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Research Article

Diet and fruit choice of the brown palm civet *Paradoxurus jerdoni*, a viverrid endemic to the Western Ghats rainforest, India

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Abstract

Brown palm civet diet was assessed by examining 1,013 scats between May 1996 and December 1999 in Kalakad-Mundanthurai Tiger Reserve, Western Ghats, India. The brown palm civet is predominantly frugivorous, with fruits of 53 native species and four species of introduced plants comprising 97% of its diet. There was high intra- and inter-annual variation in the diet of brown palm civets. Civets adapted to fluctuations in fruit resources by feeding on a diverse range of species and supplementing their year-round, primarily frugivorous, diet with invertebrates and vertebrates. Civets mainly ate fruits of trees and lianas, rarely those of herbs or shrubs. Fruits eaten by civets were mostly small (<1 cm diameter), multi-seeded, pulpy berries, and drupes with moderate to high water content, along with several large (>2 cm) fruits like *Palaquium ellipticum*, *Elaeocarpus serratus*, *Holigarna nigra*, and *Knema attenuata*. The brown palm civet is a key mammalian seed disperser in the Western Ghats rainforest by being predominantly frugivorous and dispersing a diverse array of plant species. As brown palm civets can persist in fragmented rainforest, they can play a major role in restoration of degraded fragments in these landscapes. The results emphasize the need to recognize the importance of small carnivores as seed dispersers in tropical forests.

Key-words: fruit characteristics; frugivory; small carnivore; viverrid; Western Ghats

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Introduction

Carnivores are indicative of ecosystem health and integrity [1], and can potentially affect food-web and community structure of lower trophic levels [2]. In the order Carnivora, some species in the family Viverridae, particularly in the sub-family Paradoxurinae (palm civets, including binturong *Arctictis binturong*), are known to be highly frugivorous [3-4]. Many of these species are suspected of influencing the dynamics of their forest habitats and of shaping plant community structure through effects on seed dispersal and regeneration [4-6].

Compared with the extensive literature on frugivory and seed dispersal in birds, bats, and primates [4, 7], there has been little research on factors influencing frugivory and fruit choice and seed dispersal by small carnivores [5, 8-10]. A study on the masked palm civet *Paguma larvata* in a subtropical region in Central China demonstrated civet preference for fruit and dietary shifts to animal prey such as small mammals and invertebrates during seasons of fruit scarcity [11]. It suggested that in tropical forests marked by year-round fruit availability, fruits would remain dominant in the diet through the year [11].

Apart from the abundance of resources, diet choice may also depend on fruit characteristics—morphological or nutritive. Traits influencing the vertebrate species that plants attract include fruit color, size (diameter), pulp thickness, number of seeds, and persistence of fruits on plants [5, 12-16]. Carnivore-dispersed plants have been reported to have large, many-seeded, pulp-rich, brown, and scented fruits, generally falling to the ground after ripening [5]. The few studies of mammalian carnivores (species of mustelids, canids, and viverrids) in sub-tropical and temperate regions [11, 17-19] and of bears in tropical forests [20-21] have largely focused on aspects of fruit diversity in diet and seed dispersal.

As noted by Zhou *et al.* [11], there is a lacuna of published work spanning at least one year from the Asian tropics, that would elucidate these aspects of frugivory and seed dispersal among mammalian small carnivores, especially the palm civets. Here, we present and discuss data from across three and a half years on frugivory and diet of the brown palm civet *Paradoxurus jerdoni*, a small carnivore endemic to the tropical rainforest of the Western Ghats mountains of India. Very limited information was available on the distribution of the brown palm civet until recent surveys revealed that the species occurs widely along the Western Ghats from around 8° N to about 15° 20' N but is restricted to tropical rainforest vegetation [22], including in fragmented landscapes [23]. Still, research on the ecology of the brown palm civet has been scarce [10] and the present study is the first detailed report on the diet of the species. The study addressed the following questions: (a) What is the diversity of species or food items consumed by the brown palm civet? (b) How do these vary intra- and inter-annually? (c) Do physical characteristics of fruits influence choice by civets? As the proportion and diversity of fruits in the diet of small carnivores and their effectiveness as seed dispersers have implications for the maintenance of plant communities and restoration of degraded areas [24-26], the results of the study are used to assess the functional and conservation importance of brown palm civets in the Western Ghats as well as implications for the conservation of the species.

Methods

Study site

The study was carried out in the Kalakad-Mundanthurai Tiger Reserve (KMTR, 895 km², 8° 25' – 8° 53' N and 77° 10' – 77° 35' E, Figure 1), over a period of three and half years between May 1996 and December 1999. KMTR is located in the southern extremity of the 1,600 km-long Western Ghats hill chain in India. The Western Ghats chain, along with Sri Lanka, has been identified as one of 34

biodiversity hotspots of the world [27]. High human population density and various developmental activities in this region have resulted in habitat loss, degradation, and fragmentation, particularly of the biologically rich rainforest [27].

The Agasthyamalai-Ashambu hills in which KMTR is situated include over 400 km² of relatively undisturbed and contiguous rainforest, one of the last such areas in the Western Ghats [28]. The rainforest in KMTR occurs above 600 m elevation. The mid-elevation (700 m – 1,400 m) rainforest is now categorized as the mid-elevation tropical wet evergreen forest of the *Cullenia exarillata - Mesua ferrea - Palaquium ellipticum* type [29]. The annual rainfall ranges from 1,500 mm on eastern slopes to over 3,000 mm in the western parts. The mean monthly temperature in the rainforest ranges between 19° C in January and 24° C in April–May at mid-elevations (in Sengaltheri, 1040 m). KMTR receives most of the rainfall during the north-east monsoon. The average relative humidity ranges from around 60% in March to about 97% in November–December.

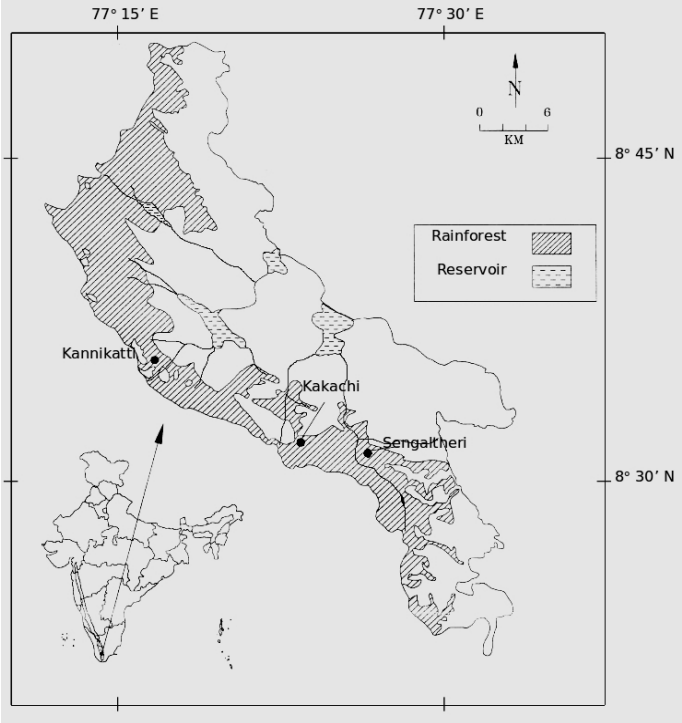

Fig. 1. Map of the Kalakad-Mundanthurai Tiger Reserve in the Western Ghats of southern India, showing locations of study sites.

Brown palm civet *Paradoxurus jerdoni (Photo by* **Kalyan Varma)**

An area of about 15 km² around the base camp in Sengaltheri (8° 31' N and 77° 26' E; 800 m – 1,100 m asl), was selected as the intensive study area in KMTR. The rainforest at Sengaltheri is contiguous with rainforest on all sides except toward the east, where the forest is adjacent to wooded grasslands. Two other sites, Kannikatti (8° 37' N and 77° 16' E; 650 m – 1,000 m) and Kakachi (8° 50' N and 77° 30' E; 1,200 m – 1,300 m), were also surveyed periodically for scats, to document the diet of the brown palm civet over a wider geographical area and altitude. Other important mammalian frugivores in these rainforest areas are the lion-tailed macaque (*Macaca silenus*), sloth bear (*Melursus ursinus*), Malabar giant squirrel (*Ratufa indica*), and at least two species of bats. Information on other dispersers and modes of dispersal from the Kakachi site are available elsewhere [30].

Diet composition

Food habits of the brown palm civet were studied using scat analysis, a technique widely used to study small carnivore diet [2, 5-6, 11, 18-19, 31-33]. As the brown palm civet is strictly nocturnal and inhabits rainforest with a dense canopy cover and understory, direct observations of feeding or camera trapping were not feasible. All scats encountered in rainforest along trails and in the interior were examined thoroughly in the field or collected for macroscopic examination at the base camp. Scats of the brown palm civet were identified based on their shape, size, and location. Brown palm civet scats are straight, cylindrical (≤2 cm in diameter), rounded at both ends and usually defecated as a single bolus on prominent places like fallen logs and rocks. This defecation behavior is typical of brown palm civets. Unlike felid scats, brown palm civet scats lacked a pungent odor. These attributes of scats were directly confirmed by comparison with scats produced by brown palm civets captured as part of a radio-telemetry study [34]. Scats that could not be conclusively identified as brown palm civet based on size, shape, odor, and location, were discarded from analysis. The other small carnivores that occurred in the rainforest are the small Indian civet *Viverricula indica*, Nilgiri marten *Martes gwatkinsi*, and the brown mongoose *Herpestes fuscus* (the common palm civet *Paradoxurus hermaphroditus* was never recorded from within the rainforest and is a species restricted to drier forest types within KMTR). The capture frequency of the other small carnivores in track-plots and camera-traps in a larger part of the study area was less than 10% and 20%, respectively, and the small Indian civet occurred very rarely within the undisturbed rainforest [23, 35].

During the study, 1,013 scats were collected from the three rainforest sites in KMTR (Sengaltheri n = 559, Kakachi n = 186, and Kannikatti n = 271 scats). While Sengaltheri and Kannikatti were surveyed across all years of the study, Kakachi was surveyed primarily in 1997. Multiple trails were surveyed around each of these sites. Systematic monthly survey for scats was carried out in Sengaltheri during 1998 and 1999, and these data are analyzed separately. As the surveyed area was much larger than the home range of individual civets [10], and visits to the same trail were usually spaced many days apart, the scats originated from a number of different individuals in the study sites. The remains in scats were identified by comparison with a reference collection of fruits, seeds, and hair samples. Seeds of all fruit species in the scats were differentiated to species level, with the exception of *Ficus spp.* Among invertebrates, insects were treated as a group, while crabs, snails, millipedes, and centipedes were dealt with as separate taxonomic groups, as they were readily identifiable in the field. Among the mammal remains, only those of the Malabar spiny dormouse (*Platacanthomys lasiurus*) was identified to species, while the other hair remains were grouped together as mammal. Henceforth, each of the species as well as taxonomic groups of species mentioned above will be referred to as food items. It must be noted that the scat analysis yields information of species that leave discernible remains in the scats (of ingested pulp and/or seed in the case of fruits or hair and hard remains in the case of animal prey). Food items such as soft-bodied animal prey, nectar, and resins may go unrecorded.

Fruit characteristics

In order to test for preference of particular physical traits of fruits by brown palm civets, characteristics of the 35 most commonly consumed species were compared with the 30 most abundant non-civet food plants in the study area. It was not possible to include all species, as data on fruit characteristics were not available for rare plant species. That these were species not eaten by civets is evidenced from their non-occurrence in scats throughout the study as well as in supplementary observations in the same and other rainforest landscapes of the Western Ghats during follow-up research [22-23]. Following Herrera [5], fruits were classified into various groups based on their physical characteristics as observed in the field or taken from published literature [36]. Plant species in the study area [37-38] were categorized as lianas, shrubs, or trees (plant form).

The fruit type categories used were: drupe, defined as an indehiscent fleshy fruit with a single seed; berry, indehiscent fleshy fruit with more than one seed, usually soft, embedded in the pulp; arillate, usually dehiscent capsules; and others, including both fleshy compound fruits, and dry, dehiscent fruits like follicles and pods. Other characteristics used were fruit size (<1 cm diameter = small, 1–2 cm = medium, >2 cm = large), color of ripe fruit (yellow, purple, brown + pink to red, blue + green), presence or absence of resin or latex, presence or absence of odor, number of seeds, seed sizes (≤ 0.5 cm = small, 0.6–1 cm = medium, >1 cm = large), pulp (0 = absent, <1 mm = thin, 1–4 mm = moderate, > 4 mm = thick), and water content (<25% = dry, 25–50% = moderate, >50% = watery).

Analyses

The contribution of each species to the diet (fruits, invertebrates, vertebrates, etc.) was calculated following Genovesi *et al.* [39] as (i) the frequency of presence (F_a) in scat (ratio of number of scats with species to total number of scats), and (ii) the absolute frequency of occurrence (F_i) of each item or species (ratio of number of occurrences of species to total number of occurrences of all species). The importance of a dietary species was assessed based on its frequency of occurrence (F_i) in the diet [39]. Any species contributing to more than 25% of the diet in a given month was considered to be an important species. F_a was calculated for the overall diet as it makes the data comparable with results of most other studies, although F_i has been recommended as being a better index [39]. Comparisons of dietary species richness (number of species in scat samples) between years were made through sample-based rarefaction analysis using the program EcoSim, Version 7.0 [40-41]. The effects of year and number of species in diet on consumption of animal matter were analyzed using analysis of covariance. The preference for particular fruit trait characteristics was assessed by χ^2 contingency table tests; if expected frequencies <5 were obtained, the chi-square tests were redone after pooling categories [42].

Results

Diet composition

Fruits constituted the predominant diet of the brown palm civets in the region—91.12% of the 1,013 scats had fruit remains (primarily seeds) of native plant species. Fruits of 53 native species of plants from 27 families (including 8 unidentified species) were consumed by brown palm civets. Fruits of four species of exotic, introduced, or domesticated plants (banana *Ensete paradisiaca*, cardamom *Elettaria cardamomum*, coffee *Coffea arabica*, and guava *Psidium guajava*) were also consumed. When exotic fruits were also included, 97.04% of scats contained fruit remains (primarily seeds). Fifteen scats (1.48%) had remains of flowers of two rainforest tree species—*Cullenia exarillata* (Bombacaceae) and *Syzygium* sp. (Myrtaceae). The civets ingested fruit pulp along with seeds, and intact seeds were defecated in all cases, except for *Palaquium ellipticum* where the scats had remains of only the pulp, rarely with damaged seeds.

Invertebrate remains (insects, millipede, centipede, snail, or crab) were found in 116 scats (11.45%). The occurrence of vertebrates, including rodents, other mammals, birds, or reptiles, in the scats was rare (3.75%, 38 scats). Twelve scats had grass plugs (usually along with vertebrate remains), and one had beeswax. A single species (or food item) was recovered from 79.86% (809) of the scats, 16.19% (164) contained remains of two species/food items, 3.36% (34) had three, and only 6 (0.59%) scats had four species/food items. None of the scats had more than four macroscopically discernible species/food items.

The six most dominant fruits in the diet were *Elaeocarpus munronii* (average absolute frequency of occurrence, F_i, across 1996–99 = 9.73%), *Holigarna nigra* (9.52%), *Acronychia pedunculata* (5.80%), *Nothopegia beddomei* (5.76%), *E. serratus* (4.66%), and *Palaquium ellipticum* (4.62%, Appendix 1). No fruit contributed more than 10% to the overall diet (average F_i across years, Fig. 2), while nearly 62% (39 species including animal matter) contributed less than 1%. Only two species, *Elaeocarpus munronii* and *Holigarna nigra*, contributed between 9% and 10% to the overall diet (Fig. 2).

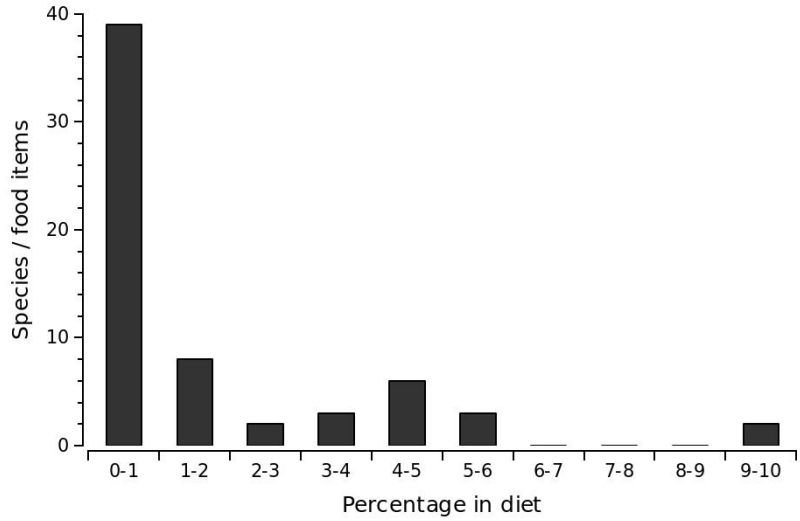

Fig. 2. Frequency distribution of the percentage occurrence of various species (or types of food items) across years in the diet of the brown palm civets in Kalakad-Mundanthurai Tiger Reserve (KMTR), India.

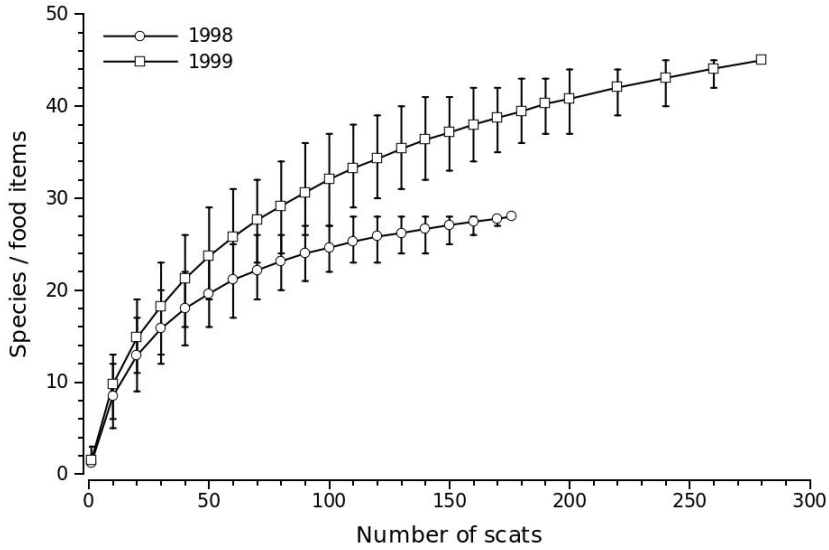

Fig. 3. Rarefaction analysis of diversity of species in brown palm civet scats in 1998 and 1999 in Sengaltheri, KMTR. Vertical bars indicate 95% confidence intervals.

Temporal variation in diet

There was considerable inter-annual variation in the food species and their frequency of occurrence in the civets' diet. Across all sites and years, the number of food items found in scats in each month varied between 2 and 22. In the systematic monthly monitoring at Sengaltheri over a 2-year period, the monthly number of fruit species found in scats varied between 2 and 13 (mean number of fruit species per month ± SE: 4.2 ± 0.64 species in 1998, 6.8 ± 0.86 species in 1999). The monthly number of fruit species in scats was significantly lower in 1998 compared with the corresponding months in 1999 (paired t-test, t = -2.50, *d.f.* = 11, P = 0.029). In Sengaltheri, during 1998, civets consumed 17 identified native plant species (28 kinds of food items in total including exotics, grass, and animal

matter, *N* = 176 scats) increasing in 1999 to 33 species (45 in total, *N* = 280 scats). Among the native plant species, only 15 species were recorded as being consumed in both years (Appendix 1). Rarefaction analysis showed that the number of species/food items was indeed higher in 1999 for comparable numbers of scats analysed (Fig. 3).

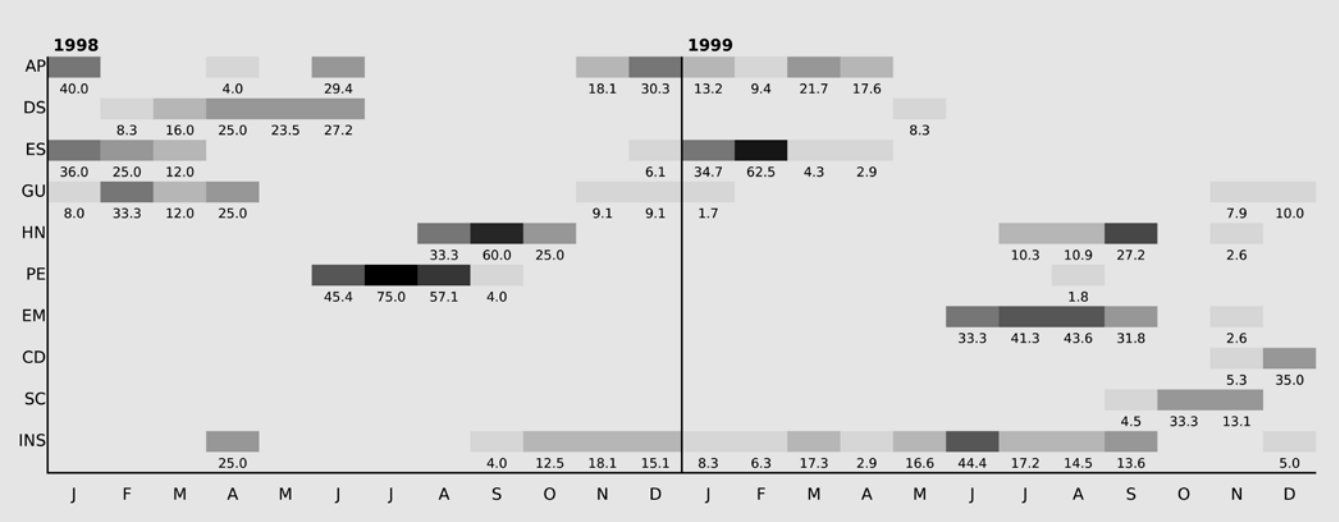

Fig. 4. Food species/items contributing to over 25% of the diet (percentage of items F_i in brown palm civet scats in Sengaltheri, KMTR, 1998–1999). Monthly percentages (F_i) are mentioned below the shades, with darker shades corresponding to higher percentages. AP – *Acronychia pedunculata*, DS – *Diospyros sylvatica*, ES – *Elaeocarpus serratus*, GU – *Gnetum ula*, HN – *Holigarna nigra*, PE – *Palaquium ellipticum*, EM – *E. munronii*, CD – *Canthium dicoccum*, SC – *Strychnos colubrina*, INS – Insects and other arthropods.

Of the 10 most commonly eaten food items in 1998 and 1999, five (*Holigarna nigra, Acronychia pedunculata, Elaeocarpus serratus*, coffee, and insects) were recorded as being consumed in both years. The relative frequency of occurrence, as well as importance (based on percentage occurrence), of the top 10 species differed between years. The species with the highest frequency of occurrence was *Palaquium ellipticum* (14.4%) in 1998 and *Elaeocarpus munronii* (12.1%) in 1999. Across months, there was a high turnover of species consumed (fruits and animal matter, Fig. 4). Each of the 10 important species (9 fruit species and insects) accounted for 25–75% of the diet in some months in the years 1998 and 1999 (Fig. 4). Among the introduced species, coffee contributed significantly to the diet. The gymnosperm *Gnetum ula* was also one of the most commonly eaten fruits. Fruits of palms such as *Bentinckia codapanna*, *Caryota urens*, *Pinanga dicksoni*, and *Calamus* sp. were also eaten. Animal matter comprised between 0% and 44.4% of items in scats across the 24 months in Sengaltheri (Fig. 5). Analysis of covariance of the monthly percentage of animal matter against year and fruit consumption revealed that animal matter tended to be higher in 1999 (coefficient = 9.09, SE = 4.60, t = 1.974, P = 0.062), and was significantly negatively related to number of fruit species in scats (slope = -1.78, SE = 0.81, t = -2.182, P = 0.041; overall R^2 = 0.147).

Characteristics of food plant species

Most fruits eaten were of trees and lianas; shrubs and herbs were rarely used (χ^2 = 23.48, *d.f.* = 3, P < 0.001; Appendix 2). Twenty-seven overstory and 7 understory tree species, 9 species of lianas and climbers, and 4 species of shrubs were used by the brown palm civet during the study period. Among fruits frequently consumed by brown palm civets, there were equal proportions of large,

medium-sized, and small fruits (Appendix 2). However, the proportion of smaller fruits tended to be higher in brown palm civet food species than among the abundant non-civet food species (χ^2 = 5.18, *d.f.* = 2, *P* = 0.075). When compared with non-consumed species, a greater proportion of fruit

species consumed by the brown palm civets were berries and drupes (80%), and most (c. 91%) had moderate to thick pulp (Appendix 2, *P* = 0.07). Fruit traits representing >50% water content, small- and medium-sized seeds, and yellow fruits, lacking odor, tended to be chosen (Appendix 2, *P* < 0.10). There was no significant difference between non-civet food species and those eaten by the civets in characteristics such as presence of resin or latex, and in the number, kind, and shape of the seeds (Appendix 2).

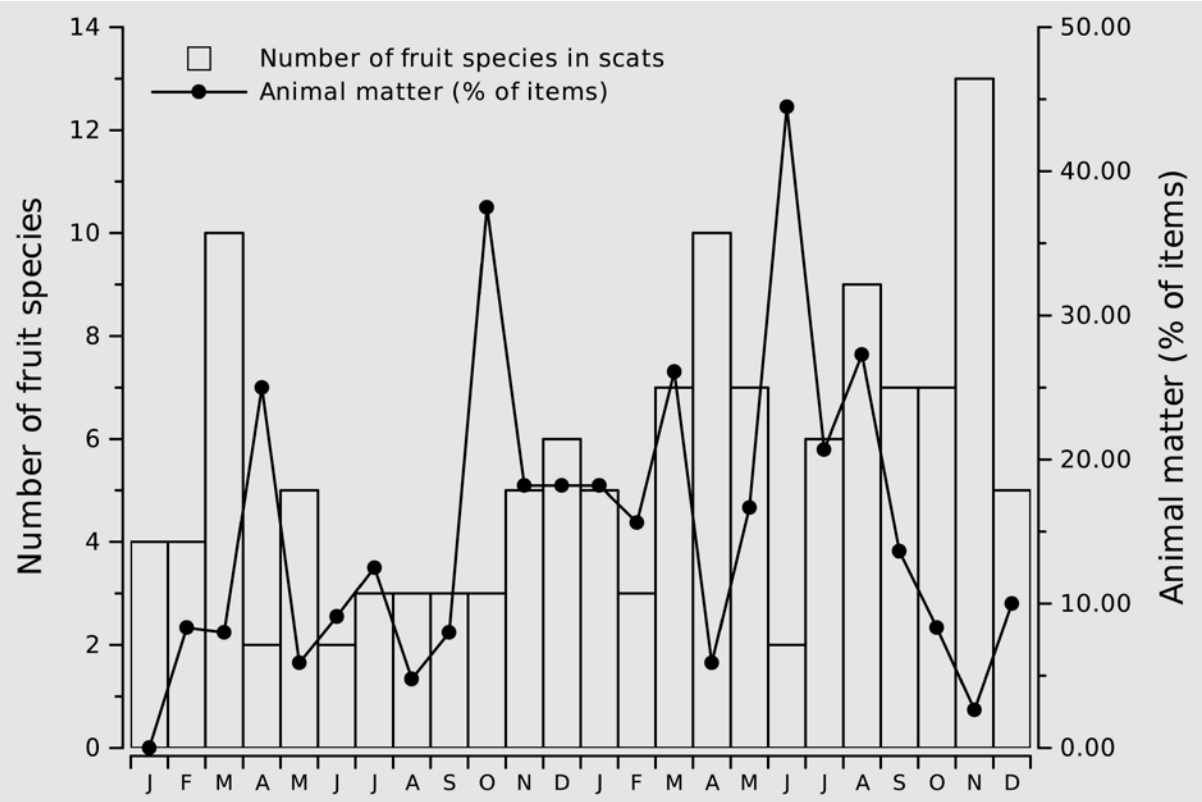

Fig. 5. Pattern of variation in diversity of fruit species and occurrence of animal matter in brown palm civet scats across two years (1998–1999) in the KMTR rainforest.

Discussion

Among the small carnivores of the families Procyonidae, Mustelidae, Herpestidae, and Viverridae, the herpestids (mongooses) are the least frugivorous, while some mustelids (badgers, martens, and weasels), procyonids (coatis and kinkajous), and viverrids (civets) are highly frugivorous (see Appendix 3, ref. [43]). Among the viverrids, the members of the sub-family Paradoxurinae or the palm civets are more frugivorous than the others [4]. In comparison with other small carnivores [6, 44-46] (Appendix 3), the brown palm civet turns out to be one of the most frugivorous, with 97.04% (91.12% if native species alone are considered) of its scats containing plant remains, predominantly seeds of fruits and rarely flowers of two native plant species. A highly frugivorous diet comparable to

that of the brown palm civet has been reported in a Neotropical procyonid, the kinkajou *Potos flavus* (99% fruit, ref. [47]).

Studies of several mustelid, herpestid, and viverrid species have shown that these species are less frugivorous than the brown palm civet (Appendix 3) and these species mainly consume fruits during seasons when fruit availability is high and alternative preferred foods are scarce. In the brown palm civet, however, fruit predominates in the diet year-round (Fig. 6). This could be due to several factors. First, the brown palm civet inhabits resource-rich tropical rainforest where, although there are marked periods of fruit abundance and scarcity, there is year-round availability of fruits [10, 48]. This is consistent with the prediction of Zhou *et al.* [11] for *Paguma larvata* that in tropical forests where fruits are available year-round, they will remain the main food throughout the year for the palm civets. Second, the "unspecialized" digestive system of the carnivores and their ability to feed opportunistically have probably enabled brown palm civets to become frugivorous (with frugivory as an evolutionary offshoot [49]), and to be able to cope with fluctuations in fruit availability. A third aspect is physiological adaptation to a diet of fruits—often nutrient-poor (particularly protein, although see [50])—including low metabolic rate and energy needs [51] and short gut passage time [52]. For the kinkajou, a nocturnal neotropical small carnivore similar in habits to the brown palm civet, the gut passage time was found to be between 35 and 215 minutes [47], and for the Sulawesi palm civet *Macrogalidia musschenbroekii*, less than 12 hours [53]. The brown palm civets had gut passage time of less than 7 hours (approximate measure based on fruit consumption and defecation during capture and release of animals for radio-collaring [34]).

Temporal variation in the diet of unspecialized, though obligate frugivores like the brown palm civet may also result from uneven temporal and spatial fruit production that is characteristic of the study area [10, 54] as in other tropical forests [48, 55-56]. Variation in species composition in the diet of the brown palm civets is pronounced, as indicated by high turnover of species across months. Although the brown palm civet diet comprised a high diversity of plant species (flowers of 2 and fruits of 53 species), there were a few species—*Holigarna nigra, Elaeocarpus serratus, Nothopegia beddomei, Gnetum ula,* and *Palaquium ellipticum*—that they consumed more frequently than the more abundant fruits of species such as *E. munronii* and *Antidesma menasu* and flowers of *Cullenia exarillata* in the study area [10]. However, in a given month not more than 13 fruit species (usually fewer than 5 species) were found in the scats, implying the need for a diverse assemblage of food species in a given area. The dominant species differed between the years, suggesting not only food preference and the generalist nature (since they use a diverse set of species) of food choice by the brown palm civets, but also that they were probably tracking fruiting episodes, as shown in other species [56-58].

Many frugivorous species are known to either migrate to habitats with greater food resource availability during times of scarcity, or shift to feeding on other rarer, aseasonal, or non-preferred fruits [55] or on animal matter [11, 32]. Despite such a high level of frugivory, brown palm civet scats contained invertebrate and vertebrate remains in 23 months during 1998 and 1999, with higher proportions in a few months when few fruit species were consumed. The increase in proportion of non-fruit items in the diet could be related to periods of relative fruit scarcity, making civets more opportunistic in their diet and consuming animal matter as a supplement [10].

The arboreal brown palm civets eat a greater number of tree and liana fruits and, unlike Mediterranean carnivores [5], the brown palm civets do not depend on fallen fruits. Although there was no statistically significant preference for other fruit traits, possibly due to low sample size, several variables approached statistical significance and are important to corroborate in future

research. It is to be noted that the comparison is made between the consumed and the more abundant non-consumed species due to the lack of information on other species. The fruits eaten by brown palm civets were, on average, smaller than those not eaten (although they did eat some of the large fruits like *E. serratus* and *P. ellipticum*), which supports Jordano [13], who points out that mammalian carnivores prefer small, pulpy fruits with small seeds, although the fruits eaten may be larger than those eaten by avian frugivores.

The dominant fruit types consumed by the brown palm civet were small-seeded drupes and berries, usually blue or green in color, with moderate to high water content in the pulp. The color of fruits apparently does not strongly influence their choice as the civets are nocturnal and tend to be color-blind [4]. The small carnivores reported from Spain also preferred multi-seeded fruits [5].

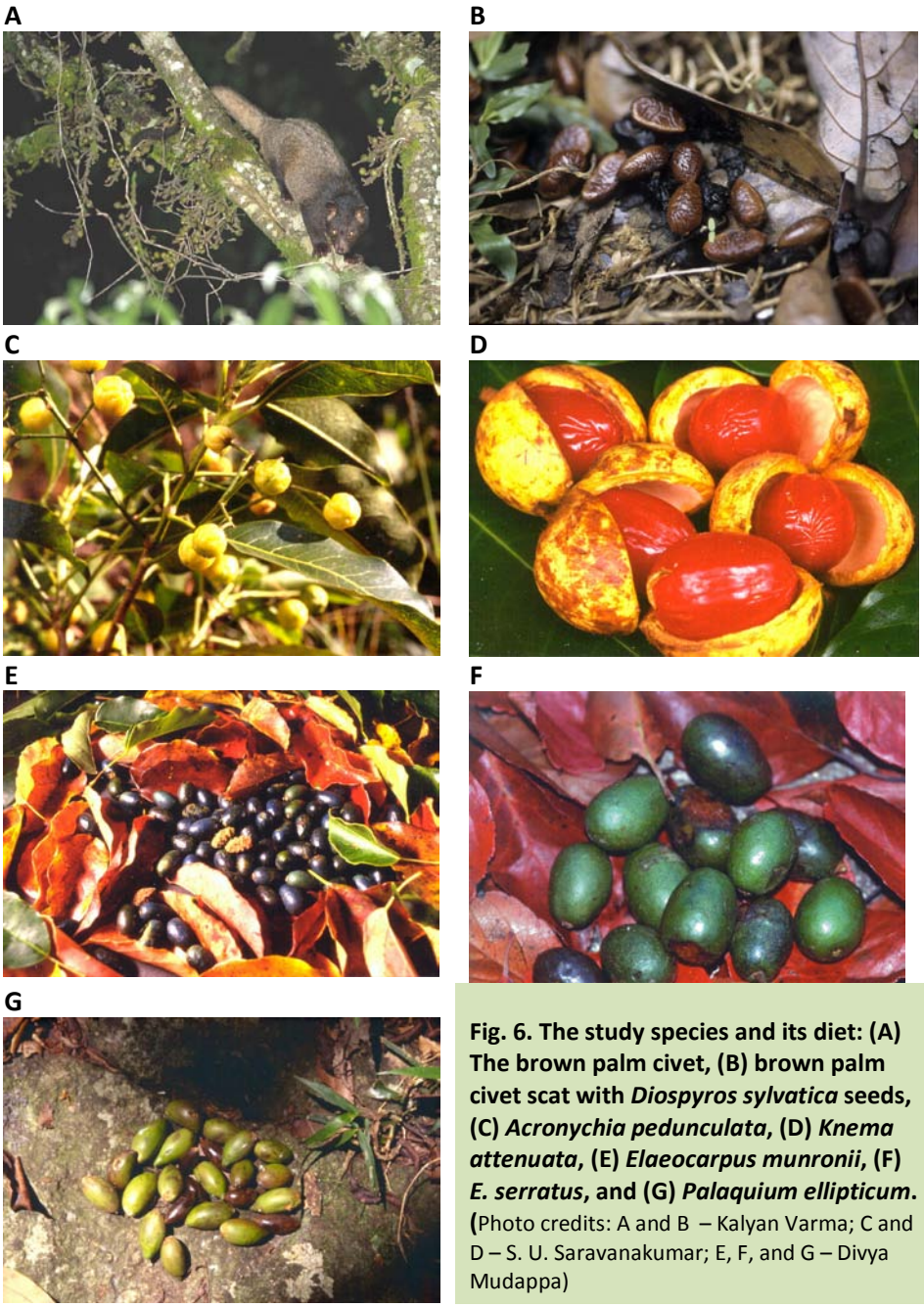

Fig. 6. The study species and its diet: (A) The brown palm civet, (B) brown palm civet scat with *Diospyros sylvatica* seeds, (C) *Acronychia pedunculata*, (D) *Knema attenuata*, (E) *Elaeocarpus munronii*, (F) *E. serratus*, and (G) *Palaquium ellipticum*. (Photo credits: A and B – Kalyan Varma; C and D – S. U. Saravanakumar; E, F, and G – Divya Mudappa)

Implications for conservation

The members of the family Viverridae are believed to be among the most important mammalian seed dispersers in Asian forests [4]. As in the case of masked palm civets in sub-tropical coniferous and broad-leaved forests [11], the present study highlights the importance of brown palm civets as frugivores and seed dispersers in Western Ghats tropical forests (Fig. 6). Brown palm civets carry seeds away from under the parent trees and defecate them virtually undamaged, with seed germination viability being retained or even enhanced in some species [10]. Of the 122 tree and liana species reported by Parthasarathy [38] in the intensive study area of Sengaltheri, 49 species (40.2%) comprising 37.3% of the 2,150 individuals in an area of 3 ha are dispersed by the brown palm civet. In the Western Ghats rainforest, the brown palm civet is a major seed disperser, along with the sloth bear (*Melursus ursinus*) and great hornbill (*Buceros bicornis*), of many large-seeded fruits like the *E. serratus*, *G. ula*, *Diospyros* spp., and *Knema attenuata*. Given the extent of frugivory and seed dispersal by brown palm civets and their ability to persist in fragmented rainforest landscapes, including small and/or degraded fragments [23], the species could play a major role in the restoration of degraded rainforest patches in the Western Ghats. Another important aspect is that the brown palm civet also consumes and disperses seeds of alien (exotic) species such as coffee *(Coffea sp.*), which may play a partial role in the spread of this understory species in relatively undisturbed forests adjacent to coffee plantations [59]. The long-term implications of this on diversity of native rainforest understory plant communities remains to be explored.

The brown palm civet is a highly frugivorous species with a year-round preponderance of fruit in its diet. The study highlights that a wide diversity of tree species are required to meet its year-round requirements. Conversion of tropical forests with high tree diversity to large-scale monoculture plantations in the Western Ghats [27-28] is likely to negatively affect the survival of the species in heavily altered landscapes. However, the brown palm civet does occur in fragmented landscapes containing remnants of tropical rainforest amid other land uses such as tea and coffee plantations [23]. Their ability to persist in such landscapes is contingent on the occurrence of a diversity of fruit tree species in remnant fragments and within other land uses in the surrounding landscape (e.g., shade trees in coffee plantations) [23]. Given that some of these areas are often depauperate in other dispersers such as larger mammals and birds like hornbills and large pigeons due to habitat loss and hunting, the brown palm civet gains additional importance as a disperser persisting in such human-impacted landscapes.

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Appendix 1. The percent occurrence of seeds and other remains in scats (percentage of items, F_i) of the brown palm civet in the tropical rainforest of Kalakad-Mundanthurai Tiger Reserve, 1996–1999 (number of scats in parentheses).

	All sites				Sengaltheri	
Species/items	**1996 (116)**	**1997 (287)**	**1998 (222)**	**1999 (388)**	**1998 (176)**	**1999 (280)**
Acronychia pedunculata	-	9.67	9.30	4.24	10.1	5.16
Annonaceae sp.	-	-	-	0.05	-	-
Antidesma menasu	-	0.16	-	-	-	-
Artocarpus heterophyllus	10.3	1.26	0.66	1.01	0.50	0.95
Bentinckia codapanna	-	1.33	0.20	0.23	-	1.44
*Bischofia javanica**	-	-	0.32	0.43	-	0.43
Calamus sp. (L)	-	0.28	0.20	-	0.33	-
Canthium dicoccum	-	-	-	3.35	-	3.35
Caryota urens	-	-	0.60	0.69	1.00	0.69
Chrysophyllum lanceolatum	4.39	2.26	2.34	3.52	2.32	3.10
Cullenia exarillata	-	0.93	-	1.14	-	1.63
*Dimocarpus longan**	-	2.22	-	-	-	-
Diospyros sylvatica	1.11	2.51	7.82	0.69	8.34	0.69
Diospyros sp. 2	-	4.05	-	-	-	-
Elaeocarpus munronii	10.5	16.3	-	12.10	-	12.7
*E. serratus**	-	3.04	6.13	9.45	6.58	9.76
Eleagnus kologa (L)	-	0.28	-	-	-	-
Embelia sp. (L)	-	2.88	0.16	0.24	0.33	0.24
*Ensete superbum** (S)	2.85	1.19	3.25	1.07	2.76	1.07
Erycibe wightiana (L)	-	-	-	0.34	-	0.37
Euonymus angulatus	-	-	-	0.69	-	0.69
Fagraea ceilanica	-	1.19	-	1.46	-	1.77
Ficus spp.*	4.34	3.02	1.60	9.31	1.53	9.09
*Filicium decipiens**	-	0.37	0.60	1.67	1.00	1.67
*Gnetum ula** (L)	-	7.53	7.31	1.68	8.04	1.62
*Holigarna nigra**	23.1	0.99	9.86	4.11	9.86	4.26
Knema attenuata	-	1.54	-	-	-	-
Lepisanthes decipiens	-	-	-	1.13	-	-
Liana sp. *1 (L)*	-	-	-	1.97	-	1.97
Ligustrum perrottetii	-	-	-	0.69	-	0.69
*Nothopegia beddomei**	19.2	-	3.33	0.50	3.46	0.53
Olea dioica	-	-	-	0.75	-	0.75
*Palaquium ellipticum**	-	3.72	14.4	0.37	15.1	0.15
Pandanus sp.* (S)	-	4.72	-	0.82	-	0.84
Pinanga dicksoni	-	0.16	-	-	-	-
Rutaceae sp. (L)	-	1.89	-	-	-	-
Sapotaceae sp.	-	-	-	0.75	-	0.69
Semecarpus auriculata	-	0.65	-	3.63	-	-
Solanum sp. (S)	-	2.22	-	0.65	-	0.68
Strychnos colubrina (L)	-	-	-	4.25	-	4.25
Strychnos sp. 2	-	-	-	0.05	-	-
Syzygium cumini/mundagam	-	-	-	0.37	-	0.45
Syzygium zeylanicum	5.93	0.48	-	-	-	-

Species/items	All sites				Sengaltheri	
	1996 (116)	1997 (287)	1998 (222)	1999 (388)	1998 (176)	1999 (280)
*Tricalysia apiocarpa**	-	-	2.11	-	1.15	-
*Viburnum punctatum**	-	-	-	0.99	-	1.30
Vitaceae sp.* (L)	-	-	2.84	0.97	2.84	0.43
Zizyphus sp. (S)	-	10.0	-	0.05	-	0.36
Banana (E)	-	-	1.21	0.42	1.42	0.42
Elettaria cardamomum (E)	-	0.09	-	0.12	-	0.15
*Coffea arabica** (E)	3.96	4.52	4.73	4.26	5.24	4.56
Psidium guajava (E)	-	-	1.96	1.34	1.96	1.34
Grass	1.42	0.58	1.02	1.01	1.02	0.95
Unknown plant matter	9.63	2.67	3.51	1.21	2.33	1.16
Other mammalian hair	-	0.70	3.00	1.80	3.26	1.98
Malabar spiny dormouse	-	0.28	2.24	0.06	-	0.06
Crab	0.88	0.91	-	0.11	-	-
Insects	1.42	2.08	7.46	11.00	6.23	12.1
Millipede	0.71	0.56	3.45	2.76	2.52	3.06
Centipede	-	-	0.25	-	0.25	-
Feather	0.41	-	0.20	-	0.33	-
Scales	-	-	-	0.06	-	0.06
Snail	-	-	-	0.06	-	0.06
Beeswax	-	0.09	-	-	-	-
Unknown animal matter	-	0.62	-	0.05	-	-

*Seeds of these species were found intact in scats and observed to germinate after ingestion by brown palm civets (seeds of other species were found intact in scats but viability could not be assessed during the study), L – liana, S – shrub, E – exotic.

Appendix 2. Comparison of brown palm civet food species (*N* = 35) and non-food species (*N* = 30) characteristics in the tropical rainforest of KMTR, Western Ghats.

	Class	**Percentage of species**				**Chi-square (*d.f.*)**	***P***
1.	Plant form*	Trees	Understory trees	Lianas	Shrubs		
	Civet food	57.4	14.9	19.1	8.5	23.48 (3)	<0.001
	Other	27.1	31.0	9.7	32.3		
2a.	Fruit type	Drupe	Berry	Arillate + other			
	Civet food	45.7	34.3	20.0		5.61 (2)	0.061
	Other	56.7	10.0	33.3			
2b.	Fruit size	Small	Medium	Large			
	Civet food	28.6	31.4	40.0		5.18 (2)	0.075
	Other	6.7	43.3	50.0			
2c.	Pulp thickness	Thick	Thin				
	Civet food	48.6	51.4			3.27 (1)	0.070
	Other	26.7	73.3				
2d.	Water content	Watery	Moderate + dry				
	Civet food	74.3	25.7			3.10 (1)	0.078
	Other	53.3	46.7				
2e.	Color	Purple	Yellow	Brown+ pink+red	Blue+ green		
	Civet food	17.1	25.7	22.9	34.3	6.28 (3)	0.098
	Other	23.3	3.3	26.7	46.7		
2f.	Odor	Presence	Absence				
	Civet food	14.3	85.7			3.30 (1)	0.069
	Other	33.3	66.7				
2g.	Resin or latex	Presence	Absence				
	Civet food	17.1	82.9			0.003 (1)	0.959 (NS)
	Other	16.7	83.3				
3a.	Seed type	Stony	Soft				
	Civet food	54.3	45.7			1.03 (1)	0.310 (NS)
	Other	66.7	33.3				
3b.	Seed shape	Globose	Ovoid	Ellipsoid + other			
	Civet food	17.1	45.7	37.1		3.47 (2)	0.176 (NS)
	Other	36.7	40.0	23.3			
3c.	Seed number	Solitary	Multi-seeded				
	Civet food	57.1	42.9			1.15 (1)	0.284 (NS)
	Other	70.0	30.0				
3d.	Seed size	Small	Medium	Large			
	Civet food	25.7	34.3	40.0		5.86 (2)	0.054
	Other	13.3	16.7	70.0			

* Sample size was larger for plant forms: *N* (civet food) = 47 species; *N* (other) = 155 species.

Appendix 3. Frequency of occurrence of flowers, fruits, and seeds in the diet of other small carnivores of families Procyonidae, Mustelidae, Herpestidae, and Viverridae.

Species (Common name)	Frequency of occurrence of plant food (%)	Number of identified species	Source
Nasuella olivacea (mountain coati)	37	1	[60]
Nasua nasua (coati)	54.5	53	[61]
Potos flavus (kinkajou)	99	78	[47]
Martes zibellina (sable)	22-38	2	[62]
Martes martes (pine marten)	5–35	9	[63]
Martes foina (stone marten)	59	16	[39]
Martes foina (stone marten)	-	11	[26]
Martes flavigula (yellow-throated marten)	43.5	13	[18]
Martes melampus (Japanese marten)	62	11	[33]
Martes melampus (Japanese marten)	57	12	[17]
Melogale moschata (small-toothed ferret badger or Chinese ferret badger)	8	-	[31]
Melogale moschata (small-toothed ferret badger or Chinese ferret badger)	33	8	[19]
Meles meles (badger)	42	9	[17]
Herpestes ichneumon (Egyptian mongoose)	<5	-	[64]
H. javanicus (= *H. auropunctatus*, small Indian mongoose)	29	4	[65]
H. naso (long-nosed mongoose)	8	-	[66]
Atilax paludinosus (marsh mongoose)	8	-	[66]
H. urva (crab-eating mongoose)	8	-	[31]
Macrogalidia musschenbroekii (Sulawesi palm civet)	62	3	[53]
5 species of civets	76	18	[6]
Paradoxurus hermaphroditus (common palm civet)	89	2	[46]
Viverricula indica (small Indian civet)	58	7	[31]
Paguma larvata (masked palm civet)	>60	67 wild, 9 cultivated	[11]
Paradoxurus jerdoni (brown palm civet)	97	55	This study