

Alternative seed-handling strategies in primates: seed-spitting by long-tailed macaques (*Macaca fascicularis*)

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Summary. The seeds in fruits consumed by primates may be chewed and digested, swallowed and defecated intact, or separated from the flesh and spat out. We show by a combination of close field observations and experiments with caged animals, that long-tailed macaques (*Macaca fascicularis*) have a remarkably low threshold of 3–4 mm for swallowing seeds and also that wild macaques rarely break them. The seeds of 69% of the ripe fruit species eaten are spat out intact or cleaned outside the mouth and dropped. Seed-spitting significantly reduces the swallowed food bulk and may lessen the risk of releasing seed toxins during mastication. However, it requires that even small fruits are processed in the mouth one or a few at a time. We suggest that fruit storage in the cheek pouches of cercopithecine monkeys allows them to spit seeds individually without excessively slowing fruit intake while feeding on patchily distributed fruit. In contrast, Apes and New World monkeys apparently swallow and defecate most ripe seeds in their diet and colobine monkeys break and digest them, detoxifying seed defenses by bacterial fermentation.

Key words: Primates – *Macaca fascicularis* – Seed dispersal – Seed size

The function of the pulp in animal-dispersed fruits is the attraction and reward of seed-dispersal agents. The function of the seed is reproduction of the parent plant. Except in those species that pay with seeds for the dispersal of other seeds (Smith and Reichman 1984), we would expect seeds to be heavily protected against destruction by fruit-eating animals and postdispersal seed predators. The literature suggests that this protection is normally chemical (Bell 1984; Janzen 1978, 1983). However heavily they are defended chemically, seeds must also be physically harder than the edible flesh or it would be impossible for a frugivore to avoid breaking them during mastication of the flesh. Hardness alone may be a defense in some species (Janzen 1978).

Fruit-eating vertebrates are thus faced with a basic problem: what to do with the potentially toxic seeds? There are three alternatives: swallow the seeds and defecate them intact; remove the fruit flesh and drop or spit out the seeds;

break and digest the seeds and detoxify any defensive compounds. The key differences between these strategies concern processing in the mouth. Seeds may be swallowed, spat or destroyed. Some large herbivores can also digest seeds that are swallowed intact, but this seems to occur only when very long passage times encourage seed germination in the gut (Janzen 1981a, b). There is no evidence that intact seeds are commonly digested by most frugivores.

In addition to the problem of seed toxicity, frugivores must also cope with the generally low nutrient content of fruit flesh (Moermond and Denslow 1985; Davies et al. 1988). Efficient fruit handling is thus an important adaptation to frugivory (Levey 1987). The alternative seed-handling strategies are likely to have different consequences for the efficiency of fruit-handling. They will certainly have different consequences for seed dispersal and thus the fitness of the fruiting plant.

Very little is known about seed-handling by Old World primates and their role in seed dispersal (Howe 1986). Currently, Southeast Asian primates are assumed to swallow or destroy the seeds of most fruit they eat (Leighton and Leighton 1983). It has even been suggested that seed-eating (and hence seed destruction) is the primitive dietary adaptation for all Old World monkeys and that this has been retained in the cercopithecines (Happel 1988). Here, however, we show by a combination of close field observations and laboratory experiments that the Southeast Asian cercopithecine monkey, *Macaca fascicularis*, has a remarkably low size threshold for swallowing seeds and spits out most intact. We discuss the potential advantages of seed-spitting over seed-swallowing and suggest how macaques and other cercopithecine monkeys minimize the consequences for the rate of oral food processing. Finally, we consider the implications of the different seed-processing methods used by primates for seed dispersal.

Methods

Macaca fascicularis (3–4 kg) is the smallest monkey in Southeast Asia. It is found from Burma to Indonesia and the Philippines and occupies all forested habitats except montane forest (Wolfheim 1983). In Singapore, we studied a group of about 30 macaques at Bukit Timah Nature Reserve, an isolated 70-ha remnant of primary and secondary rain forest (Corlett 1988, 1989). The group is sometimes fed by visitors (14% of dietary observations) and soon be-

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came tolerant of very close observation – from within 1 m in some cases.

As part of a study on the diet of the macaques (Lucas and Corlett in prep.), 510 hr of field observations were made between July 1986 and November 1987. Every 15 min during observation periods, group activity was recorded by scan sampling (Clutton-Brock 1977). For every fruit seen consumed (including those seen eaten between scan samples and during causal observations) the fate of the seeds was determined, as far as possible. Seeds were classified as dropped without entering the mouth, spat out without transport, spat out after transport in the mouth or cheek pouches, destroyed in the mouth, or swallowed. Damage to seeds in the first three categories was assessed directly from fallen seeds. Seeds were classified as destroyed on the basis of close field observations of feeding, supported by the absence of seeds in the faeces. Swallowed seeds were identified from the faeces. In total, 76 newly-deposited faeces samples were collected. These included samples from all ages and both sexes. Most samples were from observed defecations at low height above the ground and were collected intact. Seeds were extracted by sieving. For the first 68 samples, the faeces were washed through successive sieves of pore size 1 mm and 500 μm . For the remaining 8 samples, an additional 300 μm sieve was used. Samples of common seed taxa extracted from the faeces were tested for viability by germination on damp filter paper.

Where sufficient ripe fruit could be obtained, these were offered to one or more caged *M. fascicularis* of unknown provenance, at the National University of Singapore, and the fate of the seeds observed. When possible, at least 10 fruit were presented together because single fruits were often treated atypically. When the number of seeds spat out was less than the expected number in the fruit eaten, all faeces were collected and sieved until no more seeds appeared.

Seed and fruit dimensions were measured for all ripe fruit taxa that could be obtained from the forest during the study period, whether eaten by macaques or not. 'Seed' dimensions include adjacent non-fleshy, non-nutritive fruit tissues. In most cases, at least five fruits and seeds of each species were measured. Here we use maximum width as a measure of seed size because this dimension seems most likely to influence both oesophageal transit and detection of seeds between the teeth during mastication. However, the conclusions are not altered significantly if seed length is used.

Results

Fruit processing

Wild macaques usually picked fruit individually by hand. The rind, if present, was removed by the incisors in front of the mouth. The fruits of many species, particularly the smaller ones, were then transferred to a cheek pouch and others picked before any mastication took place. On one occasion, up to 20 fruits, 1 cm diameter, were apparently consigned to one cheek pouch. The macaques typically processed the fruits in the mouth one by one. With some fruit species, particularly those where the flesh adhered strongly to the seed (e.g. *Calamus* spp., Palmae), the seed was periodically taken out of the mouth by hand for visual inspection.

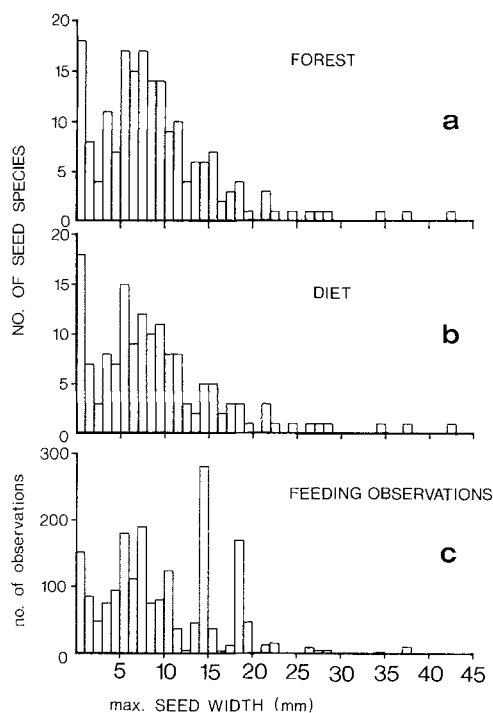


Fig. 1a-c. Seed size and fruit choice. **a** Distribution of mean seed widths of the 188 ripe fruit species collected in the forest during the study period. **b** Distribution of mean seed widths of the 151 species eaten. **c** Distribution of the number of individual observations of feeding on fruit species with seeds of different mean widths. The peaks at 14–15 mm and 18–19 mm represent intensive feeding on 4 species

Fruit consumption and seed size. We observed 185 species of ripe fruit being consumed by macaques in the field. For 151 of these, intact seeds were obtained for measurement, and for 116 species, the fate of the seeds was also reliably determined. Figure 1 compares the distribution of mean seed widths for all 188 ripe fruit species obtained during the study period, the distribution of mean seed widths for the 151 species eaten, and the distribution of the number of individual observations of feeding on fruit with seeds of different widths. The similarity of the three distributions shows that the macaques do not select fruit on the basis of seed size. The seed width distribution for the species in the diet is not significantly different from that for all the species collected in the forest (Kolmogorov-Smirnov 2 Sample Test, $P > 0.10$). Although the distribution for feeding observations is significantly different from that for species in the forest ($P < 0.05$), this results from intensive feeding on four species. There was also no evidence for selection on the basis of fruit size: the species consumed included the largest (*Artocarpus* spp., some > 30 cm diameter) and smallest (*Gynotroches axillaris*, 0.4 cm diameter) fruits found in the forest during the study period.

Seed swallowing. Seeds of 25 species (21.6%) were at least sometimes swallowed and defecated intact. This includes the minute seeds of four Melastomataceae and eight *Ficus* species that were eaten by the macaques but could not be positively distinguished from seeds of related taxa in the faeces. Figure 2a shows the distribution of mean seed widths of the species swallowed. All 6 species > 4 mm width found in the faeces were commonly spat. Of the 2900 seeds

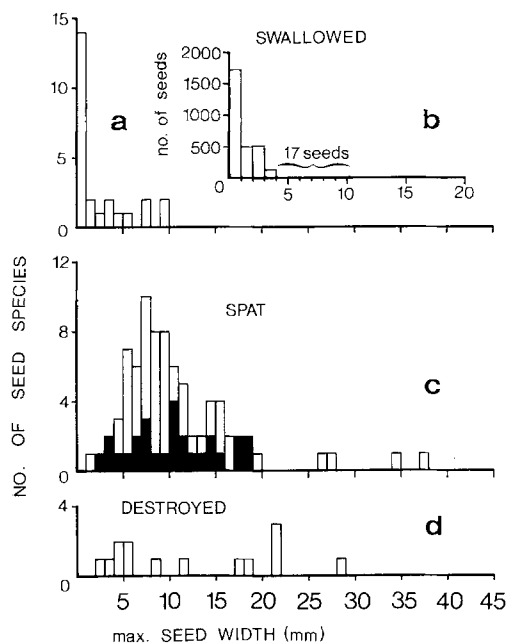


Fig. 2a–d. Seed size and seed fate. **a** Distribution of mean seed widths of the 25 species swallowed. **b** Distribution of mean seed widths of the 2900 seeds found in the faeces. **c** Distribution of mean seed widths of the 80 species spat out or dropped intact. Shading indicates the 27 species whose seeds were transported at least 20 m before being spat out. **d** Distribution of mean seed widths of the 13 species destroyed

extracted with the 1 mm and 0.5 mm sieves, only 17 seeds (0.6%) were >4 mm width (Fig. 2b). An additional 635 seeds (all Melastomataceae) were extracted from the last 8 faeces samples when the extra 0.3 mm sieve was used. Samples of common seed taxa extracted from the faeces showed >75% germination on damp filter paper, except for those of *Embelia ribes* and *Gynotroches axillaris*, where samples from both the faeces and fresh ripe fruit failed to germinate.

Seed spitting

Seeds of 80 species (69.0%) were usually either cleaned inside the mouth and then spat out intact, cleaned outside the mouth with the incisors while held in the hand and then dropped intact, or processed by a combination of these two methods. An additional 5 species (4.3%), the seeds of which were never more than partly cleaned of fruit flesh, are excluded from this total. Only the largest seeds (>ca. 20 mm width) never entered the mouth. Figure 2B shows the distribution of mean seed widths of the species spat out or dropped intact. All species >4 mm width were usually spat out or dropped. Only 4 species <4 mm were usually spat out and three of these were also often found in the faeces. The two smallest species spat out were *Timonius wallichianus*, with rod-shaped seeds (5.4 × 1.9 × 1.0 mm), and *Rhodamnia cinerea* (3.5 × 2.4 × 2.1 mm), in which the seeds are tightly clustered in the fruit and were usually spat out as a unit >4 mm width. The seeds of 27 species (shaded in Fig. 2b) were observed at least once to be carried in the cheek pouches or in the mouth for at least 20 m before being spat out. In addition, some large fruits, including *Artocarpus* spp., *Mangifera indica* and *Willughbeia coriacea*,

were sometimes carried similar distances in the hand before they were processed and the seeds spat or dropped.

Seed destruction

Seeds of 13 species (11.2%) were usually destroyed in the mouth. Most of the species in which the seeds were destroyed had non-fleshy fruits, including all Fagaceae and all wind-dispersed species. The exceptions were *Guoia pubescens*, *Prunus polystachyus* and *Xylopia malayana*, all of which have a very thin layer of flesh. Figure 2C shows the distribution of mean seed widths of the species usually destroyed. The only seeds less than 3 mm width that were destroyed were rod-shaped (7.0 × 2.5 × 2.5 mm). Seeds of the few unripe fleshy fruits eaten were also often destroyed.

Caged macaques

The experiments with caged macaques were curtailed because of the ease of close field observations and the problems of obtaining sufficient ripe, undamaged fruit. The results were similar to those from field observations except that the captives were more variable in their seed processing behaviour and much more likely to destroy seeds. The seeds of two species, *Campospermum auriculatum* and *Gnetum microcarpum*, that were apparently always spat out intact by wild macaques, were all broken and swallowed by 3 captive animals. Seeds of *Vitex pinnata* (not observed fruiting in the study area) were all destroyed by 3 individuals (one of which spat the fragments) and all spat out intact by one. Some seeds of all species were destroyed, including the very hard seeds of rattan palms. In total, the captive macaques were fed 36 fruit species. All seeds below 2 mm width (3 spp.) were swallowed and defecated intact, and all above 4 mm width mostly spat out (26 spp.) or mostly destroyed (5 spp.). Seeds of intermediate size (2 spp.) were partly spat out and partly swallowed.

Factors other than seed size

All but one of the species in which seeds were usually swallowed had multiseeded fruit. However, many multiseeded fruit had larger seeds that were always spat out. The only single-seeded species usually (apparently always) swallowed was *Embelia ribes*, with spherical seeds 2.3 mm diameter, while the slightly larger (4.1 mm diameter) but otherwise very similar seeds of *Ardisia stylosa*, in the same family, were always spat. This seems clear evidence for the controlling influence of seed size.

The fruits also varied widely in the texture of the pulp and the firmness of its attachment to the seeds. Neither factor was assessed quantitatively but we saw no evidence that either had a significant influence on seed fate.

Discussion

Seed-spitting by *Macaca fascicularis*

Three major points emerge from the results. Firstly, both field observations and feeding experiments demonstrate the existence of a surprisingly low size threshold of 3–4 mm for swallowing seeds in *Macaca fascicularis*. This is comparable with the size threshold in birds two orders of magnitude smaller in size (Johnson et al. 1985; Levey 1987). Sec-

only, the wild macaques rarely break seeds, although probably no seed in their diet is too hard for them to break (caged macaques broke some seeds of all species offered) and some are so soft that considerable care must be taken not to damage them. Finally, and presumably a direct result of this reluctance to either swallow or break seeds, both wild and caged macaques processed even small fruits individually or in small numbers.

This slow oral processing of fruits would seem to conflict with the need for efficient food handling in frugivores dependent on low nutrient fruit flesh (Levey 1987). However, the use of the cheek pouches to hold excess fruit intake while one or a few fruit are processed in the mouth may reduce or eliminate this problem. Although this would not increase food processing efficiency if food was available continuously in space and time, it does permit oral processing to continue as the macaques move between short bouts of intensive feeding on patchily distributed fruit, as they do in the rain forest (Cant 1988; our observations). Thus the average rate of nutrient and energy gain may be unaffected by the need for individual processing of fruits if seeds are to be spat out.

Other primates

There are clear differences between species of primates in the treatment of seeds in the mouth (Table 1). The data for other cercopithecines shows disagreement between field and laboratory observations. The evidence from field studies suggests that at least some species behave like *Macaca fascicularis*. The use of the cheek pouches to store excess food for later processing seems to be a constant feature of the sub-family (Murray 1975; Rowell 1984). The three *Cercopithecus* species (*C. cephus*, *C. nictitans*, *C. pogonias*) studied in the field by Gautier-Hion (1980) in Gabon, also spat the seeds of most species eaten, often after transportation in the cheek pouches. They also broke few seeds but swallowed larger seeds than *M. fascicularis*. Intact seeds formed the bulk of the faeces of *Cercopithecus aethiops* in Uganda (Jackson and Gartlan 1965), although many other seeds were apparently either spat out or dropped after removal of the flesh. Again, this species swallowed larger seeds than *M. fascicularis*. Faeces of *Papio anubis* in Ghana contained large numbers of seeds (of at least 59 species) but 76% of the seedlings germinated from the faeces were from seeds <2.5 mm in length (Lieberman et al. 1979). This suggests a possible swallowing threshold in this species, although there is no information on the range of seed sizes in the diet or the fate of larger seeds.

In striking contrast are the results of feeding trials on 5 species of captive cercopithecines (*Cercopithecus aethiops*, *C. campbelli*, *Cercocebus atys*, *Erythrocebus patas*, *Papio papio*) in Sierra Leone reported by Happel (1988). In all five species, seeds were the part of the fruit most frequently eaten. The seeds were broken with the molars and Happel suggests that the characteristic bilophodont molars of Old World monkeys are an adaptation to seed predation. *C. aethiops* destroyed the seeds in 81% of fruits tested by Happel, compared with field observations of faeces exceptionally rich in intact seeds (Jackson and Gartlan 1965). Although it is possible that the conflict between field and laboratory observations on African cercopithecines reflects differences in the monkey and/or fruit species observed, we suspect, from our own experience, that captive studies

exaggerate seed predation, particularly if fruits are offered in small numbers. The ability of the captive monkeys to tolerate seed toxins is not good evidence for seed predation being normal behaviour, because these seeds formed only a small part of their diet in captivity.

In contrast to cercopithecines, apes and New World monkeys apparently swallow and defecate intact most seeds in their diet, including very large ones (van Roosmalen 1980; Galdikas 1982; Whitten 1982; Estrada and Coates-Estrada 1984; Takasaki and Uehara 1984; Tutin and Fernandez 1985; Garber 1986; Idani 1986; Janson et al. 1986). For instance, *Saguinus mystax* and *S. fuscicollis*, although one-fifth the body weight of *M. fascicularis*, swallow seeds up to 25 mm long (Garber 1986). Species that swallow most large seeds may also spit (Howe 1980) or destroy (Galdikas 1982) significant numbers.

Colobine monkeys (Cercopithecidae, Colobinae) typically break up the seeds in the mouth and then swallow and digest them (McKey et al. 1981; Bennett 1983; Davies et al. 1988), presumably detoxifying seed chemical defenses by bacterial fermentation in their specialized digestive systems (Bauchop and Martucci 1968; Davies et al. 1988). It seems unlikely that any vertebrate gut produces, without assistance from a diverse bacterial flora, the array of enzymes needed to detoxify the diversity of defensive chemicals found in seeds. Moreover, the alternative strategy, used by many insects, of specializing on a few related seed species and thus only needing to synthesize a few enzymes, is not open to large, long-lived vertebrates. In the Neotropics, *Pithecia* and *Chiropotes* are also seed predators but apparently lack the digestive specializations of the colobines and consume mostly immature seeds (Janson 1984), which may be less toxic than mature ones (Janzen 1983a). *Brachyteles arachnoides* is also reported to consume mostly immature seeds (Milton 1984).

The available evidence thus suggests that fruit-eating primates have evolved three different ways of dealing with mature seed chemical defenses: colobines detoxify them, while the others may avoid breaking most seeds and either

Table 1. Primate species that are reported to swallow, spit or destroy most ripe seeds in the fleshy fruit they eat

Swallowers	Spitters	Destroyers
Hominoids	Cercopithecines	Colobines
<i>Pan troglodytes</i>	<i>Macaca fascicularis</i>	<i>Colobus satanas</i>
<i>P. pygmaeus</i>	<i>Cercopithecus cephus</i>	<i>Presbytis melalophos</i>
<i>Gorilla gorilla</i>	<i>C. nictitans</i>	<i>P. rubicunda</i>
<i>Pongo pygmaeus</i>	<i>C. pogonias</i>	Cercopithecines
<i>Hylobates klossii</i>		<i>C. aethiops</i> ^a
Ceboids		<i>C. campbelli</i> ^a
<i>Aloutta palliata</i>		<i>Cercocebus atys</i> ^a
<i>Ateles paniscus</i>		<i>Erythrocebus patas</i> ^a
<i>Cebus apella</i>		<i>Papio papio</i> ^a
<i>Saguinus fuscicollis</i>		
<i>S. mystax</i>		

Sources, from top to bottom, left to right: Takasaki and Uehara 1984; Idani 1986; Tutin and Fernandez 1985; Galdikas 1982; Whitten 1982; Estrada and Coates-Estrada 1984; Van Roosmalen 1980; Janson et al. 1986; Garber 1986; this paper; Gautier-Hion 1980; McKey et al. 1981; Bennett 1983; Davies et al. 1988; Happel 1988

^a Based on field observations except those from Happel (1988)

swallow and defecate most of them (apes and New World monkeys) or spit them out (at least some cercopithecines). Ripe seed treatment may distinguish taxonomic groups (Table 1) and may be of evolutionary significance.

Why spit seeds?

The nutritional value of many seeds is high (Davies et al. 1988; Davies and Baillie 1988) – certainly higher than the pulp. There must therefore be a strong selective pressure for the evolution of detoxifying mechanisms. However, there are also likely to be costs associated with fermentative detoxification, including relatively slow passage of food and the apparent sensitivity of fermentation systems to chemical disruption (Davies et al. 1988). Moreover, the restriction of fore-stomach fermentation to a taxonomically distinct group suggests the possibility of phylogenetic inertia. For those primates that cannot detoxify seed chemical defenses, there are several possible selective advantages in spitting out seeds rather than swallowing them. The seeds may contribute more than half of the weight of typical forest fruits (Garber 1986; Whitten 1982): for instance, a male *Hylobates klossii* (weighing about 6 kg) ingested over one kilogram of seeds in a day (Whitten 1982). Their elimination may thus significantly reduce total body weight. It will also avoid filling the gut with indigestible bulk. This seems likely to both increase the rate and efficiency of digestion and reduce the necessary investment in gut tissues. Spitting may also permit more thorough mastication of the fruit pulp than is possible when there is a danger of damaging toxic seeds.

Implications for seed dispersal

Seed-destroying colobines probably disperse few, if any, seeds, although very small ones may escape mastication and be defecated intact. Seed swallows may be better dispersal agents than spitters for larger seeds, because the seeds are likely to be dropped further from the parent tree. Over 50 percent of the seeds ingested by *Saguinus mystax* and *S. fuscicollis* were defecated more than 200 m from the parent tree (Garber 1986). This advantage may be partly counteracted if swallowed seeds are deposited in large fecal clumps, as were the small seeds swallowed by *M. fascicularis*. However, in *Hylobates klossii* (Whitten 1982) and *Ateles paniscus* (van Roosmalen 1980) the faeces break up and become widely scattered while falling, and large seeds are often defecated singly by *Saguinus* species (Garber 1986).

M. fascicularis usually dropped or spat out larger seeds singly. Although only a small proportion of the seeds were carried more than 20 m in this study, it seems probable that macaques in undisturbed forest, where they are subject to predation, would spend less time congregated in fruiting trees and carry more fruit away before processing, as reported for other cercopithecines (Lindburg 1971; Murray 1975; Gautier-Hion 1984; Rowell 1984). In relatively undisturbed rain forest in northern Sumatra, Cant (1988) reports *Macaca fascicularis* 'moving rapidly between feeding sites and spending very brief periods at each' – behavior likely to maximise seed dispersal effectiveness. In Singapore, which has not had apes in historical times, macaques (including the now extinct *M. nemestrina*) may have been the major dispersal agents for some large-seeded trees, such as *Artocarpus* species.

The potentially very different consequences for plant fitness of seeds being spat, destroyed or swallowed must exert a strong selective pressure on plants to evolve ways of influencing seed fate. Seed swallowing could be promoted by preferential attraction of swallowers, or by reduction of seed size below the swallowing threshold of spitters. Reduction in seed size, however, is likely to have major consequences for other components of fitness (Foster and Janson 1985). Janzen (1983b) suggested that lubricating chemicals in the fruit pulp may make seeds more slippery and thus more difficult to sort from the pulp for spitting. They may also make them more difficult to detect. Gautier-Horn (1984) reported that the fate of large seeds eaten by *Cercopithecus* species was determined by the firmness of attachment of the fruit pulp. Where the seeds were very easily separated from the flesh, they were spat out under the parent tree. Seeds less easily separated were transported in the cheek pouches and spat elsewhere, while seeds with firmly attached flesh were swallowed. We, however, found no evidence for the influence of lubricating chemicals or firmness of flesh attachment on seed fate in fruits eaten by *M. fascicularis*. The sharpness of the size threshold, despite a wide range of fruit textures, argues against the significance of such influences for the fruits in our sample. The few species which apparently transgress the size threshold are more easily explained by the influence of seed dimensions other than width on seed detection or by seed clumping. Size was the major determinant of seed fate in fleshy fruits eaten by *Macaca fascicularis*.

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