Dietary adaptations of temperate primates: comparisons of Japanese and Barbary macaques

Goro Hanya, Nelly Ménard, Mohamed Qarro, Mohamed Ibn Tattou, Mieko Fuse, Dominique Vallet, Aya Yamada, Moe Go, Hino Takafumi, Riyou Tsujino, Naoki Agetsuma and Kazuo Wada

G. Hanya, A. Yamada, M. Go, K. Wada: Primate Research Institute, Kyoto University, Inuyama, Japan
N. Ménard, D. Vallet: Station Biologique, CNRS-université Rennes, Paimpont, France
M. Qarro: Ecole Nationale Forestière d'Ingénieurs, Salé, Morocco
M. Ibn Tattou: Institut Scientifique, Université Mohammed V-Agdal, Rabat, Morocco
M. Fuse: Sasayama Field Station, Kobe University, Sasayama, Japan
H. Takafumi and N. Agetsuma: Field Science Center for Northern Biosphere, Hokkaido University
R. Tsujino: Research Institute for Humanity and Nature

Correspondence to: G. Hanya: Primate Research Institute, Kyoto University, Kanrin 41-2, Inuyama, Aichi, 484-8506 Japan. E-mail: hanya@pri.kyoto-u.ac.jp, Tel: +81-568-63-0542, Fax: +81-568-63-0564

Short title: Diet of temperate macaques

Abstract

Habitat, diet and leaf chemistry are compared between Japanese and Barbary macaques in order to reveal the similarities and differences in dietary adaptations of temperate primates living at the eastern and western extremes of the genus *Macaca*. Tree species diversity and proportion of fleshy-fruited species are much higher in Japan than in North Africa. Both species spend considerable annual feeding time on leaves. Japanese macaques prefer fruits and seeds over leaves and Barbary macaques prefer seeds. These characteristics are adaptive in temperate regions where fruit availability varies considerably with season, since animals can survive during the lean period by relying on leaf and other vegetative foods. The two species are different with respect to the higher consumption of herbs by Barbary macaques, and the leaves consumed contain high condensed and hydrolysable tannin for Barbary but not for Japanese macaques. Barbary macaques supplement less diverse tree foods with herbs. Because of the low species diversity and high tannin content of the dominant tree species, Barbary macaques may have developed the capacity to cope with tannin. This supports the idea that the digestion of leaves is indispensable to survive in temperate regions where fruit and seed foods are not available for a prolonged period during each year.

KEY WORDS: Barbary macaque, condensed tannin, Japanese macaque, leaf chemistry, temperate forest

Introduction

Primates originated in the tropical rain forests (Fleagle 1999), but they have radiated into various marginal habitats, such as woodlands, savanna and high mountains. Temperate forest is one of those marginal habitats harboring approximately 20 genera within 8 families (Lemuridae, Indriidae, Cheirogaleidae, Lorisidae, Cebidae, Callitrichidae, Cercopithecidae and Hylobatidae), if we define the border between temperate and tropical regions as the tropics of Cancer and Capricorn (Fleagle 1999). Among them, five species (Japanese and Barbary macaques, Sichuan and Guizhou golden monkeys, and golden langurs) are distributed exclusively in the temperate regions (Fleagle 1999). Although temperate primates are a minority within the order, it is expected that adaptations to temperate habitat have evolved in various lineages.

Temperate forest is characterized by high seasonal variations in temperature and day length. In addition, fruiting phenology in temperate forest is more seasonal than in tropical forest (Ting et al. 2008), and the fruiting peak tends to occur in a more limited time of the year (autumn). Consequently, fruiting phenology tends to be more seasonal and predictable in temperate forest than in tropical forest (Ting et al. 2008). In the former, fruit is commonly absent for several months of the year (Herrera 1984; Hanya et al. 2004). In some tropical forests, plant reproductive phenology is aseasonal or weakly seasonal (Sakai 2002). In most tropical forests, however, fruiting peaks are predictable, but not all species peak in the same month (van Schaik et al. 1993; Ting et al. 2008). Based on a review of 51 temperate and tropical forests all over the world, fruit fall in the tropical forests is, on average, 1.71 times larger than that in temperate forests (Hanya and Aiba, in press). The proportion of fleshy-fruited species, potential foods for primates, is also smaller in temperate than in tropical forests (Willson et al. 1989). Therefore, fruit food availability (biomass of edible parts of fruits) seems to be smaller in temperate than in tropical forests.

Availability of young leaves, as well as fruits, may also be limited in temperate forests. Young leaves are usually available throughout the year in the tropics (van Schaik et al. 1993), but the period of leaf flushing is confined to spring and early summer in temperate regions (Agetsuma 1995; Komiyama et al. 2001). Therefore, protein-rich young leaves cannot be used as a fallback food when fruits are not available, particularly in winter.

Hanya (2004) revealed that Japanese macaques have two dietary characteristics that are adaptive in temperate forests: 1) They eat substantial amounts of leaves and other vegetative parts, while fruits and seeds are only minor foods; 2) Even in the fruit-poor environments, they prefer fruits and seeds and eat them whenever they are available. To survive in a fruit-poor environment, monkeys must adapt by eating a large amount of leaf foods. In fact, the proportion of fruit-feeding time of temperate macaques (*Macaca fuscata*, *M. cyclopis*, and *M. mulatta*: 9-54%) is lower than that of tropical macaques (*M. fascicularis*, *M. radiata*, *M. nigra*, and *M. nemestrina*: 59-70%) (Hanya 2004). At the same time, preference for fruit is also useful in temperate regions because food ingested in excess of daily requirements can be saved as fat to help animals survive in the fruit-poor winter (Wada 1975). Since the fruiting phenology and climate are highly annually periodic in temperate forests, it is possible for animals to predict when to start fat deposition and how long a food shortage will last. In fact, patterns of seasonal change in deposited fat are quite similar among different populations of Japanese macaques, having peaks in early spring and late autumn, corresponding to the seasonal change in food availability (Muroyama et al. 2006). Therefore, dependence on deposited fat is a safe strategy in temperate regions, and fat deposition is in fact prevalent in temperate and arctic endotherms (Pond 1978).

This paper compares habitat, diet and leaf food selection by two species of temperate macaques, Japanese and Barbary macaques. We chose these species because

1) they are among the most-studied temperate macaques and 2) they are the most distantly located, at the eastern- and western-most extremes of the distribution of genus *Macaca*. Japanese macaques are distributed widely throughout the Japanese archipelago (30—41° N). Their habitat includes both warm-temperate broad-leaved evergreen forest and cool-temperate broad-leaved deciduous forest. They also live in coniferous forests in high mountains (Izumiyama 2002; Hanya et al. 2004). Barbary macaques live in isolated forest patches in Morocco and Algeria (31—36 ° N). They live from lowland thermophilous scrub through mid-altitude mixed deciduous and evergreen oak forest and high-altitude coniferous forest (Fa 1984b). Among the extant macaques, Barbary macaques represent a relatively ancient branch (Fa 1989). Some data on other temperate species are available, but we have not examined them in detail, as we have done for the Barbary and Japanese macaques because data for those other species are scanty, in particular habitat data.

Based on our original data and review of published articles, we examine 1) the difference in tree species diversity and composition between the two habitats; 2) the annual diet of the two species, with special reference to fruit/seed- and leaf-eating; 3) the relationship between fruit/seed availability and fruit/seed-eating in the two species, in order to clarify the preferences for fruit/seeds by these macaques; and 4) leaf chemistry of food and non-food tree leaves, in order to reveal the difference in selection criterion of leaf foods in response to the habitat differences.

Methods

Vegetation

Data on the vegetation of macaque habitats were derived from our published (Ménard and Vallet 1988; Hanya et al. 2003) and unpublished data. Data from six sites in Japan and two sites in Algeria were compared. We sampled trees of >5 cm in diameter at breast height (DBH). The number of species and the Shannon-Wiener diversity index (Clutton-Brock 1977) were compared. In the calculation of the diversity index, each species was evaluated either by basal area or coverage. We controlled for the effect of area on species diversity by comparing plot sizes of 0.5 ha, in some cases obtained by extrapolation (Colwell and Coddington 1994), using the software program 'EstimateS'.

Diet

Annual dietary composition was compared primarily by using observational data of 12 months or more, expressing dietary composition according to feeding time. Data were available for three sites (lowland and coniferous forest of Yakushima and deciduous forest of Kinkazan) for Japanese macaques (Hill 1997; Hanya 2004; Tsuji et al. 2006) and two sites for Barbary macaques (deciduous oak forest of Akfadou and coniferous/evergreen broad-leaved forest of Djurdjura, Algeria) (Ménard 1985; Ménard and Vallet 1986). For comparative purposes, data on annual diet of three species of tropical macaques (*M. nigra*, *M. fascicularis* and *M. radiata*), studied by scan sampling (Ali 1986; Yeager 1996; O'Brien and Kinnaird 1997), are also shown. Data on monthly changes were not available for the tropical macaques. At Kinkazan, data were obtained over several years and included all 12 calendar months. At other sites, data were taken for at least 12 consecutive months. In the lowland forest of Yakushima, data were taken for 1.5 years, but we used data for only the first 12 consecutive months.

At the two North African sites, we used the scan sampling method, recording the activity of the first five animals seen every 10 min. At Yakushima, we used focal sampling of adults and recorded behavior by instantaneous 1-min sampling (lowland habitat) or continuous sampling (coniferous forest). At Kinkazan, both scan sampling (every ten or five minutes) of all visible individuals and continuous focal-animal sampling of adult females were used. There are methodological differences among the studies, but for rough comparison of major food items, these can be neglected (Fragaszy et al. 1992). In lowland Yakushima, annual dietary composition described by scan sampling (Agetsuma and Nakagawa 1998; data not used because observations for January were lacking) is similar to that obtained by focal animal sampling (Hill 1997; data used in this paper). Dietary data were expressed as the proportion of the food in the annual feeding time. The actual proportion of each food's intake may be different from the value expressed by feeding time. However, this should not matter for comparative purposes, such as the evaluations in this study. Other types of data, e.g. data representing diet by energy intake or data of less than one year, were used ad libitum.

Leaf chemistry

Data on leaf chemistry for Japanese macaques in Yakushima are taken from Hanya et al. (2007), but the data for Barbary macaques in Moyen Atlas, Morocco, are original. In Yakushima and Moyen Atlas, both food and non-food leaves were sampled. In Yakushima, food leaves were determined from our observational data covering a one-year period in the coniferous and lowland forests (Hanya et al. 2007). For non-food leaves, all of the species which appeared in two vegetation plots but were not eaten by macaques were examined. The vegetation plots were 50 m × 50 m and 5 m × 1500 m in lowland and coniferous forests, respectively. Both plots, although having different sizes and shapes, reflect typical macaque habitat characteristics (Hanya et al. 2007). Since there was no essential difference in leaf selection between the two habitats (Hanya et al. 2007), data on coniferous and lowland forests were combined. Leaves were sampled in September 2000, 2004 and 2005. In Moyen Atlas, leaves of all species listed in Table 6.4 of Drucker (1984) (except introduced species), representing food species and major trees in Moyen Atlas, were sampled. Among them, food leaves were determined using the comprehensive food list of Barbary macaques in Appendix II of Fa (1984a). Leaves were sampled in late September and early October 2005. The numbers of food and non-food leaf species sampled were, respectively, 24 and 54 in Yakushima and 13 and 16 in Moyen Atlas. Sampling periods were determined by the following conditions: 1) several months after the leaf flush in spring, 2) before the deciduous species shed leaves in late autumn 3) when at least some leaf eating was observed. Since the sites' sampling periods roughly matched, data were comparable.

Sampling was conducted for at least four individual trees, except when the species was rare (2 species for each area, sampled for only one tree). At least 20 leaves were sampled for each species. Collected leaves were kept in paper envelopes and brought to field stations where they were immediately dried at 40°C for 24 hours. Pre-dried leaves were kept in plastic bags and brought to the laboratory at the Primate Research Institute, Kyoto University, where they were dried again at 40°C for 48 hours by a vacuum incubator. After weighing, leaves were ground, sieved through a 0.5-mm mesh, put in plastic tubes, and kept in a desiccator.

All of the chemical analyses were done at the Primate Research Institute, Kyoto University, under the same protocol. Crude protein was determined using the Kjeldahl procedure for total nitrogen and multiplying by 6.25 (Hasegawa 1993). Crude lipid was measured as diethyl-ether extract by the Soxhlet method (Hasegawa 1993).

Crude ash was determined by ashing at 550°C (Hasegawa 1993). Neutral detergent fiber (NDF) was estimated following the methods of van Soest et al. (1991). Condensed tannin was extracted with 50% methanol and determined by the buthanol-HCl method (Porter 1989). Condensed tannin concentration was calibrated from the absorbance at 550 nm, using the known concentration of cyanidin chloride. Hydrolysable tannin extracted with 70% aqueous acetone was determined by the potassium iodine method (Willis and Allen 1998). Hydrolysable tannin concentration was calibrated as a tannic acid equivalent from the absorbance at 550 nm. The available standards of tannins substantially overestimate or underestimate tannin concentration (Rautio et al. 2007) , so the reported values of tannin are used only for comparative purposes (food vs. non-food or Yakushima vs. Moyen Atlas) in this study.

With respect to leaf chemistry, we conducted two kinds of analysis. First, in order to analyze leaf selection at each study site, we used the generalized linear model (GLM) based on whether macaques ate the species (0 = non-food, 1 = food) as a dependent variable and the above-mentioned six chemical properties as independent variables. This analysis was conducted separately for each site. All possible combinations of independent factors were examined, and the model fitness was assessed by Akaike's Information Criterion, or AIC (Burnham and Anderson 2002). We examined only the model having a ΔAIC (difference with the smallest AIC) of less than two. In order to assess the relative likelihood of these models, we calculated Akaike weight as: exp(-0.5 * ΔAIC score for that model)/sum of exp(-0.5 * ΔAIC score) for all of the models (Burnham and Anderson 2002). Second, in order to determine the difference in the chemical properties of food leaves between the two macaque species, we compared the six chemical properties of food leaves between the sites by the t-test.

Since six analyses were run, the alpha level was set to 0.05/6 = 0.0083, using Bonferroni correction (Curtin and Schulz 1998).

Results

Habitat

Habitats of Japanese macaques were richer in tree species, in particular fleshy-fruited species, than those of Barbary macaques, although the same genera or families were often dominant in both regions. When comparing the number of species per 0.5 ha, the Japanese forests had 18-61 tree species, including 7-35 fleshy-fruited species. On the other hand, the North African forests had only four or five tree species (all non-fleshy). As for the diversity index, quantitative comparison is difficult due to the difference in plot size and sampling method (basal area is used in most of the Japanese forests, and coverage is used in the North African forests). However, all of the Barbary macaque habitats had lower diversity indices than the Japanese macaque habitats (Table I). In one study site where the diversity index was calculated from both coverage and basal area, coverage resulted in a higher index than did basal area. If this held true for North African sites, the difference in diversity between Algeria and Japan may have been larger than shown in Table I. Even when a much broader area was covered (84 forests over 20 km × 70 km), both number of species and diversity were lower in the Barbary macaque habitat (Ajbilou et al. 2006) than in any of the Japanese macaque habitats. Fleshy-fruited species constituted more than half of the tree species in Japanese forests but only a small portion (0-33%) in North African forests. In both habitats, oaks (*Quercus*) were dominant in lowlands and conifers (*Cedrus* and *Pinus* in North Africa and *Abies*, *Cryptomeria* and *Tsuga* in Japan) were dominant in high-altitude forests.

Diet

Among the five populations, the proportion of time spent feeding on leaves was highest for Barbary macaques in the coniferous/evergreen broad-leaved forest of Djurdjura (48%) and second highest in Japanese macaques in the coniferous forest of Yakushima (41%) (Fig. 1). The proportion of time spent feeding on seeds was highest for Japanese macaques in the deciduous forest of Kinkazan (44%), followed by two Barbary macaque populations (26% and 32%) and Japanese macaques in the lowland forest of Yakushima (34%); however, this value was low in the coniferous forest of Yakushima (4%). The proportion of fruit-eating time was higher for Japanese macaques (10-24%) than Barbary macaques (0.8-4.3%). Lichen constituted a considerable proportion of feeding time of the Barbary macaques in the deciduous oak forest of Akfadou (14%). It has not been reported that Japanese macaques eat lichens. In the coniferous forest of Yakushima, the macaques also spend considerable time feeding on mushrooms (14%). Compared with tropical macaques, time spent feeding on fruits was considerably lower (54-67% for tropical vs. 0.8-25% for temperate macaques).

Barbary macaques eat more herbs than Japanese macaques. Barbary macaques in the coniferous/evergreen broad-leaved forest of Djurdjura spent 54% of their annual feeding time on herbs, constituting 35% leaves, 8% root and 11% seeds, and those in the deciduous oak forest of Akfadou spent 32% of feeding time on herbs (19% leaves, 7% roots and 6% seeds) (Ménard 2002). Japanese macaques in the coniferous forest of Yakushima spent only 15% of annual feeding time on herbs (9% leaves, 3% roots, 1% seeds) (Hanya 2004), and those at Kinkazan spent 28% of annual feeding time on herbs (leaves 25% and fruits 3%) (Tsuji et al 2006; Tsuji et al. unpublished data). Hill (1997) does not report the herb feeding time. However, according to Agetsuma and Nakagawa (1998), who reported the food composition of Japanese macaques in the lowland of Yakushima for 11 calendar months, herb feeding time was only 3% of the annual feeding time.

Seasonal changes in diet were similar in the two species, although the absolute feeding time was considerably different (Fig. 2). In the case of Japanese macaques, leaf eating was dominant in winter (January-March) or spring (April-June), since fruits and seeds were not available and macaques ate mature leaves as fallback foods (Hanya 2004) or because protein-rich young leaves are available. Fruit and seed eating occurred most often in autumn (September-November) and intermediately in summer (July and August, except in the coniferous forest of Yakushima). Mushroom-eating was observed in various months for Japanese macaques, most often in summer. In summary, Japanese macaques ate young leaves in spring, various foods such as fruits, mature leaves, fungi, seeds and animals (mostly insects) in summer, and fleshy fruits and seeds (in particular acorns) in autumn. In winter, after consuming the fruits and seeds produced in the preceding autumn, they ate mature leaves of evergreen trees in evergreen forests or bark and winter buds in deciduous forests. The same pattern has also been reported at other sites, such as the warm-temperate forest of Koshima or the cool-temperate forest of Shiga Heights (Suzuki 1965; Iwamoto 1982). Barbary macaques also ate leaves in spring, various foods such as fruits, seeds, leaves, lichens and roots in summer, acorns and conifer (*Abies* and *Cedrus*) seeds in autumn, and leaves and lichens (Akfadou only) in winter. Similar patterns have been reported from Rif or Moyen Atlas (Drucker 1984; Mehlman 1988; Ménard and Qarro 1999).

Japanese macaques prefer fruits and seeds, while Barbary macaques also prefer seeds but not fruits. It has already been shown that Japanese macaques in the coniferous forest of Yakushima increased their feeding time on fruits and seeds with increasing availability (Hanya 2004). We analyzed the relationship between fruit/seed eating and availability for Barbary macaques in Moyen Atlas using the data by Drucker (1984), expressing monthly dietary composition by energy intake. They ate fleshy fruits of lianas from February to April and acorns from August to November. Monthly feeding time on seeds and seed availability correlated significantly ($r = 0.969$, $P < 0.0001$). However, correlation between the monthly feeding time on fruits and fruit availability was not significant ($r = 0.569$, $P = 0.523$).

Leaf chemistry

Condensed tannin and lipid content affected leaf selection of Japanese macaques, but no chemical factor significantly affected leaf selection of Barbary macaques (Tables II and III). GLM analysis revealed that all of the models having Δ AIC < 2 included condensed tannin, hydrolysable tannin, and crude lipid (all negative effect), and thus the effects of these three factors were robust. On the other hand, in the analysis of Barbary macaques, a null model having no independent factor had the smallest AIC, and none of the other models having Δ AIC < 2 were significant.

In comparing food leaves between Japanese and Barbary macaques (Fig. 3), the food leaves of Barbary macaques included significantly higher condensed tannins, hydrolysable tannin, and crude lipid (condensed tannin: $t = 3.92$, $P = 0.004$; hydrolysable tannin: $t = 3.13$, $P = 0.0035$; crude lipid: $t = 4.17$, $P = 0.0002$). On the other hand, the content of crude protein, neutral detergent fiber and crude ash did not differ significantly between the two macaques (crude protein: $t = 2.12$, $P = 0.041$;

neutral detergent fiber: $t = 2.75$, $P = 0.0093$; crude ash: $t = 0.838$, $P = 0.41$).

Discussion

We established that tree species diversity, in particular fleshy-fruited species, is higher in Japan than in North Africa. Both Japanese and North African forests are dominated by *Quercus* (lowland) and conifers (high altitude forests), but North African forests consist almost exclusively of those dominant species. This difference significantly affected the feeding ecology of the two macaque species.

Similarities

In response to the pronounced seasonal changes in temperature and fruiting phenology, which is a more-or-less universal pattern among temperate forests (Ting et al. 2008), both Japanese and Barbary macaques showed qualitatively similar patterns of seasonal dietary change. They eat young leaves in spring, various foods including fruits, mature leaves, and fungi in summer, fruits and/or seeds in autumn, and leaves and other vegetative foods such as mature leaves, buds and bark in winter. A similar pattern can also be seen for Taiwanese macaques (Su and Lee 2001). The dietary pattern of rhesus macaques in Pakistan seems a bit different; since they increase fruit eating in the monsoon season (July-September) between dry early summer and dry autumn (Goldstein and Richard 1989). In this area, the greatest fruit diversity and biomass is available for macaques in the monsoon season (Goldstein and Richard 1989).

Barbary macaques share many dietary characteristics with Japanese macaques, which have been proposed by Hanya (2004) as adaptive strategies to survive in temperate habitat. Barbary macaques also rely considerably on leaves. It is known that primates in Asia, in particular cercopithecines, tend to use leaves as fallback foods compared to primates in other regions (Hemingway and Bynum 2005). The dependence on leaves may have been an important prerequisite for macaques to survive in temperate forests. At the same time, they prefer seeds, which contain less fiber and more digestible carbohydrates than leaves (Janson and Chapman 1999), such as those of *Quercus*, *Cedrus* and fir (*Abies*), and they eat them whenever available. Although this tendency was statistically confirmed for only Moyen Atlas, Ménard (2002) mentioned that in North African forests, acorns are available from autumn to winter, which coincides with the acorn-eating period of Barbary macaques. Likewise, fir seeds are a major component of the Barbary macaque diet in the Rif Mountains when they are abundant (Mehlman 1988).

Differences

Japanese and Barbary macaques differ with respect to their degree of reliance on herbs and fleshy fruits, and their leaf selection. These differences seem to be related to the lower tree species diversity in North Africa than in Japan.

Barbary macaques rely on herbs more than do Japanese macaques. Barbary macaques compensate for low tree species diversity by consuming herbs. In the two North African forests (Djurdjura and Akfadou), the two most dominant species (*Quercus* and *Cedrus*) account for more than 95% of the trees in coverage (Ménard and Vallet 1988). Barbary macaques eat the leaves and seeds of both species, but seeds are available only for a limited period. Leaves of herbs may be more palatable than tree leaves due to their low fiber (Waterman 1984). In addition, excessive consumption of the leaves of one or a few species may overload the detoxifying capacity of animals for a particular toxin contained in the leaves (Janson and Chapman 1999). Japanese macaques at Kinkazan relied more heavily on herbs than those at Yakushima. The forests of Kinkazan have been degraded by overgrazing of sika deer, and some forests were converted to grasslands (Tsuji and Takatsuki 2004), so Japanese macaques also supplement their diet with herbs when food resources are scarce. Even stronger dependence on herbs has been reported for another temperate primate, the rhesus macaques in northwest Pakistan (Goldstein and Richard 1989). They live in a degraded habitat where vegetation has been damaged by logging, overgrazing by cattle, and natural disturbances. Feeding on herbs constituted 68% of the total feeding time of this population. Macaques mostly utilize forest habitat (Hanya et al. 2002), but they seem to be able to subsist largely on herbs, especially in poor temperate habitats.

Both Barbary and Japanese macaques often consumed considerable amounts of seeds, but most populations consumed fruits when they were available (Fig. 2). Seeds preferred by Barbary macaques came from the dominant plants of the forest (e.g. *Quercus*, *Cedrus* and *Abies*), whereas fleshy-fruited species were only a minority of the community. Therefore it was difficult to determine whether Barbary macaques actually preferred fleshy fruits over seeds. On the other hand, Japanese forests harbor many fleshy-fruited tree species. Many of these are common and supply a considerable amount of food for the macaques (Hanya et al. 2003).

Chemical properties, as well as relative availability, affect the selection of food leaves by Japanese macaques (Hanya et al. 2007). In North Africa, however, the effect of chemical properties may be masked by the effect of uncertain availability. The more palatable leaves may be simply not available for the Barbary macaques in this low-diversity forest.

We found that Japanese macaques avoided leaves with high condensed tannin, hydrolysable tannin, and crude lipid content. It is not evident why Japanese macaques avoided leaves with high crude lipid, but they may dislike the non-fat constituents included in crude lipid, such as waxes, cutins and pigments (Bleisch et al. 1998). On the other hand, the food leaves of Barbary macaques contained more tannin (both condensed and hydrolysable) and crude lipid than those eaten by Japanese macaques. In Yakushima, coniferous leaves, such as *Abies*, *Tsuga* and *Cryptomeria*, contain large amounts of condensed tannin (1.9%, 1.3% and 0.5%, respectively), and Japanese macaques never eat these leaves. The condensed tannin contents of these leaves were 4.1-15.7 times higher than the average for the food leaves (0.12%). In Moyen Atlas, conifer leaves such as *Cedrus* and *Juniperus* also contain much condensed tannin (2.4% and 3.7%, respectively), but Barbary macaques eat conifer leaves not only in Moyen Atlas but also in other habitats, such as Rif (Mehlman 1988) and Djurdjura (Ménard and Vallet 1986). In addition, condensed tannin content was higher in Moyen Atlas than in Yakushima not only for dominant species but also on average. The same pattern was found for hydrolysable tannins (Hanya et al., unpublished data). Barbary macaques survive in an environment where tree species diversity is low and leaves contain much tannin. On the other hand , most Japanese macaque habitats are covered with broad-leaved trees, and conifers are dominant only in high mountains (Yamagiwa and Hill 1998). However, broad-leaved trees are available even in coniferous forest (Table I), so Japanese macaques do not need the capacity to tolerate high levels of condensed tannin. It remains an open question whether Barbary and Japanese macaques have developed different detoxifying abilities for tannins. Interestingly, similar situations are reported in two species of closely related rodents (Skopec et al. 2008). However, the evidence is equivocal, since specialists on tannin-rich oaks are known to have higher detoxifying abilities for tannins than sympatric generalist species, but these two species showed similar responses of body weight and survival in a feeding experiment on oak leaves (Skopec et al. 2008). Experimental studies are necessary for the two macaque species.

Conclusions and future directions in the study of temperate primates

This study has shown that both Japanese and Barbary macaques adapt to temperate habitats in similar ways. They spend much time eating leaves and other vegetative foods and select seeds and fruits when they are available. Barbary macaques appear to have a high tolerance for secondary compounds in leaves, which may be expected in their environment with lower tree species diversity. Animals can survive during the lean period by consuming leaf and other vegetative foods and by metabolizing the fat deposited from eating fruits and seeds during the food-abundant period. This will lead to decreases in body weight during winter (Wada 1975; Kurita et al. 2002). Such dietary switching is a common response to the deterioration of food resources in many tropical forests as well (van Schaik and Pfannes 2005). It has already been reported that the degree of seasonal dietary variability increases with increasing latitude (Hemingway and Bynum 2005), and our close examination of the two temperate species confirmed this. Temperate primates may show the extreme of this strategy because of the prolonged period of fruit scarcity and the lack of fallback fruits, such as *Ficus* or *Musanga*, which are often available to tropical primates even when other fruits are not available (Terborgh 1983; Furuichi et al. 2001). In fact, Japanese and Barbary macaques depend on leaf and other vegetative foods (45% and 55% of diet, respectively, for one population of each), as do the “folivorous” colobines (average for 24 species: 52% of diet) (Kirkpatrick 1999). These temperate macaques consume no fruits/seeds and rely exclusively on fallback foods such as fibrous foods and lichen in some months of the year (Fig. 2), a pattern not seen in tropical macaques (Ali 1986; Yeager 1996; O'Brien and Kinnaird 1997). Therefore, leaves and lichen are ‘staple’, not ‘filler’ fallback foods for temperate macaques (Marshall and Wrangham 2007). Fat deposition is commonly reported for temperate endotherms (Pond 1978), including Japanese macaques (Wada 1975), but data on this are scarce for tropical primates. Interestingly, fat deposition has been reported in orangutans living in a habitat experiencing considerable supra-annual mast fruiting (Knott 1998). Future work on physiological and genetic analyses of fat deposition, digestion and detoxification abilities of temperate macaques would further support our conclusion.

In order to generalize these findings, more work is needed on other species. A comparison with *Rhinopithecus*, another lineage radiated in temperate regions, would be particularly interesting. The dependence on leaves and the preference for fruits are compatible in macaques because they are caeco-colic-fermenters which can digest both leaves and fruits (Lambert 1998), but this may not be so in the case of forestomach-fermenting colobines. Interestingly, *Rhinopithecus* prefer young leaves but rely heavily on lichens as fallback foods (Grueter et al. 2009), which are also eaten by Barbary macaques. Lichens are composed of largely water-soluble carbohydrates, whose digestibility is higher than NDF (Kirkpatrick et al. 2001), so they might be a better food than mature leaves. A comparison between *Macaca* and *Rhinopithecus* would be useful in helping us understand the kinds of adaptations required for primates to survive in temperate forests.

Acknowledgements

We would like to thank our friends and colleagues who supported our fieldwork in Japan, Morocco and Algeria. The Ministry of Environment and Forestry Agency, Japan, and Haut Commissariat aux Eaux et Forêt et à la Lutte Contre la Désertification, Morocco gave us permission to study in the area. Dr. Y. Tsuji kindly provided his published data. This study was financed by the JSPS Core-to-core Program HOPE, Cooperation Research Program of KUPRI and the MEXT Grant-in-Aid for JSPS Fellows, Grant-in-Aid for Young Scientists (#20770195 and #22687002) to GH, the 21st Century COE Program (A14) and Global COE Program “Formation of a Strategic Base for Biodiversity and Evolutionary Research: from Genome to Ecosystem.”

References

Agetsuma N (1995) Dietary selection by Yakushima macaques (*Macaca fuscata yakui*): the influence of food availability and temperature. Int J Primatol 16: 611—627.

Agetsuma N, Nakagawa N (1998) Effects of habitat differences on feeding behaviors of Japanese monkeys: Comparison between Yakushima and Kinkazan. Primates 39: 275—289.

Ajbilou R, Maranon T, Arroyo J (2006) Ecological and biogeographical analyses of Mediterranean forests of northern Morocco. Acta Oecol 29: 104—113.

Ali R (1986) Feeding ecology of the bonnet macaque at the Mundanthurai Sanctuary, Tamil Nadu. J Bombay Nat Hist Soc 83: 98—110.

Bleisch W, Liu Z, Dierenfeld E, Xie J (1998) Selected nutrient analysis of plants in the diet of the Guizhou snub-nosed monkey (*Rhinopithecus* [*Rhinopithecus*] *brelichi*).

In: Jablonski N (ed) The Natural History of the Doucs and Snub-nosed Monkeys. World Scientific Publishing, Singapore, pp 241—254

Burnham KP, Anderson DR (2002) Model Selection and Multi-model Inference. 2nd Edition. Springer, New York.

Clutton-Brock TH (1977) Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes. Academic Press, Brighton.

Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. Philos Trans R Soc Lond Ser B-Biol Sci 345: 101—118.

Curtin F, Schulz P (1998) Multiple correlations and Bonferroni's correction. Biol Psychiatry 44: 775—777.

Drucker GR (1984) The feeding ecology of Barbary macaque and cedar forest conservation in the Moroccan Moyen Atlas. In: Fa JE (ed) The Barbary Macaque: A case study in Conservation. Plenum Press, New York, pp 135—164

Fa JE (1984a) The Barbary Macaque: A Case Study in Conservation. Plenum Press, New York.

Fa JE (1984b) Habitat distribution and habitat preference in Barbary macaques (*Macaca sylvanus*). Int J Primatol 5: 273—286.

Fa JE (1989) The Genus *Macaca*: a review of taxonomy and evolution. Mammal Rev 19: 45—81.

Fleagle JG (1999) Primate Adaptation and Evolution. Second Edition. Academic Press, London.

Fragaszy DM, Boinski S, Whipple J (1992) Behavioral sampling in the field: Comparison of individual and group sampling methods. Am J Primatol 26: 259—275.

Furuichi T, Hashimoto C, Tashiro Y (2001) Fruit availability and habitat use by chimpanzees in the Kalinzu Forest, Uganda: Examination of fallback foods. Int J Primatol 22: 929—945.

Goldstein SJ, Richard AF (1989) Ecology of rhesus macaques (*Macaca mulatta*) in northwest Pakistan. Int J Primatol 10: 531—567.

Grueter CC, Li DY, Ren BP, Wei FW, Xiang ZF, van Schaik CP (2009) Fallback foods of temperate-living primates: a case study on snub-nosed monkeys. Am J Phys Anthropol 140: 700—715.

Hanya G (2004) Diet of a Japanese macaque troop in the coniferous forest of Yakushima. Int J Primatol 25: 55—71.

Hanya G, Kiyono M, Takafumi H, Tsujino R, Agetsuma N (2007) Mature leaf selection of Japanese macaques: effects of availability and chemical content. J Zool 273: 140—147.

Hanya G, Noma N, Agetsuma N (2003) Altitudinal and seasonal variations in the diet of Japanese macaques in Yakushima. Primates 44: 51—59.

Hanya G, Yamada H, Arakane T (2002) Expeditionary ranging by a Japanese macaque troop in Hieizan. Anthropol Sci 110: 415—420.

Hanya G, Yoshihiro S, Zamma K, Matsubara H, Ohtake M, Kubo R, Noma N, Agetsuma N, Takahata Y (2004) Environmental determinants of the altitudinal variations in relative group densities of Japanese macaques on Yakushima. Ecol Res 19: 485—493.

Hasegawa K (1993) Nutritional Analysis (in Japanese). Baifukan, Tokyo.

Hemingway C, Bynum N (2005) The influence of seasonality on primate diet and ranging. In: Brockman DK, van Schaik CP (eds) Seasonality in Primates: Studies of

Living and Extinct Human and Non-Human Primates. Cambridge University Press, Cambridge, pp 57—104

Herrera CM (1984) A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. Ecol Monogr 54: 1—23.

Hill DA (1997) Seasonal variation in the feeding behavior and diet of Japanese macaques (*Macaca fuscata yakui*) in lowland forest of Yakushima. Am J Primatol 43: 305—322.

Iwamoto T (1982) Food and nutritional condition of free ranging Japanese monkeys on Koshima Islet during winter Primates 23: 153—170.

Izumiyama S (2002) Above the forest limit (in Japanese). In: Oi T, Masui K (eds) Natural History of Japanese Macaque: Their Ecological Diversity and Conservation. Tokai University Press, Tokyo, pp 67—77

Janson C, Chapman C (1999) Resources and primate community structure. In: Fleagle J, Janson C, Reed K (eds) Primate Communities. Cambridge Univ Press, Cambridge, pp 237—267

Kirkpatrick RC (1999) Colobine diet and social organization. In: Dolhinow P, Fuentes A (eds) The Nonhuman Primates. Mayfield Publishing Company, Mountain View, pp 93—105

Kirkpatrick RC, Zou RJ, Dierenfeld ES, Zhou HW (2001) Digestion of selected foods by Yunnan snub-nosed monkey *Rhinopithecus bieti* (Colobinae). Am J Phys Anthropol 114: 156—162.

Knott CD (1998) Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. Int J Primatol 19: 1061—1079.

Komiyama A, Kato S, Teranishi M (2001) Differential overstory leaf flushing contributes to the formation of a patchy understory. Journal of Forest Research 6: 163—171.

Kurita H, Shiniomura T, Fujita T (2002) Temporal variation in Japanese macaque bodily mass. International Journal of Primatology 23: 411—428.

Lambert JE (1998) Primate digestion: Interactions among anatomy, physiology, and feeding ecology. Evol Anthropol 7: 8—20.

Ménard N (1985) Le régime alimentaire de *Macaca sylvanus* dans différents habitats d'Algérie: I. Régime en chênaie décidue. Revue d'Ecologie (La Terre Et La Vie) 40: 351—466.

Ménard N (2002) Ecological plasticity of Barbary macaques (*Macaca sylvanus*). Evol Anthropol 11: 95—100.

Ménard N, Qarro M (1999) Bark stripping and water availability: A comparative study between Moroccan and Algerian Barbary Macaques (*Macaca sylvanus*). Revue d'Ecologie (La Terre Et La Vie) 54: 123—132.

Ménard N, Vallet D (1986) Le régime alimentaire de *Macaca sylvanus* dans différents habitats d'Algérie: II. Régime en forêt sempervirente et sur les sommets roucheux. Revue d'Ecologie (La Terre Et La Vie) 41: 173—192.

Ménard N, Vallet D (1988) Disponibilités et utilisation des ressources par le magot (*Macaca sylvanus*) dans différents milieux en Algérie. Revue d'Ecologie (La Terre Et La Vie) 43: 201—250.

Marshall AJ, Wrangham RW (2007) Evolutionary consequences of fallback foods. Int J Primatol 28: 1218—1235.

Mehlman PT (1988) Food resources of the wild barbary macaque (*Macaca sylvanus*) in high altitude fir forest, Ghomaran Rif, Morocco. Journal of Zoology 214: 469—490.

Muroyama Y, Kanamori H, Kitahara E (2006) Seasonal variation and sex differences in the nutritional status in two local populations of wild Japanese macaques. Primates 47: 355—364.

O'Brien TG, Kinnaird MF (1997) Behavior, diet, and movements of the Sulawesi crested black macaque (*Macaca nigra*). Int J Primatol 18: 321—351.

Pond CM (1978) Morphological aspects and ecological and mechanical consequences of fat deposition in wild vertebrates. Annual Review of Ecology and Systematics 9: 519—570.

Porter LJ (1989) Tannins. In: Dey PM, Harborne JB (eds) Methods in Plant Biochemistry, vol1 Plant Phenolics. Academic Press, London, pp 389—419

Rautio P, Bergvall UA, Karonen M, Salminen JP (2007) Bitter problems in ecological feeding experiments: Commercial tannin preparations and common methods for tannin quantifications. Biochem Syst Ecol 35: 257—262.

Sakai S (2002) General flowering in lowland mixed dipterocarp forests of South-east Asia. Biol J Linnean Soc 75: 233—247.

Skopec MM, Haley S, Torregrossa AM, Dearing MD (2008) An oak (*Quercus agrifolia*) specialist (*Neotoma macrotis*) and a sympatric generalist (*Neotoma lepida*) show similar intakes and digestibilities of oak. Physiol Biochem Zool 81: 426—433.

Su HH, Lee LL (2001) Food habits of Formosan rock macaques (*Macaca cyclopis*) in Jentse, northeastern Taiwan, assessed by fecal analysis and behavioral observation. Int J Primatol 22: 359—377.

Suzuki A (1965) An ecological study of wild Japanese monkeys in snowy areas: focused on their food habits. Primates 6: 31—72

Terborgh J (1983) Five New World Primates. Princeton University Press, Princeton.

Ting S, Hartley S, Burns KC (2008) Global patterns in fruiting seasons. Glob Ecol Biogeogr 17: 648—657.

Tsuji Y, Fujita S, Sugiura H, Saito C, Takatsuki S (2006) Long-term variation in fruiting and the food habits of wild Japanese macaques on Kinkazan Island, northern Japan. Am J Primatol 68: 1068—1080.

Tsuji Y, Takatsuki S (2004) Food habits and home range use of Japanese macaques on an island inhabited by deer. Ecol Res 19: 381—388.

van Schaik CP, Pfannes K (2005) Tropical climates and phenology: a primate perspective. In: Brockman DK, van Schaik CP (eds) Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge University Press, Cambridge, pp 23—54

van Schaik CP, Terborgh JW, Wright SJ (1993) The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annu Rev Ecol System 24: 353—377.

van Soest PJ, Robertson JB, Lewis BA (1991) Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. J Dairy Sci 74: 3583—3597.

Wada K (1975) Ecology of wintering among Japanese monkeys in Shiga Heights and its adaptive significance. Physiol Ecol Jpn 16: 9—14.

Waterman P (1984) Food acquisition and processing as a function of plant chemistry. In: Chivers DJ, Wood BA, Bilsborough A (eds) Food Acquisition and Processing in Primates. Plenum Press, New York, pp 177—211

Willis RB, Allen PR (1998) Improved method for measuring hydrolyzable tannins using potassium iodide. Analyst 123: 435—439.

Willson MF, Irvine AK, Walsh NG (1989) Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. Biotropica 21: 133—147.

Yamagiwa J, Hill D (1998) Intraspecific variation in the social organization of Japanese macaques: Past and present scope of field studies in natural habitats. Primates 39: 257—273.

Yeager CP (1996) Feeding ecology of the long-tailed macaque (*Macaca fascicularis*) in Kalimantan Tengah, Indonesia. Int J Primatol 17: 51—62.

Table I. Number of tree species and diversity in Japanese and north African forests

Study site	Country*	Vegetation	Area (ha)	#Tree Species	#Fleshy-fruited tree species	#Tree Species/0.5 ha**	#Fleshy-fruited tree species/ 0.5ha**	H (BA based)	H (cover based)	Dominant species (Top3)	Source
Yakushima, 100 m	J	Evergreen broad-leaved forest	0.5	52	31	52	31	3.17	-	*Ardisia sieboldii* (Myrsinaceae), *Lithocarpus edulis* (Fagaceae), *Litsea acuminata* (Lauraceae)	Takafumi, Agetsuma, Tsujino, unpublis
Yakushima, 600 m	J	Evergreen broad-leaved forest	0.25	18	10	18	10	2.04	-	*Distylium racemosum* (Hamamelidaceae), *Quercus salicina* (Fagaceae), *Neolitsea aciculata* (Lauraceae)	Hanya *et al*. (2003)
Yakushima, 1050 m	J	Coniferous/evergreen broad-leaved forest	0.5	21	10	21	10	2.10	2.57	*Abies firma* (Pinaceae), *Cryptomeria japonica* (Taxodiaceae), *Tsuga sieboldii* (Pinaceae)	Hanya, unpublished
Koshima	J	Evergreen broad-leaved forest	0.5	55	35	55	35	2.45	-	*Machilus thunbergii* (Lauraceae), *Podocarpus macrophyllus* (Podocarpaceae), *Prunus jamasakura* (Rosaceae)	Go, unpublished
Shiga Heights	J	Deciduous broad-leaved forest	0.22	48	10	61	13	2.97	-	*Betula ermanii* (Betulaceae), *Quercus crispula* (Fagaceae), *Fagus crenata* (Fagaceae),	Wada, unpulished
Muroo	J	Deciduous broad-leaved forest	0.04	14	5	25	7	2.25	-	*Quercus serrata* (Fagaceae), *Quercus glauca* (Fagaceae), *Acanthopanax sciadophylloides* (Araliaceae)	Yamada, unpublished
Akfadou	A	Deciduous oak forest	0.5	4	0	4	0	-	0.77	*Quercus afares* (Fagaceae), *Quercus faginea* (Fagaceae), *Quercus suber* (Fagaceae)	Ménard and Vallet (1988)
Djurdjura	A	Coniferous/evergreen broad-leaved forest	0.5	5	0	5	0	-	0.73	*Cedrus atlantica* (Pinaceae), *Quercus ilex* (Fagaceae), *Pinus clusiana* (Pinaceae)	Ménard and Vallet (1988)
Northen Morocco (Rif)	M	Mixed oak evergreen and semidiciduous forests	NA***	15	5	-	-	1.85	-	*Pinus pinaster* (Pinaceae), *Quercus canariensis* (Fagaceae), *Quercus coccifera* (Fagaceae)	Ajbilou *et al*. (2006)

H: Shannon-Wiener's diversity index, calculated by the proportion of of each species either as basal area (BA) or coverage.
*: J: Japan, A: Algeria, M: Morocco
**: Underlined are estimated values by the method of Colwell and Coddington (1994)
***: Vegetation data of 84 forests of northern Morocco (scattered over an area of 20 km*70 km), sapmled by 'nearest neighb

Table II. Summary of the generalized linear models on the effect of chemical properties on leaf food selection

a) Japanese macaques in Yakushima

Adopted factors	AIC	△AIC	Akaike weight
Protein+, Lipid-, Condensed-, Hydrolysable-	**75.4**	**0.0**	**21%**
Ash+, Lipid-, Condensed-, Hydrolysable-	**76.9**	**1.6**	**9%**
Lipid-, Condensed-, Hydrolysable-	**77.0**	**1.7**	**9%**
Protein+, Lipid-, Condensed-, Hydrolysable-	**77.1**	**1.7**	**9%**
Protein+, NDF+, Lipid-, Condensed-, Hydrolysable	**77.4**	**2.0**	**8%**

b) Barbary macaques in Moyen Atlas

Adopted factors	AIC	△AIC	Akaike weight
(Null model)	43.1	0.0	8%
Condensed+	44.2	1.2	5%
Hydrolysable-	44.3	1.2	4%
Protein-	44.4	1.4	4%
Ash+	44.6	1.5	4%
Ash+, Condensed+	44.7	1.7	4%
Lipid-	45.0	1.9	3%
NDF-	45.0	2.0	3%

Protein: crude protein; NDF: neutral detergent fiber; Ash: crude ash; Lipid: crude lipid; condensed: condensed tannin; Hydrolysable: hydrolysable tannin
△AIC: Difference with the smallest AIC
Akaike weight: exp(-0.5*△AIC)/Σ exp(0.5*△AIC) (Burnham and Anderson, 2002)
+ denotes positive effect (more likely to select as a food) and - denotes negative effect on food selection.
Bold indicates that the model is significant (compared with the null model).

Table III. Best-fit generalized linear model on the effect of chemical properties on leaf food selection

a) Japanese macaques in Yakushima

Adopted factors	Coefficient	SE	p
Crude protein	19.4	10.5	0.064
Crude lipid	-37.8	14.2	0.01
Condensed tannin	-387	139	0.0053
Hydrolysable tannin	-24.5	12.4	0.048

In this best-fit model, df=72, AIC=75.4, p<0.0001 in the likelihood ratio test using χ^2 distribution
Coefficient: coefficient by maximum likelihood estimation; SE: standard error of the coefficient, p: the probability that the coefficient is not different from zero by Wald test.

b) Barbary macaques in Moyen Atlas
Null model had the smallest AIC: AIC=43.1

Legends for figures

Fig. 1. Comparisons of annual diet of temperate and tropical macaques. Percentage to total annual feeding time of each food category is shown. Data from (Ménard 1985; Ali 1986; Ménard and Vallet 1986; Yeager 1996; Hill 1997; O'Brien and Kinnaird 1997; Hanya 2004; Tsuji et al. 2006).

Fig. 2. Seasonal variations in the diet of Japanese and Barbary macaques. Percentage to total monthly feeding time of each food category is shown. Data from (Ménard 1985; Ménard and Vallet 1986; Hill 1997; Hanya 2004; Tsuji et al. 2006).

Fig. 3. Leaf chemistry of food and non-food leaves of Yakushima (Japanese macaques) and Moyen Atlas (Barbary macaques). Y-axis is the proportion of dry matter. Average+SD is shown. Note that the scale is different among graphs.

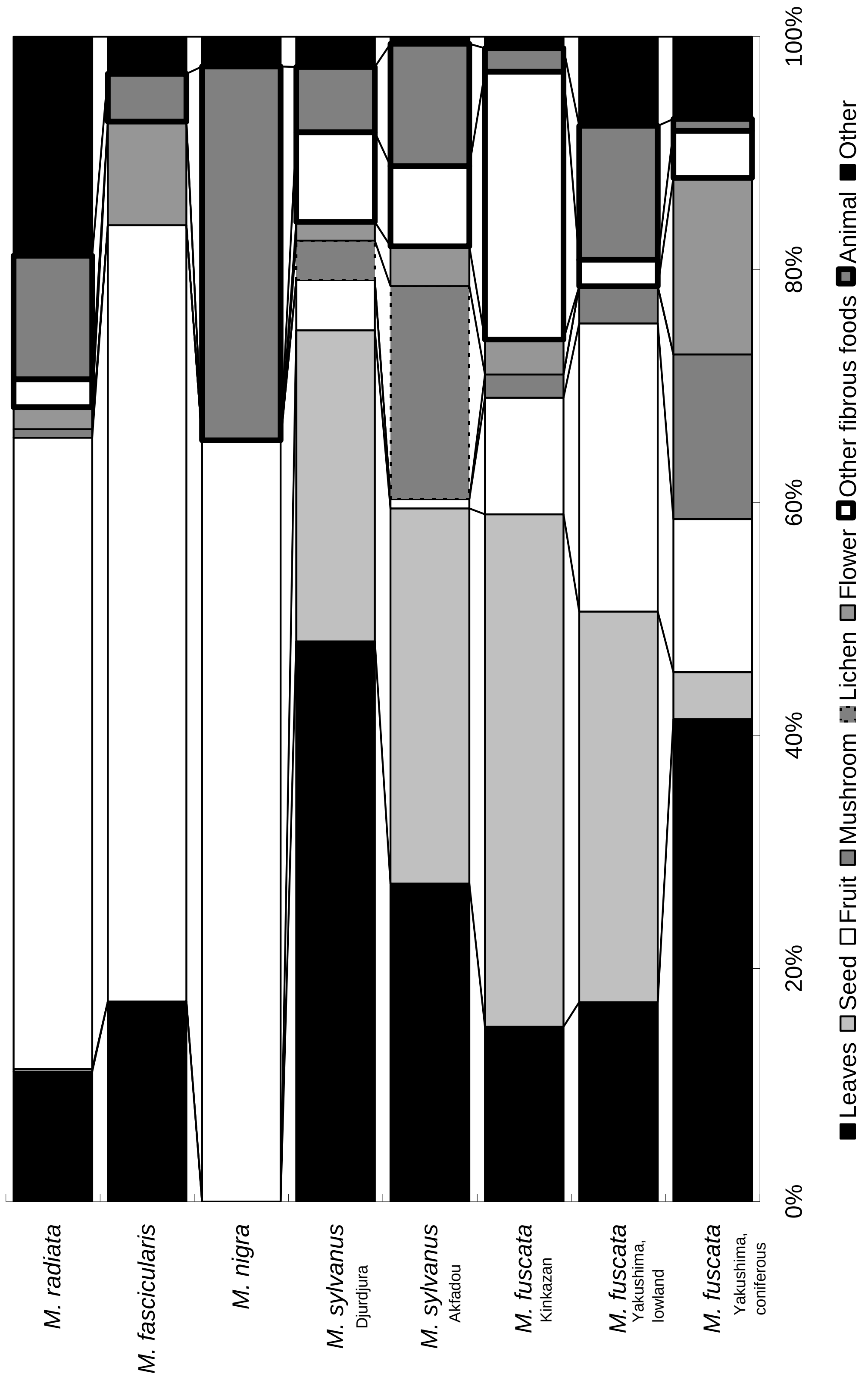
0%
20%
40%
60%
80%
100%
M. radiata
M. fascicularis
M. nigra
M. sylvanus Djurdjura
M. sylvanus Akfadou
M. fuscata Kinkazan
M. fuscata Yakushima, lowland
M. fuscata Yakushima, coniferous
■ Leaves
▨ Seed
☐ Fruit
▨ Mushroom
▨ Lichen
▨ Flower
☐ Other fibrous foods
▣ Animal
■ Other

Fig. 1

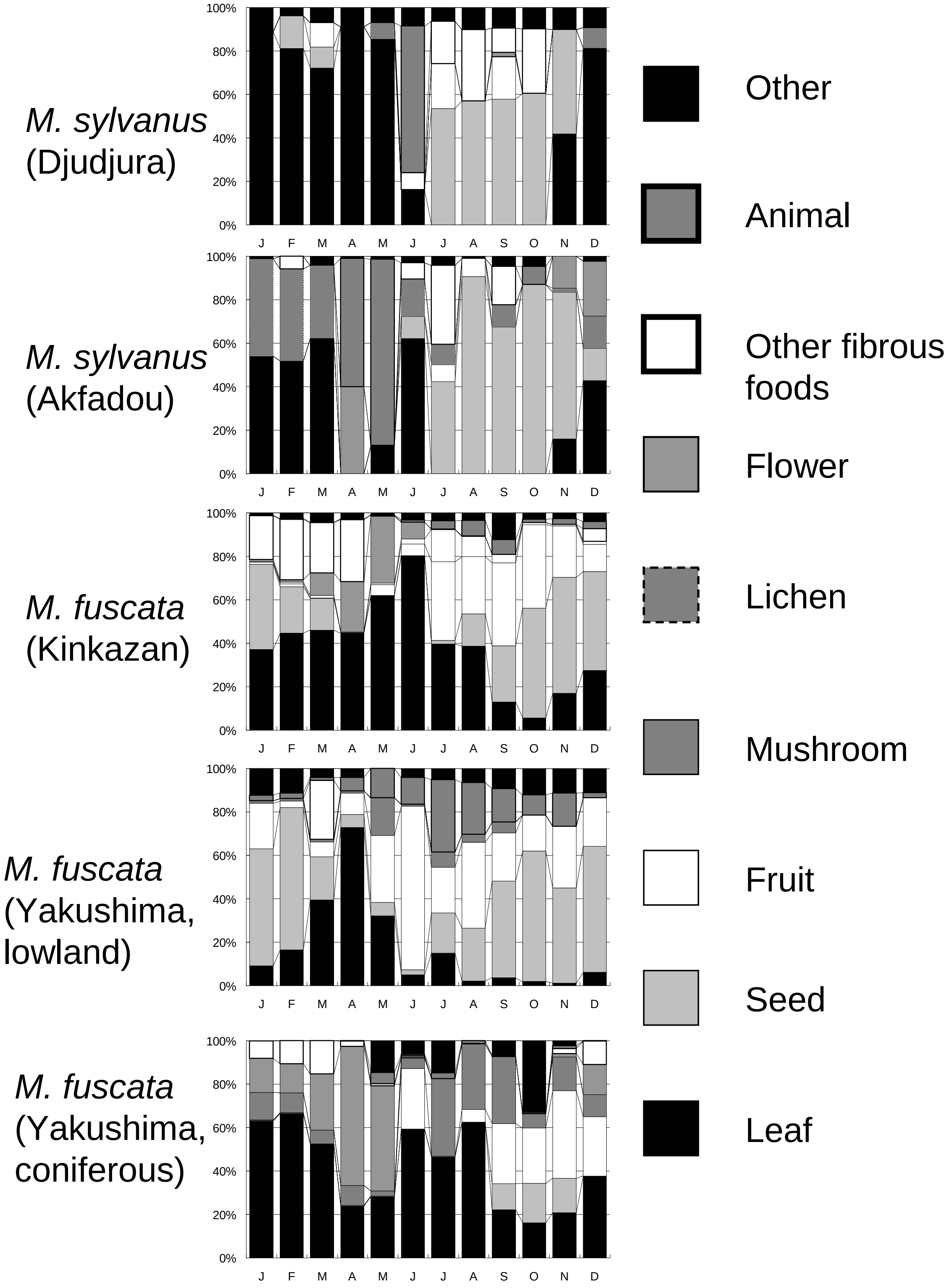
M. sylvanus (Djudjura)
M. sylvanus (Akfadou)
M. fuscata (Kinkazan)
M. fuscata (Yakushima, lowland)
M. fuscata (Yakushima, coniferous)
0%
20%
40%
60%
80%
100%
J F M A M J J A S O N D
Other
Animal
Other fibrous foods
Flower
Lichen
Mushroom
Fruit
Seed
Leaf

Fig. 2

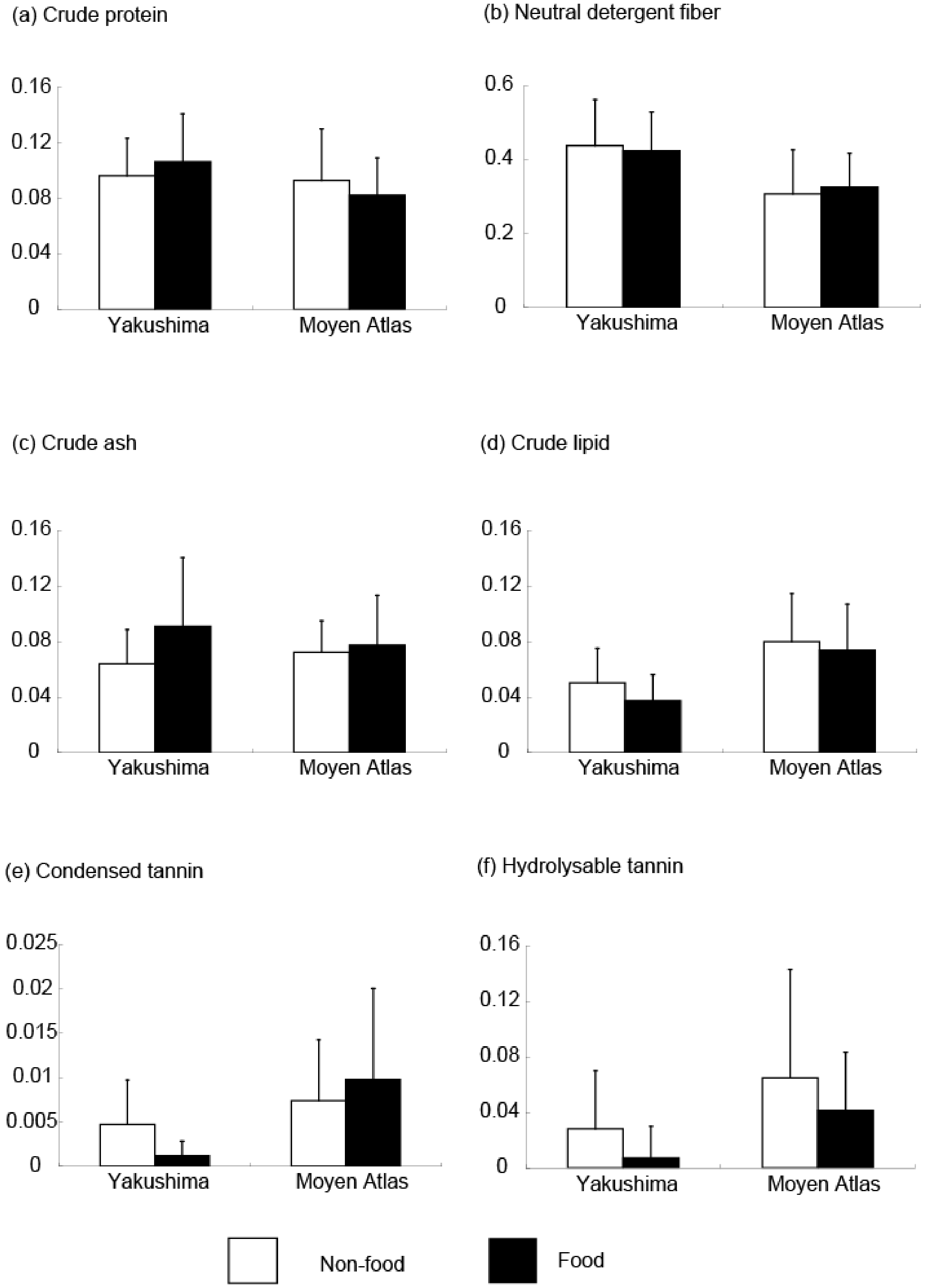
(a) Crude protein
0.16
0.12
0.08
0.04
0
Yakushima
Moyen Atlas
(b) Neutral detergent fiber
0.6
0.4
0.2
0
Yakushima
Moyen Atlas
(c) Crude ash
0.16
0.12
0.08
0.04
0
Yakushima
Moyen Atlas
(d) Crude lipid
0.16
0.12
0.08
0.04
0
Yakushima
Moyen Atlas
(e) Condensed tannin
0.025
0.02
0.015
0.01
0.005
0
Yakushima
Moyen Atlas
(f) Hydrolysable tannin
0.16
0.12
0.08
0.04
0
Yakushima
Moyen Atlas
Non-food
Food

Fig. 3