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RH: GLEANING ASSOCIATION OF DEER WITH COLOBINES

“Deer” friends: feeding associations between colobine monkeys and deer

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We observed an inter-species association between wild Javan lutungs (*Trachypithecus auratus*) and rusa deer (*Rusa timorensis*). In this association, the former drops plant items that the latter subsequently consumes (glean). We investigated whether the association is beneficial for deer that inhabit tropical regions characterized by drastic seasonal changes. Between 2011 and 2013, we conducted field surveys in the Pangandaran Nature Reserve, Indonesia. We observed 248 gleaning events; the total duration (60.1 h) of these gleaning events corresponded to approximately 4% of the lutung observation time. Deer consumed 39 items dropped by lutungs; these items belonged to 28 plant species and included leaves, fruits, and flowers. Gleaning events occurred more frequently during months when rainfall was low and few herbaceous plants grew in grassland patches. Gleaned foods were significantly heavier than non-gleaned foods. Our findings imply that the lutung–deer association is beneficial to deer, by improving nutritional condition during seasons with low food resources.

Key words: feeding association, Indonesia, nutritional analysis, Pangandaran, primates, *Rusa timorensis, Trachypithecus auratus*, ungulates

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Animal species belonging to different taxa sometimes form multi-species associations (Stensland et al. 2003; Anderwald et al. 2011). Multi-taxon groups can serve several purposes such as predator defense and improved access to resources (Diamond 1981). For example, coyotes (Canis latrans) and badgers (Taxidea taxus) increase their feeding efficiency by cooperating when they search for ground squirrels; this association improves the hunting success of both species (Minta et al. 1992). Aardwolfs (Proteles cristata) are able to capture ants and termites by forming associations with aardvarks (Orycteropus afer), which excavate ant and termite mounds with their strong claws (Taylor and Skinner 2000). In marine systems, seabirds, cetaceans, and sea lions catch fish more efficiently by preying in groups (Bräger 1998; Bearzi 2006; Anderwald et al. 2011).

Gleaning behavior is a type of food-related association formed worldwide between primates and terrestrial mammals; in this association, the primates drop plant items that the terrestrial mammals subsequently consume (Newton 1989). Gleaning behavior has been reported between baboons (Papio spp.) and bushbuck (Tragelaphus scriptus) or impala (Aepyceros melampus) in Africa (Morgan-Davies 1960; Elder and Elder 1970); common langurs (Semnopithecus entellus) and axis deer (Axis axis—Newton 1989; Ramesh et al. 2012), and Japanese macaques (Macaca fuscata) and sika deer (Cervus
nippon—Majolo and Ventura 2004; Tsuji et al. 2007) in Asia; and howler monkeys (Alouatta seniculus) and white-tailed deer (Odocoileus virginianus) or collared peccaries (Tayassu tajacu) in South America (Robinson and Eisenberg 1985; Agoramoorthy 1997). All these associations are considered to be beneficial only for the ungulates (i.e., commensalism) through predator avoidance and increased foraging success (Majolo and Ventura 2004; Tsuji 2008). In the present study, we evaluated whether such primate–ungulate relationships are truly beneficial to the ungulates.

Newton (1989) and Majolo and Ventura (2004) postulated that plant items dropped by monkeys were attractive and beneficial for deer, because gleaning occurred more frequently than expected for the density; moreover, deer beneath trees frequently competed for leaves dropped by monkeys. This type of episodic behavioral information is important; however, it does not provide the quantitative data required to confirm the benefits of gleaning. To address the adaptive meaning of gleaning, it is necessary to observe ungulates over an entire day and to evaluate the relative contribution of dietary items dropped by primates to the foraging success of ungulates in terms of energy intake. In instances where behavioral observation of ungulates is impractical, it is important to describe the circumstances under which frequent gleaning occurs (Boinski...
and Scott 1988; Tsuji et al. 2007) and to verify whether the nutritional value and availability of gleaned foods is higher than that of non-gleaned foods (Tsuji et al. 2007).

The availability and phenology of tropical plants show clear seasonality (Lieberman 1982; Hanya et al. 2013). Therefore, the gleaning association formed between primates and ungulates in tropical regions is likely to display seasonal variation in terms of the frequency, duration, and number of participants. In the present study, we observed a gleaning association between wild Javan lutungs (Trachypithecus auratus) and rusa deer (Rusa timorensis) in the Pangandaran Nature Reserve, western Java, Indonesia. We hypothesized that feeding behavior of deer should be sensitive to its current nutritional state and food abundance, and gleaning association with lutungs is beneficial to them in food-scarce seasons, being in poor nutritional state. Based on that overarching hypothesis, we tested 3 predictions: 1) frequency and duration of gleaning events and number of deer participating in these gleaning events become greater when normal foods of deer are abundant, 2) gleaned foods have higher nutritional values than staple foods consumed by deer, 3) nutritional condition of the deer participating in gleaning is related to abundance of their normal foods.

**MATERIALS AND METHODS**
Study area.—The Pangandaran Nature Reserve is located on the southern coast of west Java, Indonesia (latitude 7°43’S; longitude 108°40’E—Sumardja and Kartawinata 1977; Tsuji et al. 2013). Average elevation is approximately 100 m above sea level (Mitani et al. 2009). The reserve is divided into 2 sections, namely, a 38-ha forest park and a 370-ha nature reserve (Mitani et al. 2009; Tsuji et al. 2015). Between 2005 and 2013, average annual rainfall was 3,272 mm (AccuWeather.com 2015, http://www.accuweather.com (accessed: 14 Jan 2015)). Average annual air temperature (25–30°C) and humidity (85–95%) in the region were relatively stable (Brotoisworo 1991; Kool 1993). We divided a typical year into 2 seasons, namely, a rainy season that lasts from October to March and a dry season that occurs between April and September (Brotoisworo 1991). The main vegetation in the forest park consists of Tectona grandis, Swietenia macrophylla, Vitex pubescens, Cratoxylum formosum, and Dillenia excelsa (Sumardja and Kartawinata 1977; Tsuji et al. 2015). Several grassland patches occur (Sumardja and Kartawinata 1977; Tsuji et al. 2015); within these grassland patches, the main dietary items of deer, including herbaceous plants and shrub species (de Garin-Wichetitsky et al. 2005; Kangiras 2009), are abundant. Vegetation along the forest path (5 m wide) differs from that found elsewhere in the forest park because of
Study subjects.—Six groups of Javan lutungs inhabit the forest park. In this study, we observed 3 lutung groups inhabiting the northeastern part of the forest (approximately 13 ha). Lutungs in the Pangandaran Nature Reserve feed mainly on young leaves, fruits, and flowers (Brotoisworo 1991; Kool 1993). They typically prefer the leaf petiole and drop remaining leaf parts from trees while feeding (Kool 1993). Lutungs consume whole fruits and flowers, but sometimes accidentally drop these food items on the ground (Y. Tsuji pers. obs.).

We believe that in June 2013, 68–78 deer inhabited the forest park (Bambang Prayitno, Natural Resources Conservation Center, Ciamis, Java West, pers. comm., Dec 2014). Deer in the Pangandaran Nature Reserve mainly feed on the leaves and stems of herbaceous plants, and feed supplementarily on the leaves and fruits of shrub species (Kangiras 2009). Deer in the forest park are habituated to tourists, and therefore close observation (at a distance of < 15 m) was possible. With the exception of feral dogs and raptors (Tsuji et al. 2014), no predators of lutungs or deer were present.

Observation of gleaning.—Between 2011 and 2013, we conducted 5 intermittent field surveys; during each of these surveys, we observed the 3 selected lutung groups
from dawn until dusk (observation time 1,568 h). We recorded 248 gleaning events. We
defined the start of a gleaning event as the time when deer began to feed on plant items
dropped by lutungs feeding in a particular tree. During each gleaning event, we
recorded all the food items consumed by deer. We independently recorded multiple
items consumed during a single gleaning event. In addition, we recorded the number of
deer beneath the tree crown every 10 min to obtain the maximum number of deer during
a given gleaning event. We defined the end of a given gleaning event as the time when
the deer stopped feeding and the last animal had left the feeding tree. For 198 gleaning
events, we calculated the duration of the gleaning event (min) by subtracting the start
time from end time. We were unable to calculate the duration of the remaining 50
gleaning events, because we failed to observe the start or the end times of these events.
Hence, we may have under- (or over-) estimated the average duration of the gleaning
events. We obtained the total duration of 198 gleaning events by summing the duration
of each event.

To obtain group size of deer during non-gleaning periods, we recorded the number
of deer observed per group as we walked along the forest path once per month during
our study seasons (August, November, and December 2011; April, October, November,
and December 2012; and September, October, and November 2013) and recorded the
sizes of 146 groups. We did not consider the age–sex class of deer since the effect of
group composition on gleaning is not a focus of this study. All the research methods
used in this study complied with the guidelines of the American Society of
Mammalogists (Sikes et al. 2011) and adhered to Indonesian legal requirements
(research permission no: RISTEK 207/SIP/FRP/SM/VI/2013).

Food quality and quantity.—In order to quantify abundance of typical food items of
deer (non-gleaning foods), we conducted plant sampling. We selected 3 sampling sites
in the study area (inter-site distance of > 200 m) and collected non-gleaned foods in
these sites. At each sampling site, we randomly selected 6 quadrats in each of the 3
vegetation types (forest, forest edge, and grassland); within each quadrat, we cut the
aboveground parts of herbaceous plants and shrubs (3 sites \( \times \) 3 vegetation types \( \times \) 6
quadrats = 54 quadrats). The size of each quadrat was as follows: forest, 50 cm \( \times \) 50 cm;
forest edge, 20 cm \( \times \) 20 cm; and grassland, 10 cm \( \times \) 10 cm. We conducted the plant
sampling 9 times (August and October 2011; April, October, and December 2012; June,
August, October, and December 2013).

To evaluate the nutritional contents of consumed food items, we collected gleaned
foods (36 items from 27 plant species) and non-gleaned foods (22 items from 21 plant
species previously recorded as deer dietary food items; Appendix I—Kangiras 2009).
We dried and weighed these food items and estimated the amount of non-gleaned foods per unit area (to the nearest 0.1 g). For each food item \( (i) \), we analyzed the following nutritional characteristics on a dry weight basis: 1) % neutral detergent fiber (NDF); 2) % crude protein (CP); 3) % crude lipid (CL); and 4) % crude ash (CA). In each instance, we conducted duplicate analyses and calculated the average values. In addition, we calculated gross energy content \( (GE_i; \text{kcal} \cdot \text{g}^{-1}) \) by summing the carbohydrate content, which was calculated as follows: 
\[
[100 - (\% CP_i + \% CL_i + \% CA_i)] \text{ at } 0.0415 \text{kcal} \cdot \text{g}^{-1}; \%
\]
\[
\% CP \text{ at } 0.0565 \text{kcal} \cdot \text{g}^{-1}; \% \text{ CL at } 0.0940 \text{kcal} \cdot \text{g}^{-1—Maynard et al. 1979; Tsuji et al. 2008}.\n\]

_Evaluation of deer nutritional condition._—To evaluate nutritional condition of deer, we used the physical condition index (Riney 1960). For each deer group, we photographed the nearest individual to observers that was standing upright and relaxed in a normal posture, by using a digital SLR camera (EOS Kiss Digital E5; Canon, Tokyo, Japan). We categorized physical condition of deer into 5 levels, from “1” (lean) to “5” (fat), according to the degree of apparent fat accumulation at 5 checkpoints (Riney 1960). To sample randomly and avoid multiple data sampling from the same individuals, we photographed deer at different places throughout the study area.
Statistics analyses.—We used chi-square tests of independence to evaluate monthly changes in gleaning frequency and frequency of animals with a nutritional condition score of “5.” We applied the 2-sample Kolmogorov–Smirnov test to assess differences in group size of deer between gleaning and non-gleaning periods. We conducted Spearman’s rank correlation analyses to test the relationship between monthly rainfall (AccuWeather.com 2015, http://www.accuweather.com (accessed: 14 Jan 2015)) and amount of non-gleaned foods in forest, forest edge, and grassland. We applied the Kruskal–Wallis test to evaluate seasonal changes in 1) amount of non-gleaned foods for each of the three vegetation types, 2) mean duration of gleaning events, and 3) maximum number of deer. We conducted post-hoc analyses using the Steel–Dwass test (Zar 1999).

We used generalized linear models (GLMs) to evaluate effects of monthly rainfall and amount of non-gleaned foods on 1) the frequency of gleaning events (error structure, negative binomial; offset term, observation time); 2) duration of a single gleaning event (error structure, gamma); 3) mean maximum number of deer during a gleaning event (error structure, gamma); and 4) nutritional condition of deer (error structure, negative binomial; offset term, total number of animals with scored nutritional conditions).
Finally, we employed Mann-Whitney $U$-tests to compare the nutritional composition of gleaned and non-gleaned foods. In each statistical test, we set $\alpha$ at 0.05.

**RESULTS**

We observed 248 gleaning events during 1,568 h of observation (0.16 times per hour) and we recorded 251 items consumed by deer (Table 1). Rusa deer fed on 39 items belonging to 28 plant species; these items mainly comprised the leaves of *Swietenia macrophylla*, the flowers and fruits of *Pterospermum javanicum*, and the leaves of *Kleinhovia hospita* (Table 1). The food consumed during gleaning events comprised leaves (55.4%), fruits (28.7%), and flowers (15.9%; Table 1). The gleaning frequency varied seasonally; it occurred more frequently in August and less frequently in November and December (chi-square test: $\chi^2_{14} = 90.4$, $P < 0.001$; Fig. 1). The maximum number of deer observed beneath a tree during a gleaning event ranged from 1 to 15 (median = 2; $n = 248$; Fig. 2) and the group size did not differ from that recorded in non-gleaning periods (range = 1–18; median = 2; $n = 146$; 2-sample Kolmogorov–Smirnov test: $\chi^2_2 = 3.3$, $P = 0.388$). Group size of deer in a gleaning event did not differ between months (Kruskal–Wallis test: $\chi^2_{14} = 7.5$, $P = 0.912$), and duration of a single gleaning event ranged from 1 to 87 min (median = 10; $n = 198$; Fig. 3). Total duration of 198 gleaning events was 60.1 h, which corresponded to 3.8% of lutung...
observation time (1,568 h). Duration of gleaning did not differ between months

(Kruskal–Wallis test: $\chi^2_{14} = 22.4, P = 0.071$).

The amount of non-gleaned foods within quadrats varied seasonally for each

vegetation type (Kruskal–Wallis test: grassland: $\chi^2_8 = 58.7, P < 0.001$; forest edge: $\chi^2_8 = 44.7, P < 0.001$; forest: $\chi^2_8 = 45.6, P < 0.001$). Further, the results of post-hoc analysis revealed a greater amount of non-gleaned foods in the grassland during December 2012 and December 2013, and a greater amount of non-gleaned foods along the forest edge during August 2011 and December 2013 than in other study months (Fig. 4; Steel–Dwass tests, $P < 0.05$). There was no correlation between monthly rainfall and amount of non-gleaned foods in any of the 3 vegetation types (Spearman’s rank correlation test: grassland: $r_s = 0.517, d.f. = 13, P = 0.162$; forest edge: $r_s = 0.200, d.f. = 13, P = 0.613$; forest: $r_s = 0.000, d.f. = 13, P = 1.000$).

Frequency of gleaning events was greater during months with lower rainfall (GLM: $z_{13} = -2.755, P = 0.006$) and during months with lower amounts of non-gleaned foods in grassland (GLM: $z_7 = -2.687, P = 0.007$), while not during months with lower amount of non-gleaned food in the forest (GLM: $z_7 = -0.766, P = 0.444$) or along the forest edge (GLM: $z_7 = -0.426, P = 0.670$). Deer group size was not related to monthly rainfall (GLM: $t_{12} = 1.389, P = 0.190$) or to the amount of non-gleaned foods (GLM:
grassland: $t_7 = 1.492, P = 0.179$; forest edge: $t_7 = 1.155, P = 0.286$; forest: $t_7 = 0.593, P = 0.572$). Mean duration of gleaning was not related to monthly rainfall (GLM: $t_{12} = 0.911, P = 0.380$) or the amount of non-gleaned foods (GLM: grassland: $t_7 = 0.435, P = 0.677$; forest edge: $t_7 = −0.890, P = 0.403$; forest: $t_7 = −0.644, P = 0.540$).

The % CL, % CA, % NDF, % CP, and GE did not differ between gleaned foods ($n = 36$) and non-gleaned foods ($n = 22$; Mann-Whitney $U$-tests: % CL: $U = 392.5, P = 0.962$; % CA: $U = 407.5, P = 0.860$; % NDF: $U = 401.0, P = 0.943$; % CP: $U = 309.5, P = 0.168$; GE: $U = 407.5, P = 0.856$). Dry mass of the gleaned foods (1.06 ± 1.03 g), however, was significantly greater than that of non-gleaned foods (0.69 ± 0.40 g; Mann-Whitney $U$-test: $U = 549.0, P = 0.014$) (Table 2).

Nutritional condition of deer varied seasonally (Fig. 5). In particular, the percentage of deer with a nutritional score of “5” (i.e., fat) differed between months (chi-square test: $\chi^2_{14} = 146.9, P < 0.001$). Deer had high nutritional scores during months when the amount of non-gleaned foods in the grassland was low (GLM: $z_{13} = −2.148, P = 0.032$); the nutritional score did not differ significantly according to monthly rainfall ($z_7 = −1.780, P = 0.075$) or the amount of non-gleaned foods along the forest edge ($z_{13} = 0.518, P = 0.640$) and in the forest ($z_{13} = −1.556, P = 0.120$).

**DISCUSSION**
We observed that rusa deer in the Pangandaran Nature Reserve fed on leaves, fruits, and flowers dropped by sympatric Javan lutungs. Leaves comprised > 50% of the gleaned foods and seemed to be an important food source for deer. Leaves are found in the tree crown above the ground (> 10 m in height—Tsuji et al. 2015), and therefore deer are unable to access these food items on their own. While feeding on leaves, lutungs individually remove plant parts from the branches. After consuming the petiole, lutungs drop most of the leaves (Kool 1993); further, they accidentally drop flowers and fruits during feeding. From the perspective of the deer, this “wasteful” (Morgan-Davies 1960; Senzota 1983) feeding strategy and larger dry mass of gleaned foods contribute to increased amounts of food on the forest floor. We did not calculate the amount of dropped foods; however, a troop of 20 common langurs dropped approximately 1.5 tons of foliage annually, of which 0.8 tons provided suitable forage for axis deer (Axis axis—Newton 2001). Therefore, we expect the leaves, fruits, and flowers dropped beneath the trees by lutungs could provide a substantial food source for deer.

The frequency of gleaning in the PNR (0.12 times per h) corresponded to approximately 4% of the time we observed lutungs. High gleaning frequency in this area was likely related to the high population density of both lutungs and deer in this nature reserve (370 lutungs per km² and 180 deer per km², respectively). In addition,
lutungs and rusa deer predominantly inhabit small home ranges (5–10 ha for each group—Kool and Croft 1992; Kangiras 2009).

Gleaning events by deer did not occur evenly throughout the year; frequency of gleaning events was greater during months with lower rainfall and reduced availability of non-gleaned foods in grassland, which was a main feeding site of deer (Kangiras 2009). In contrast, the amount of food in the forest and along the forest edge did not influence the frequency of gleaning events. Other deer species were reported to increase their browsing in forested habitats when the availability (and nutritious quality) of herbs decreased (Asada and Ochiai 1996; Marshall et al. 2004), which implies that the forest (including the forest edge) is an alternative feeding site for deer. On the basis of the high population density of deer in the forest park, intraspecific competition for food was likely severe. Hence, we believe gleaning behavior during the dry season was a behavioral response to shortage of food at typical feeding sites.

Contrary to our prediction, the nutritional condition score of deer was higher in the dry season than in the rainy season. A plausible reason for higher nutritional condition during the dry season is a function of a lag effect of the accumulation of body reserves during the wet season, as reported in mule deer (*Odocoileus hemionus*—Monteith et al. 2013); the deer would have begun the dry season at their highest fat levels. The size of a
deer group during a gleaning event did not differ from that recorded in non-gleaning periods. This finding implies that deer gather beneath trees opportunistically.

Alternatively, the considerable variation in the body condition of deer inhabiting the Pangandaran Nature Reserve indicates that these deer may be at risk from starvation, and therefore food items dropped by lutungs may be beneficial (i.e., gleaned food items represent “bonus food” for these deer).

To date, few investigations of primate–ungulate relationships have evaluated the benefits of these associations (Tsuji 2008; Heymann and Hsia 2014). In the present study, we showed that food availability influenced some gleaning characteristics. Our data suggest that the feeding association between lutungs and deer is an important behavioral traits to overcome seasonal limitations in food abundance in high density populations of deer. Future studies should address the manner in which primate–ungulate associations contribute to foraging and reproductive success in deer, by combining behavioral observations of deer with dietary nutritional analyses.

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FIGURE LEGENDS

FIG 1.—Seasonal changes in gleaning frequency (times per h) observed during the study period. The numbers above each month denote the observation year.

FIG 2.—Distribution of deer group size during gleaning events (filled bars, \( n = 248 \)) and non-gleaning periods (open bars, \( n = 146 \)).

FIG 3.—Distribution of the duration of a single gleaning event (\( n = 198 \)).

FIG 4.—Seasonal changes in the abundance of non-gleaned foods (g/m²) in a) grassland, b) forest edge, and c) forest. Horizontal bars represent significant differences (post-hoc tests, \( P < 0.05 \)). The numbers above each month denote the observation year.

FIG 5.—Seasonal changes in deer nutritional condition scores [ranging from “1” (lean) to “5” (fat)]. The numbers above each month denote the observation year.
### TABLE 1.


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TABLE 2.—U- and P-values (Mann-Whitney U-test) of comparisons of nutritional compositions between the gleaned foods and the non-gleaned foods of rusa deer in Pangandaran Nature Reserve, West Java, Indonesia. DM: dry mass of feeding unit, %NDF: neutral detergent fiber content, %CP: crude protein content, %CL: crude lipid content, %CA: crude ash content, GE: gross energy. *: P < 0.05.

<table>
<thead>
<tr>
<th>Nutritional fraction</th>
<th>Gleaned foods (n = 36)</th>
<th>Non-gleaned foods (n = 22)</th>
<th>U</th>
<th>P</th>
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<tr>
<td>DM</td>
<td>1.063 ± 1.034</td>
<td>0.692 ± 0.400</td>
<td>549.0</td>
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<tr>
<td>%NDF</td>
<td>66.58 ± 0.37</td>
<td>65.28 ± 3.10</td>
<td>401.0</td>
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<td>%CP</td>
<td>9.81 ± 0.26</td>
<td>11.62 ± 0.32</td>
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<td>%CL</td>
<td>1.39 ± 0.14</td>
<td>2.03 ± 0.16</td>
<td>392.5</td>
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<td>%CA</td>
<td>6.53 ± 0.27</td>
<td>7.71 ± 0.20</td>
<td>315.5</td>
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<td>GE (kcal·g⁻¹)</td>
<td>4.10 ± 0.20</td>
<td>4.11 ± 0.30</td>
<td>407.5</td>
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