lumped together (e.g., Ketambe, Danum Valley) and non-dominant habitat types within sites (e.g., swamp in Gunung Palung, hill in Suaq Balimbing). Lowland sites in particular typically include mixed habitat, making it difficult to judge which predominates or which was the focus of study. Habitat type effects are likely to be weak owing to this dilution.

We assessed habitat quality in terms of logging, treating Sabangau, Tuanan, Beratus, Kinabatangan, and Bukit Tigapuluh as logged sites and all other sites as unlogged.

(r = −0.28, p = 0.33) were relatively strong but not significant. Using Spearman correlations to dampen Ketambe's influence produced the same overall pattern plus significant correlations for bark and 'other' plant parts. Findings confirm that short term studies underestimate the number of taxa eaten at a site and perhaps the proportion of plant food species used for bark and 'other' parts.

We focused interpopulation analyses on plant foods because plant foods overwhelmingly define orangutan diets and non-plant food items were less systematically reported and identified. We compared food lists between sites via fixed-effects manovas with study time span included as a covariate. The number of sites compared was relatively small so we could not test all variables within one manova or test interaction effects (insufficient error degrees of freedom). We used two manovas to test for main effects of island, habitat type, habitat quality, and status on diet—one for dietary breadth (number of plant food taxa) and one for intensity of use (average number of parts eaten per species,

Box 9.3 Limitations

The sites providing lists represent only a fraction of the orangutan populations surviving in forest habitat, each site's contribution is limited by the focus (ecology, behavior, cognition) and duration (0.5–33 years) of generating research, and the degree to which target factors are represented varies widely. Representation is much better for Borneo than Sumatra, for instance. Orangutans on the two islands are now considered distinct species, *Pongo pygmaeus* and *Pongo abelii* respectively (Xu and Arnason 1996), so combining Bornean and Sumatran food lists may conceal inter-island differences in diet that reflect genotypic rather than phenotypic differences (e.g., reproduction, life history; Wich *et al.* 2006b). Three *P. pygmaeus* subspecies are also now recognized on Borneo: *morio* (east), *wurmbii* (central-west), and *pygmaeus* (north-west) (Groves 2001). Diets for *morio* and *wurmbii* are well represented but no sites represent *pygmaeus*.

Rehabilitant food lists reflect different circumstances than wild orangutan food lists. Briefly, rehabilitant sites represent species but not subspecies; three of the four rehabilitant sites represent Bornean habitat and the most extensively studied are in east Borneo; supplemental provisions were available to rehabilitants during some data collection periods at three of the four sites (Sungai Wain, Beratus, Sungai Rayu); and rehabilitant diets mainly represent immatures with atypical and varied feral knowledge who live in atypical orangutan communities (for details see Chapter 23). However, some rehabilitants eventually abandon provisions or provisioning ceases; all the rehabilitant food lists we used include rehabilitants with over 2 years' experience in their release forest; and all the rehabilitant sites we included are empty of a resident wild population so there is virtually no chance that rehabilitants were familiar with the release forest prior to being transferred there or were influenced by resident wild orangutans.

The combined food list represents only what food species and items were reported to have been eaten. Some lists did not report everything eaten: some derive from studies that focused primarily on fruit foods so other food items are underrepresented, and foods from non-plant sources tend to be less systematically reported and less carefully identified than plant foods. No list represents what food species were available. Differences in availability affect any such list and issues such as dietary choice cannot be resolved without companion information on availability (Tutin *et al.* 1994). The latter is an important dimension to explore with respect to models of diet choice and to the contribution of social learning and innovation to food knowledge, e.g., how easily particular food items can be learned. Finally, the importance of a food taxon or item within the local diet cannot be determined in standard fashion via this or similar lists, although common use across sites may be of some value. These lists show an item's presence in the diet at a given site but not how much community members rely on it.

Taxonomic identifications are not uniformly reliable. Those from recent studies are relatively reliable because they are based on systematic collection of food samples in the field and formal identification in consultation with botanical experts familiar with the area's biology, including specialists from Indonesia's Kebun Raya (Bogor), Wanariset Herbarium (Samboja, Kalimantan Timur), CIMTROP Herbarium (Centre of International Management and Cooperation of Tropical Peatlands, Palangkaraya, Kalimantan Tengah), National Herbarium (Leiden, the Netherlands), Harvard Herbarium (Cambridge, USA), and Danum Valley Field Centre (Sabah, Malaysia). Identifications from early studies may be less reliable because biological expertise was less readily available; chances of correcting identification errors are slim, however, especially where research has long since ceased (e.g., Mentoko, Ulu Segama, Ranun Langkat). Errors probably result in underestimating diversity within sites and overestimating overlap between sites at the species level; generic and family level identifications are probably more reliable (Rodman 2002).

Not all differences between sites in identifying food taxa and food items could be resolved. Variable and in some cases large numbers of food taxa were identified only locally (0–53 taxa per site, 0–53% of taxa distinguished at the site), for instance, or were identified only to genus or family levels. This limits the accuracy of diet comparisons between sites. Food items were also distinguished differently across sites; several distinctions with important ecological, nutritional, or learning implications were not always made systematically (e.g., seed ingestion, young vs mature leaves), and at some sites large numbers of plant items were reported only as undifferentiated plant matter. The consequence for the compiled list is that food items can only be distinguished at gross levels. Some of these difficulties are unavoidable given field conditions, but they limit the validity of both individual and comprehensive food lists.

Table 9.2 Orangutan plant food taxonomic richness by site

Site[1]	Plant families	Plant genera		Plant species		Genera per family[2]	Species per family[2]	Species per genus[2]
		Total[2]	Identified	Total[2]	Identified			
Kinabatangan 07	59	123	122	179	118	2.24	3.19	1.46
Ulu Segama 07	36	63	62	92	56	1.75	2.56	1.46
R02	35	57	56	84	48	1.63	2.40	1.47
Danum Valley 07	40	59	58	87	44	1.55	2.25	1.47
Mentoko 07	32	63	62	103	66	2.06	3.31	1.63
R02	64	156	153	196	176	2.44	3.06	1.26
Sungai Wain 07	52	117	116	195	128	2.46	3.96	1.67
R02	54	124	111	201	125	2.30	3.72	1.62
Beratus 07	48	117	116	189	120	2.52	4.02	1.62
Tuanan 07	43	74	73	109	45	1.79	2.09	1.18
Sabangau 07	53	84	83	108	54	1.64	2.08	1.27
Tanjung Puting 07	58	108	107	203	142	1.95	3.16	1.65
R02	54	98	96	154	120	1.81	2.85	1.57
Sungai Rayu 07	29	43	43	46	13	1.48	1.59	1.07
Gunung Palung 07	53	123	122	183	79	2.36	3.49	1.49
R02	53	121	121	183	80	2.28	3.45	1.51
Bukit Tigapuluh 07	21	33	32	94	21	1.57	2.00	1.27
Ranun-Langkat 07	12	21	21	25	12	1.75	2.08	1.19
Ketambe 07	84	221	220	379	278	2.67	4.17	1.57
R02	44	80	74	105	67	1.82	2.39	1.31
Suaq Balimbing 07	34	57	57	73	64	1.68	2.12	1.26
Overall (all sites) 07	122	449	440	1486	839	1.96	2.80	1.42
R02	86	283	261	620	425	1.95	2.97	1.52

1. Sites ordered by location (east to west). First row values (07) are calculated from the expanded food list, 2007 version. Second row values (R02), where present, are from Rodman (2002)
2. Total counts represent taxa included in the comparative version of the combined food list.

proportion of plant species in the diet used per food type). Multivariate F tests are derived from Pillai's trace. All statistics were calculated with SAS 9.1 for Windows (SAS Institute Inc., 2002–3), with the significance level set at 0.05. Fig. 9.1 shows plots of least squares means for each fixed effect.

9.4.3.2 *Island*

Manovas comparing food lists between the two islands confirm that Bornean and Sumatran orangutans differ in number of plant food taxa (multivariate $F_{3,6} = 11.40$, $p = 0.007$) but not intensity of plant species use (multivariate $F_{6,3} = 2.25$, $p = 0.27$). Univariate tests support several predicted differences: Borneans feed on significantly more families, genera, and species than Sumatrans, consume more plant parts per species, and eat cambium and possibly leaves from a larger proportion of their plant food species (see Table 9.5, Fig. 9.1a).

9.4.3.3 *Habitat type*

Manovas compared three broad habitat types: swamp, lowland/hill, lowland/riverine (Table 9.6, Fig. 9.1c). We found a significant effect for habitat type on number of plant taxa eaten ($F_{6,14} = 3.08$, $p = 0.04$) but not for intensity of plant food species use ($F_{12,8} = 1.26$, $p = 0.38$). As predicted, however, orangutans ate from most taxa in swamps, fewer in hill forest, and fewest in riverine habitat; differences were significant for families and genera but not species (see Table 9.6). No significant differences were found across habitat types for intensity of use

Table 9.3 Orangutan food items: comparative compiled list and Rodman's (2002) list

Orangutan food list	Plant part	Families Total	Genera		Species		% species total
			Total	Identified	Total	Identified	
2007	All	122	449	440	1486	839	
	Fruit	95	331	323	1029	619	69.2
	Seed	49	113	112	220	120	14.8
	Flower	45	86	83	126	77	8.5
	Leaf	94	232	224	488	266	32.8
	Pith	27	66	59	113	48	7.6
	Bark	63	136	131	280	162	18.8
	Other	59	138	131	187	99	12.6
Rodman	All	86	283	261	620	425	
	Fruit	70	198	190	442	326	71.3
	Seed	37	69	69	105	54	16.9
	Flower	17	22	21	26	13	4.2
	Leaf	49	97	86	136	79	21.9
	Pith	13	26	24	39	26	6.3
	Bark	32	62	52	103	59	16.6
	Other	36	66	54	80	35	12.9

Rodman values are reproduced from Rodman (2002).

Total counts represent taxa included in the comparative food list.

% species total: cells show percentage of plant food species from which a food type is eaten (based on the comparative version of the combined food list).

measures but nominally, least square mean differences followed predicted patterns: orangutans eat fruit from a lower proportion of their plant food species in swamps than in either type of lowland habitat, for instance.

9.4.3.4 Habitat quality

We tested habitat quality influences in terms of logging (Table 9.7, Figure 9.1d). Neither number of taxa consumed nor intensity of plant food species use differed as a function of logging (multivariate $F_{3,6} = 0.08$, $p = 0.97$ and $F_{6,3} = 1.62$, $p = 0.37$ respectively). Nominally, least square means for number of plant food families, genera, and species were higher and for all intensity of use measures were lower in unlogged versus logged forests, as predicted. However, none of these differences neared significance.

9.4.3.5 Status

Table 9.8a (all sites) and Figure 9.1b compare rehabilitant with wild orangutan diets. Manovas detected no overall differences between wild and rehabilitant orangutans in number of plant food taxa (multivariate $F_{3,6} = 0.61$, $p = 0.60$) or intensity of use (multivariate $F_{6,3} = 6.50$, $p = 0.08$) although the latter neared significance. At the univariate level, rehabilitants eat pith from a significantly larger proportion of their plant food species (see Table 9.8a). Nominally, but not statistically, rehabilitants versus wild orangutans: eat from more taxa, eat more parts per plant food species, and eat fruit from a smaller proportion and non-preferred items (leaves, cambium) from a larger proportion of their plant food species. Pith findings conform to predictions.

This comparison is confounded by habitat differences known to affect diet, most obviously island and forest type. Food list differences attributable to rehabilitant–wild status should be most obvious when both groups range in similar habitat. Our best option for improving habitat similarity was to limit comparisons to the six sites in East Borneo. Only univariate tests were possible; none

Table 9.4 Orangutan plant food items by sites (comparative list)

Sites	Time span (years)	Total plant species	Food types—total species used								Total veg. items	Mean veg. items/sp	Plant food types – % of plant species					
			Fr	Fl	L	P	B	Vg	An	Oth			Fr	Fl	L	P	B	Vg
Kinabatangan	8	179	78	9	123	0	63	9	2	1	282	1.58	44	5	69	0	35	5
Ulu Segama	2	92	85	1	4	1	4	5	0	0	100	1.09	92	1	4	1	4	5
Danum Valley	1	87	58	5	44	0	10	0	1	0	117	1.34	67	6	51	0	11	0
Mentoko	4	103	94	0	13	0	11	2	0	0	120	1.17	91	0	13	0	11	2
Sungai Wain	6	195	143	15	37	28	32	16	11	3	271	1.39	73	8	19	14	16	8
Beratus	4	189	100	10	40	43	36	26	4	3	255	1.35	53	5	21	23	19	14
Tuanan	3	109	84	31	63	12	15	20	7	3	225	2.06	77	28	58	11	14	18
Sabangau	1.5	108	70	24	67	4	18	1	4	3	184	1.70	65	22	62	4	17	1
Tanjung Puting	4	203	156	12	41	2	50	20	6	6	281	1.38	77	6	20	1	25	10
Sungai Rayu	0.5	46	24	3	25	7	6	0	0	0	65	1.41	52	7	54	15	13	0
Gunung Palung	8	183	115	13	35	7	28	57	6	1	255	1.39	63	7	19	4	15	31
Bukit Tigapuluh	2	94	73	4	14	16	3	2	6	2	112	1.19	78	4	15	17	3	2
Ranun-Langkat	0.75	25	25	0	0	0	0	0	0	0	25	1.00	100	0	0	0	0	0
Ketambe	33	379	330	20	85	16	49	12	16	3	512	1.35	87	5	22	4	13	3
Suaq Balimbing	5	73	25	1	3	0	0	46	4	4	75	1.03	34	1	4	0	0	63

Column headings: Fr, fruit; Fl, flower; L, leaves; P, pith; B, bark; Vg, other vegetation; An, animal; Oth, other items.

Total vegetation items: sum of scores for all food parts from plants.

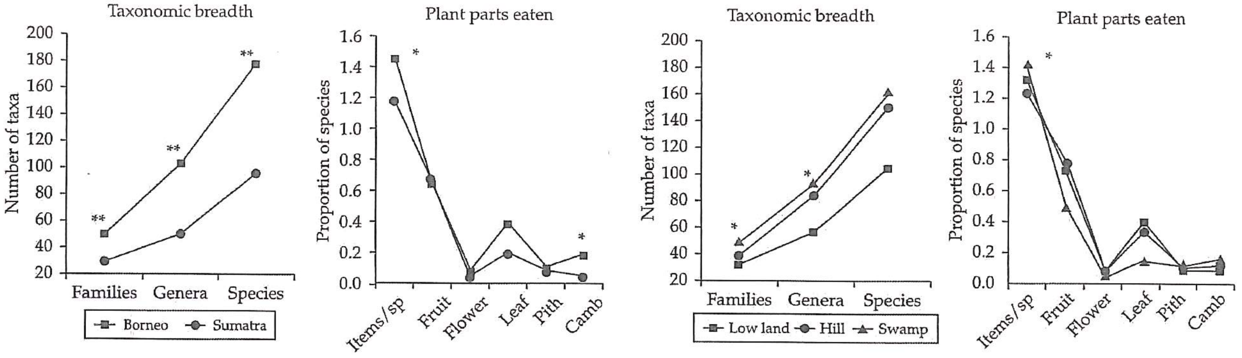
Mean vegetation items/species: total vegetation items/total species at each site.

Plant food types—% of plant species: percentage of plant food species from which each plant part is taken at each site.

Suaq Balimbing: food list does not report plant food parts systematically.

(a) Island: Borneo vs Sumatra

(c) Habitat type: lowland (riverine) vs hill vs swamp



(b) Status: Rehabilitant vs Wild

(d) Habitat quality: logged vs unlogged

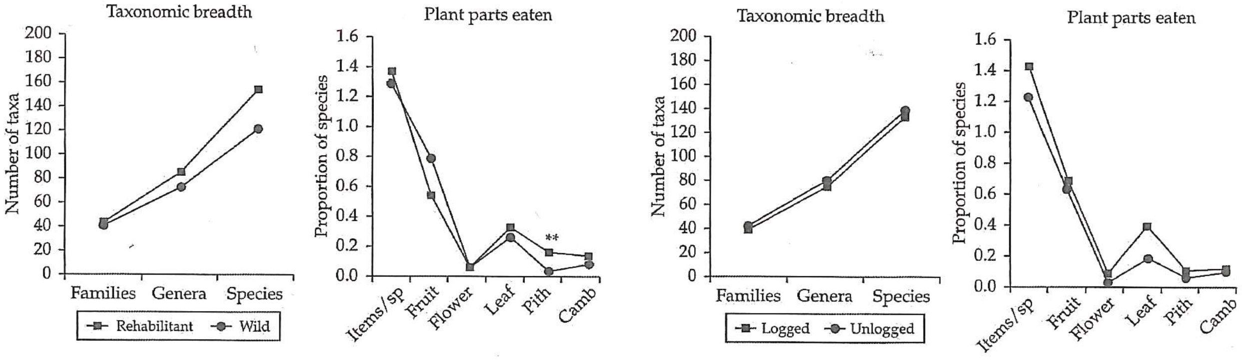


Figure 9.1 Factors influencing between site differences in plant food repertoires: (a) Island (Borneo-Sumatra), (b) Status (rehabilitant–wild), (c) Habitat type (Lowland-swamp), d) Habitat quality (unlogged-logged). Two graphs are shown for each factor, one showing taxonomic diversity (total number of families, genera, species) and the other showing the distribution of food items (average number of items per species, proportion of species from which fruit, flowers, leaves, pith, and cambium are eaten). Points shown are least square means. (*, ** difference significant at 0.05, 0.01 level, respectively.)

Table 9.5 Differences in food repertoires (plant foods) as a function of island (Borneo, Sumatra)

Variable	Borneo (n = 11)			Sumatra (n = 4)			Univariate $F_{1,9}$	p
	Mean	sd	ls mean	Mean	sd	ls mean		
Items/species	1.40	0.23	1.40	1.13	0.15	1.18	5.96	0.04
Fruit	0.69	1.15	0.69	0.75	0.28	0.68	0.08	0.78
Flowers	0.07	0.07	0.08	0.03	0.02	0.04	1.33	0.28
Leaves	0.33	0.21	0.39	0.10	0.10	0.20	3.83	0.09
Pith	0.06	0.08	0.10	0.05	0.08	0.08	0.81	0.39
Cambium	0.16	0.08	0.19	0.04	0.06	0.04	10.94	0.01
No. of families	45.45	10.54	49.03	38.25	31.92	28.56	28.48	0.0007
No. of genera	89.82	30.21	102.47	83.00	93.21	50.23	42.75	0.0002
No. of species	151.00	54.39	176.40	149.00	167.85	95.12	12.90	0.007

ls mean: least squares mean (after adjusting for study time span) (see text).

Univariate F tests compare least squares means (ls mean) for Borneo and Sumatra.

Table 9.6 Differences in plant food repertoires as a function of habitat type (lowland/riverine, lowland/hill, swamp)

Variable	Lowland (n = 4)			Hill (n = 6)			Swamp (n = 5)			Univariate $F_{2,8}$	p
	Mean	sd	ls mean	Mean	sd	ls mean	Mean	sd	ls mean		
Items/sp.	1.31	0.15	1.32	1.22	0.16	1.23	1.47	0.33	1.42	1.02	0.40
Fruit	0.74	0.15	0.72	0.76	0.18	0.77	0.59	0.20	0.48	2.03	0.19
flowers	0.04	0.03	0.05	0.04	0.03	0.04	0.10	0.09	0.09	0.44	0.66
Leaves	0.33	0.20	0.40	0.13	0.09	0.14	0.38	0.26	0.34	3.60	0.08
pith	0.04	0.06	0.08	0.10	0.10	0.10	0.03	0.39	0.09	0.41	0.68
cambium	0.14	0.04	0.11	0.09	0.08	0.08	0.17	0.13	0.16	1.06	0.39
No. of families	46.00	25.82	31.63	36.67	16.56	36.97	49.80	10.55	48.16	4.96	0.04
No. of genera	97.00	83.19	55.75	79.50	46.67	82.42	91.00	27.25	91.03	6.18	0.02
No. of species	167.75	155.21	102.21	138.67	73.89	146.13	150.80	55.94	158.94	2.03	0.19

ls mean: least squares mean (after adjusting for study timespan) (see text).
Univariate F tests compare least square means for three broad habitat types.

Table 9.7 Differences in plant food repertoires as a function of habitat quality (logged, unlogged)

Variable	Logged (n = 5)			Unlogged (n = 10)			Univariate $F_{1,8}$	p
	Mean	sd	lsmean	Mean	sd	lsmean		
items/sp	1.50	0.28	1.42	1.25	0.17	1.22	2.39	0.16
Fruit	0.64	0.16	0.68	0.74	0.20	0.64	0.10	0.76
Flowers	0.11	0.09	0.09	0.04	0.03	0.03	1.98	0.20
Leaves	0.41	0.23	0.39	0.20	0.18	0.19	3.84	0.09
Pith	0.11	0.10	0.11	0.04	0.05	0.07	3.19	0.11
Cambium	0.17	0.12	0.12	0.11	0.08	0.11	0.12	0.07
No. of families	44.80	14.11	38.32	42.90	19.75	39.52	0.08	0.78
No. of genera	86.80	36.18	74.26	88.60	57.81	78.54	0.25	0.63
No. of species	150.00	38.22	133.76	150.70	109.68	137.77	0.03	0.87

1. lsmean: least squares mean (after adjusting for study time span) (see text).
2. Logged sites: Sabangau, Tuanan, Kinabatangan, Beratus, Bukit Tigapuluh.
3. univariate F tests compare ls means for logged and unlogged sites.

showed significant wild–rehabilitant differences. Nominally, however, rehabilitant–wild differences within East Borneo were virtually identical to those seen across all sites (see Table 9.8b).

9.4.4 Food items

As an exploratory step toward understanding how orangutans learn to identify food items and their uses, we examined the combined food list for plant food species that are common to multiple sites and plant foods that may have pharmacological properties.

For plant food species common to several sites, we examined species for which the parts eaten differ between sites. If differences are difficult to explain on genetic and ecological terms, they are potentially products of social learning (van Schaik and Knott 2001). For species where fruit is eaten at all sites but leaves, pith, or cambium at only a few, for instance, differences between sites could reflect ecological differences because non-fruit items are

Table 9.8a and b Differences in plant food repertoires as a function of status (wild, rehabilitant)

	Wild (n = 11)			Rehabilitant (n = 4)			Univariate	p
	Mean	sd	ls mean	Mean	sd	ls mean	$F_{1,8}$	
(a) All sites								
Items/species	1.33	0.27	1.28	1.34	0.13	1.36	0.37	0.56
Fruit	0.72	0.20	0.78	0.64	0.12	0.54	2.74	0.14
Flowers	0.06	0.07	0.06	0.05	0.01	0.06	0.00	0.98
Leaves	0.27	0.23	0.26	0.28	0.19	0.33	0.35	0.57
Pith	0.02	0.03	0.03	0.17	0.05	0.16	30.24	0.0006
Cambium	0.13	0.10	0.08	0.14	0.08	0.14	1.30	0.29
No. of families	45.91	18.67	37.25	37.00	14.17	40.59	0.55	0.48
No. of genera	91.55	53.17	69.85	78.25	46.67	82.95	2.00	0.19
No. of species	153.45	97.57	118.93	142.25	78.64	152.60	1.64	0.24
(b) East Borneo sites								
Items/species	1.27	0.22	1.28	1.34	0.00	1.40	0.19	0.74
Fruit	0.73	0.22	0.71	0.62	0.14	0.54	0.80	0.53
Flowers	0.03	0.03	0.02	0.06	0.01	0.07	0.62	0.58
Leaves	0.32	0.30	0.31	0.20	0.01	0.33	0.00	0.98
Pith	0.00	0.00	0.02	0.19	0.07	0.19	28.96	0.12
Cambium	0.16	0.14	0.17	0.16	0.03	0.18	0.05	0.86
No. of families	41.75	11.95	44.17	49.00	2.83	47.32	0.04	0.88
No. of genera	77.50	30.44	85.55	118.50	2.12	111.07	2.31	0.37
No. of species	125.50	36.77	130.59	208.00	18.38	198.99	21.51	0.14

ls mean: least squares mean (after adjusting for study timespan) (see text).

Food type values represent the proportion of species from which each type is eaten.

Univariate F tests compare lsmeans for wild and rehabilitant orangutans.

East Borneo sites: Wild (Kinabatangan, Ulu Segama, Danum Valley, Mentoko), Rehabilitant (Beratus, Sungai Wain); to enable statistical analyses, habitat type was collapsed into two categories, lowland (lowland alluvial, swamp) vs higher land.

typically eaten when and where fruit is scarce; patchy flower eating also makes ecological sense because flowers are nutritionally rich but rarely available (McConkey *et al.* 2003).

Most plant food species are used at only one site (n = 599), consistent with presumed differences in plant species composition between sites, but a substantial number are used at multiple sites (n = 243, maximum 7 sites using the same food species). The extent of sharing may be underestimated, given rates of unidentified species. We examined plant food species shared by four or more sites (n = 39) for patterns in the plant parts eaten. The set of plant parts eaten was identical across sites for only 5/39 of these species; for the remaining 34 species, differences seemed easy to explain ecologically for only 17 species. Table 9.9 offers examples of species for which site differences seem easy and difficult to explain. The first three species show patterns that may reflect ecological factors. Orangutans eat fruit from *Dracontomelum dao* and *Garcinia parvifolia* at all sites where these species are eaten, but other parts only where productivity is probably low (logged, swamp). They eat from *Shorea leprosula* at four sites: they eat its fruit at Danum Valley but not the other three sites, probably because *S. leprosula* is a dipterocarp with an irregular, supra-annual fruiting cycle and sampling probably did not include a fruiting period.

The other four species in Table 9.9 offer examples of patterns that seem difficult to explain ecologically. Orangutans eat from *Durio kutejensis* at four

East Borneo sites; they only eat its fruit at Beratus and Sungai Wain, only its leaves at Kinabatangan, and both at Danum Valley. The fruit is large and nutritious and orangutans are fruit pursuers so not eating fruit is difficult to explain ecologically. This species may not fruit annually (Yumoto 2000) so length of study might explain not eating this fruit, but probably not at Kinabatangan. *Gironniera nervosa* provides food at five Bornean sites. Ecological conditions may underpin differences

Table 9.9 Examples of differential plant part consumption across sites

Species	Site	W/R	Ecology	Fruit	Flower	Leaf	Camb	Pith
Dracontomelum dao	GP	W	B H U	√				
(Anacardiaceae)	KN	W	B S L	√		√	√	
	BE	R	B H L	√		√		
	MN	W	B L U	√				
	KET	W	S L U	√				
Garcinia parvifolia	KN	W	B S L	√		√		
(Clusiaceae)	BE	R	B H L	√				
	SW	R	B H U	√				
	TN	W	B S L	√		√		
	TP	W	B S U	√				
	KET	W	S L U	√				
	RL	W	S H U	√				
Shorea leprulosa	DV	W	B H U	√			√	
(Dipterocarpaceae)	KN	W	B S L				√	
	MN	W	B L U			√		
	SQ	W	S S U					
Durio kutejensis	DV	W	B H U	√		√		
(Bombacaceae)	KN	W	B S L			√		
	BE	R	B H L	√				
	SW	R	B H U	√				
Gironniera nervosa	GP	W	B H U			√		
(Ulmaceae)	KN	W	B S L		√	√	√	
	BE	R	B H L	√	√	√	√	
	SW	R	B H U	√		√	√	
	TP	W	B S U	√		√	√	
Koompassia malaccensis	GP	W	B H U			√	√	
(Leguminosae)	KN	W	B S L			√	√	
	SE	W	B S L				√	
	SW	R	B H U	√			√	
	TN	W	B S L			√		
	TP	W	B S U	√		√	√	
Artocarpus elasticus	GP	W	B H U	√	√	√	√	
(Moraceae)	KN	W	B S L	√		√		
	BE	R	B H L				√	
	SW	R	B H U	√				
	B30	R	S H U	√				
	KET	W	S L U	√			√	

Ecology: Cell entries represent island (B, Borneo; S, Sumatra), habitat quality (L, lowland/riverine; H, lowland/hill; S, swamp), and habitat quality (L, logged; U unlogged) W/R: W, wild; R, rehabilitant.

Food item columns: Cells are checked if that item is eaten for that species and site. 'Other' vegetation items were dropped as uninterpretable.

between sites for flowers (ephemeral availability) but they do not easily account for eating fruit at only three sites and not eating cambium at only one. *Koompassia malaccensis* provides food at six Bornean sites including Tuanan and Sabangau. Puzzling is that orangutans eat pith at all sites except Tuanan, although Tuanan is very close to Sabangau and very similar ecologically. *Artocarpus elasticus* is eaten at six sites. The greatest number of parts is eaten at Gunung Palung, probably the most productive of the four Bornean sites with a study area of particularly high habitat diversity as well as a project focus on diet. These four patterns are more consistent with social learning than with learning shaped by ecological pressures. Patterns could change with better botanical identification and more extensive observation, so they require confirmation and careful analysis.

Orangutan food lists also include items with known medicinal value for humans. The compiled food list shows geophagy (soil consumption), for instance, at seven sites. All except Tuanan (swamp soil) and Kinabatangan (no details) report eating clays. Analyses of the clay soils that orangutans consume at Ketambe and Sungai Wain identified minerals (bioavailable iron, manganese, sodium, iodine), which may provide nutritional supplements, and kaolins and smectite, which could relieve gastrointestinal distress from harmful dietary organics and excessive intestinal tract water (Stambolic-Robb 1997; Voros 2000). Site specific and compiled food lists may be similarly useful for highlighting other items in orangutan diets that may have medicinal properties. Kissler (2003) used an earlier version of the combined food list to determine whether any of 54 plant items identified in traditional dayak medicine occur in orangutan diets. Her comparison turned up 18 orangutan plant food taxa known to have medicinal properties for humans. Whether orangutans eat the specific plant parts that have medicinal value and whether they obtain medicinal benefits remains to be assessed. As with food knowledge, the value of food lists lies in narrowing the range of possibilities worth examining.

9.5 Orangutan and great ape diets compared

We compared our extended orangutan food list with food lists that Rodman (2002) compiled for each great ape (Fig. 9.2, Table 9.10). Three patterns stand out. First, our extended food list alters Rodman's picture of orangutan diet range substantially. Wich's updates to the Ketambe food list, for instance, show Ketambe orangutans eating the most species per plant family of the six populations Rodman included whereas the older Ketambe food list available to Rodman showed Ketambe orangutans eating the fewest (see Table 9.2). The extended list also shows greater interpopulation variation in number of species eaten per plant family than Rodman's list (2.00–4.17 vs 2.39–3.72) (see Table 9.2) and orangutans eating flowers, leaves and bark from higher percentages of their food species (see Table 9.3). These patterns do not adjust for length of study. Rodman (2002) included little information

Table 9.10 Comparing great ape plant diets

Great ape taxa	No. of sites	Families	Comparable		Identified	
			Genera	Species	Genera	Species
Orangutan 2007	15	122	449	1486	440	839
Gorilla	11	105	360	662	347	551
Chimpanzee	13	94	348	631	340	571
Orangutan 2002	6	86	283	620	261	425
Bonobo	4	57	169	257	167	227

Two entries are listed for orangutans: 2007 (the current food list) and 2002 (Rodman's 2002 list).
Values for gorillas, chimpanzees, and bonobos are taken from Rodman (2002).
Great ape taxa are listed in order of dietary diversity (highest, first).

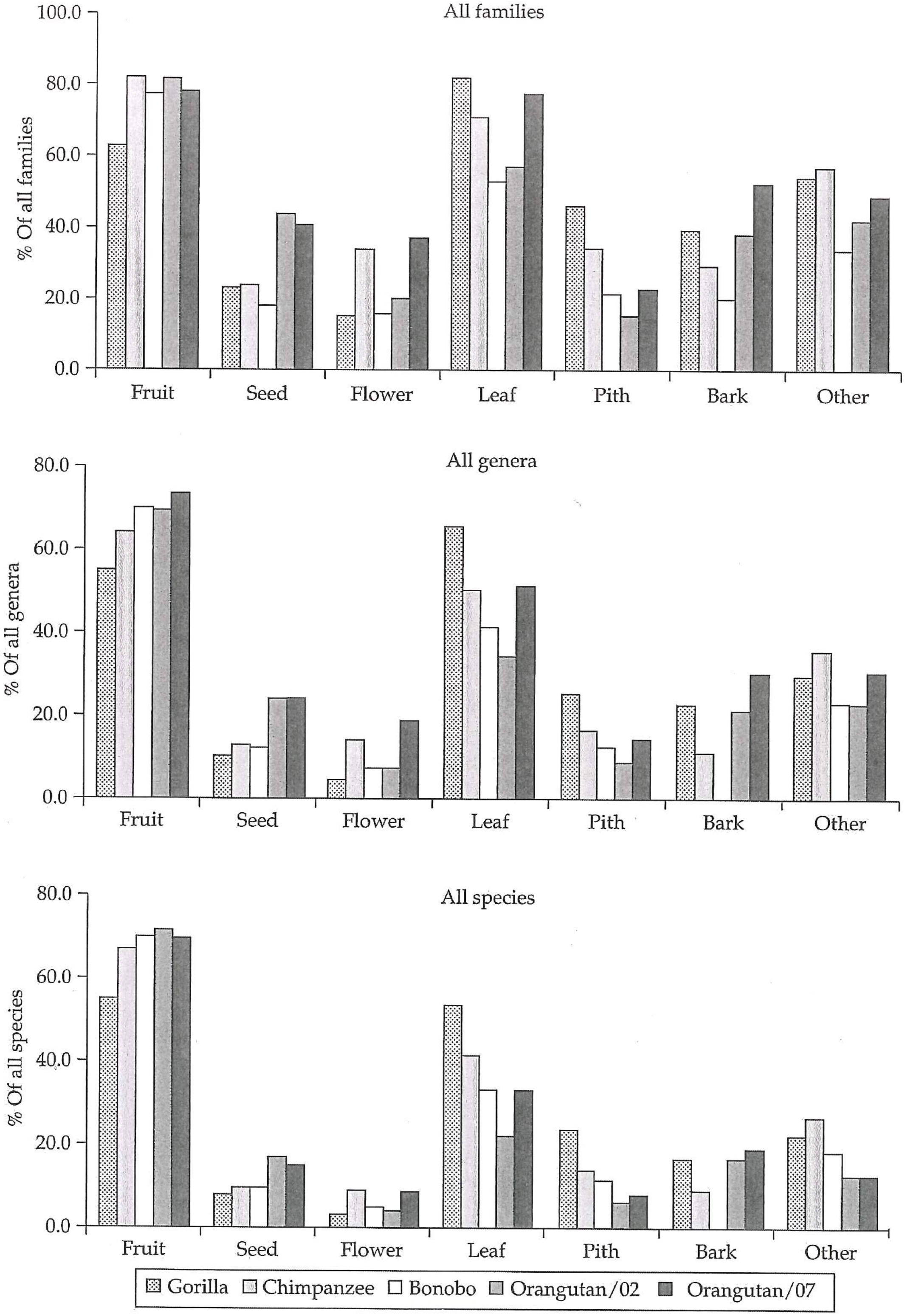


Figure 9.2 Comparing dietary range between great apes. Figures compares percentages of food plant families, genera and species that serve as sources for individual plant food items across great ape taxa. Two sets of values are shown for orangutans to illustrate the changes generated by updating the food list. Orangutan/07 values are derived from the present updated food list. Orangutan/02 and all African great ape values are taken from Rodman (2002) with one exception (*Pan paniscus*, total number of genera for 'Other': published value (4) is assumed to be in error; the value 40 was substituted).

on the methods used to collect the food data he included, so there is no immediate way to incorporate this factor.

Second, we reconsidered Rodman's comparison of food lists across the great apes using the extended orangutan list. Table 9.10 clearly shows a positive correlation between the number of sites represented in each great ape's food list and taxonomic richness: the more sites included, the broader the food list. Apparent differences between great ape taxa are most likely due to habitat variation, which would almost inevitably increase with more contributing sites. Food lists for orangutans, chimpanzees, and gorillas now represent similar numbers of sites (11–15) so chances are better that food list differences represent differences between these taxa. For the same reason, however, the bonobo dietary pattern is probably unreliable.

Third, food list updates change the position of orangutans relative to African great apes in diet. Data available to Rodman indicated that orangutans feed on narrower ranges of plant taxa than African great apes, except bonobos. Updated data show orangutans feeding on wider ranges of plant taxa than African great apes and perhaps more species per plant family (Wilcoxon two sample test, $p < 0.08$, comparing Rodman's values for African great ape sites with updated orangutan values, per Table 9.3, for sites with data covering at least one year). These patterns are consistent with lower productivity and perhaps more floristically diverse forests in Asian than African great ape habitat (Yamagiwa 2004), which probably oblige orangutans to tap a wider range of plant taxa than African great apes to fulfill their nutritional needs. Changes in the proportion of plant food species that orangutans tap for individual food types also increase similarities between orangutan and African great ape diets (see Table 9.3). Rodman's (2002) analyses led him to conclude that great ape diets are homogeneous; updates to the orangutan list reinforce this interpretation.

9.6 Discussion

Several inter-population differences in food lists conform to predictions based on habitat productivity. Orangutans ranging less vs more productive habitat feed on more taxa (Borneo vs Sumatra, swamp vs hill vs riverine habitat), feed more intensively on their plant food species (Borneo vs Sumatra), and eat low-quality foods from higher proportions of their plant food species (Borneo vs Sumatra). Not all predicted differences were supported statistically, but most differences were consistent with the view that habitat productivity has an inverse effect on dietary breadth and intensity of food species use.

Findings also suggest internal effects on diet, in particular, rehabilitant versus wild orangutans may feed on relatively more taxa and eat pith from a larger proportion of their plant food species. Greater pith consumption could reflect rehabilitants' relatively greater terrestriality (Harrisson 1969; Borner and Stonehouse 1979; Peters 1995; Chapter 23 this volume); this could lead to heavier use of terrestrial vegetation, which is one of their major sources of pith (e.g., gingers, pandans, pinangs). Rehabilitants' wider range of food taxa may also indicate greater exploration. Sociocultural support in the wild should focus learners on the better food taxa in their area; rehabilitants, who lack such guidance, may rely on trial and error and ultimately use a larger range of taxa. This is consistent with suggestions that they may be the more innovative (Chapter 20 this volume).

This food list also shows orangutan diets to be as taxonomically rich as African ape diets or even more so, consistent with the view that orangutan habitat is less productive and more variable in fruit production than African ape habitat (Yamagiwa 2004). It shows orangutans eat plant food parts in proportions more similar to African great apes than the food lists available to Rodman (2002) indicated. It shows greater similarity in the items that orangutans and African great apes eat—notably invertebrates (substantial), vertebrates (rare but rather widespread), and medicinal items. Orangutans eat meat, albeit very rarely, at Gunung Palung, Suaq Balimbing and Ketambe, and some rehabilitants eat fish (chapter 20). Nonhuman primate meat eating occurs beyond great apes (Utami and van Hooff 1997) but finding it in multiple orangutan populations increases the likelihood that it is a dietary feature common to great apes, not one that emerged newly in chimpanzees. The immediate interpretation for the differences between Rodman's and the updated orangutan food list is that the latter represents a wider range of habitats, sites, and timeframes. Alternatively, the differences might represent changes to orangutan diets caused by habitat degradation. All but two of the lists Rodman used (Gunung Palung, Sungai Wain) represent the late 1960s and the 1970s; all sites added to the updated list represent the 1990s or later. Forest degradation through logging and 'conversion' became increasingly widespread in Sumatra and Borneo from the 1970s, so differences between the two lists may represent habitat change over time rather than stable habitat differences. Both factors probably enter into play.

Various factors complicate the picture. First, the external and internal factors explored here cannot be entirely disentangled. Island differences could reflect species factors, given that Bornean and Sumatran orangutans are now considered distinct species, and rehabilitant–wild differences are generally consistent with lower productivity at rehabilitant sites although our measures do not suggest productivity differences. The weak habitat-linked differences in diet found here may be due in part to orangutans' flexible foraging strategies. Their contingent use of two main strategies in response to food scarcities, shifting diet and traveling in search of preferred foods, combined with the fact that they typically range in areas that provide a mosaic of habitat types, is probably designed to buffer or mute the impact of ecological factors.

Second, some weak results may reflect methodological factors, such as limitations to current food list data or conditions in effect when and where food data were collected (Fox *et al.* 2004). Logging effects, for instance, may be unclear because of habitat recovery post logging. Normal orangutan densities have been found in disturbed forest that has had time to regenerate (Knop *et al.* 2004; Ancrenaz *et al.* 2005) and none of the food lists used here represents feeding only immediately after logging. Habitat type effects may be diluted because we tested dominant rather than pure habitat types and research sites typically include a mix of habitat types. Assessing habitat type using only each site's plant food species specific to each type might produce greater differences. Length of study affected orangutan diet patterns, as expected. Short-term studies may misrepresent how orangutans apportion food types across plant food species, notably bark/cambium, and underestimate the range of foods they eat. Long-term studies are more likely to include fruit scarcity periods, so the bark finding is consistent with evidence that orangutans respond to seasonal fruit scarcities by increasing use of fallback items like bark but do not readily reduce fruit consumption.

Several recommendations for further work issue from this project. First, we recommend revising data collection standards for reporting food items and for identifying food species. Existing standards (Morrogh-Bernard *et al.* 2002) are valuable in identifying essential distinctions across sites but they do not distinguish some items with important biological implications. Orangutans are considered important seed dispersers and seed predators, for instance, so seed ingestion is worth distinguishing from seed predation. Orangutans themselves often distinguish young from mature leaves, the former being less toxic so easier to digest. Pith, in the sense of relatively spongy tissue in the center of any stems, remains a catch-all category that is biologically heterogeneous (food lists report as pith, meristem, parenchyma, inner leaf stems). Cambium is the bark-related item most often consumed, but orangutans may eat the whole of the bark in some species. Finally, orangutans consume significant numbers of non-plant items that are worth distinguishing in field reports and identifying formally, especially invertebrates. Invertebrate foods have been formally identified for chimpanzees and the study of chimpanzee invertebrate consumption has been informative, so similar efforts could prove informative for orangutans. We therefore recommend the following revisions to recording standards for orangutan foods (Table 9.11).

While comparisons of orangutan food lists across orangutan populations did not, for the most part, go beyond supporting recognized diet patterns, comparisons with other great apes did change the picture of the variability and composition of orangutan diets relative to African great apes. The compiled food list may also suggest starting points for studying how orangutans acquire knowledge about food items and the extent to which they obtain medicinal benefits from items they ingest.

Table 9.11 Standards for recording orangutan food items

Item	Description
Fruit	The pulp (mesocarp) and skin (exocarp) of the fruit of a plant. Part(s) eaten (pulp, skin); stage of maturity (ripe, unripe mature-large but not ripe, unripe immature); for all stages describe color and softness.
Seed	The seed (endocarp) of a plant, if ingested. Parts ingested; stage of maturity
Flower	Part(s) eaten, stage of maturity (bud, flower)
Young leaf	Immature leaves, including shoots Parts eaten (blade with/without veins, petiole, tip, stem)
Leaf	Mature leaves (includes epiphyte leaves); parts eaten (per young leaves)
Pith	Inner matter within the stems of plants (e.g., meristem, parenchyma) Part(s) eaten (meristem, parenchyma), part(s) discarded after processing (e.g., fibrous material after sap extracted), growth form (e.g. rattan, palm, pandan, liana, ginger, grass, other terrestrial herbaceous vegetation)
Bark	Bark, including inner layers (cambium, or phloem) part(s) eaten (e.g., cambium, cambium plus bark)
Other plant	Any other plant parts (e.g. root, fern, other parts of epiphytes, dead wood) part(s) eaten
Invertebrates	part(s) eaten; stage of maturity/caste; describe source
Vertebrates	part(s) eaten, stage of maturity
Water	describe source
Other non-plant	Any other items (e.g., honey, fungi, soil) part(s) eaten, describe items

Together, findings illustrate that food lists can be useful for understanding orangutan diets. With further improvements, e.g., standardized food data collection, food species linked to habitat type, and extended study duration, findings also suggest it is worth revisiting the factors tested here and exploring additional ones. Further comparisons between orangutans and other great apes are also worth pursuing, although these also entail updating African great ape food lists. Newer food lists have become available for some African great apes: western lowland gorillas, for instance, have been found to be more dedicated to fruit than previously believed (Rogers *et al.* 2004). Newer food data also show marked dietary differences within both gorillas and orangutans, suggesting the merits of comparing great apes along other lines than the traditional chimpanzee–gorilla–bonobo–orangutan.

Finally, with orangutans and other great apes at risk of extinction, conservationists urgently need to understand the ecological conditions in which each species can survive in order to design effective protection programs. Meeting nutritional needs is fundamental to survival, so knowing what items orangutans can use as food is essential to identifying forest areas that are suitable for them, gaining protection for these areas, and perhaps enriching them. This orangutan food list has already proven valuable as a basis for identifying orangutan food species available in a given forest block. Rogers *et al.* (2004) suggested similar applications for their western lowland gorilla food list. Finding suitable habitat for the world's remaining great apes is increasingly crucial to ensuring their survival, and broad databases like these offer one basis for assessing and demonstrating suitability.

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