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## Selection of the young coconut mesocarp by the Sulawesi babirusa (*Babyrusa celebensis*)

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**Abstract.** The feeding behaviours of the Sulawesi babirusa (*Babyrusa celebensis*) in terms of its preference to eat the mesocarp, or husk, of immature coconuts (*Cocos nucifera*) and the feeding marks on leftover coconuts were observed. Additionally, to explore the physicochemical factors behind this preference, a comparative study was conducted on the basal and apical parts of the coconut mesocarp. The breaking load, macronutrient content, and volatile compounds were examined. The findings were as follows: 1) Babirusas always sniffed the cut surface of the coconut before eating. They then scooped out the basal part of the mesocarp where the fibres are more visibly scarce with their mandibular incisors and ate more than 7.6 times the surface area at this end than at the apical end. 2) The preferred basal part of the immature mesocarp had a lower breaking load. 3) The gas chromatography-mass spectrophotometry (GC-MS) chromatogram of the basal sample showed larger peak areas for 2-methylbutanal and 3-methylbutanal. In conclusion, the babirusa preferred the basal part of the immature coconut mesocarp, and the preferred basal part had distinctive features in terms of hardness and volatile profile, which is probably characterised by the presence of 2-methylbutanal and 3-methylbutanal.

**Key words:** breaking load, food preference, volatile compound, wild pig, young coconut husk.

The babirusa (genus *Babyrusa*) is a wild pig endemic to Sulawesi and the neighbouring islands of Indonesia (Macdonald 1993, 2017). These animals primarily inhabit tropical rainforest on the banks of rivers and ponds and low-lying areas near coasts (Leus et al. 2016; Macdonald et al. 2016; Macdonald and Pattikawa 2017). Along the coastal areas and interior water courses of Indonesia, coconut palms (*Cocos nucifera*) are widely distributed. Historically, they have been planted by small-scale farmers for copra production.

In the Togian Archipelago of Central Sulawesi, some of the babirusa's range of distribution extends into agricultural areas including coconut groves. As a consequence, babirusas have come into conflict with the local Muslim farmers, particularly in vegetable gardens

(Ito et al. 2005; Akbar et al. 2007; Ito et al. 2008). At the same time, the population trend of babirusas on the Togian islands is decreasing due to forest clearance and forest fires, illegal hunting, and predation by dogs (Macdonald et al. 2016; Ito and Melletti 2017).

A questionnaire conducted in 2007 revealed that local farmers' knowledge of the feeding habits and reproduction of the babirusa was limited (Ito et al. 2008; Ito and Melletti 2017). Although some babirusas have been observed to forage in coconut groves (Akbar et al. 2007; Meijaard et al. 2011), it remains unclear which growth stage or part of coconut fruits were consumed and how the animals ate the coconuts. Some local farmers believe that animals can crack open intact mature coconuts to eat the kernel. Others have expressed excessive fear and

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aversion towards the animals. To overcome these negative beliefs, it is necessary to clear the misconceptions surrounding the ecology of babirusas (Ito et al. 2008; Indonesian Ministry of Forestry 2013; Ito and Melletti 2017). For this purpose, it is important to generate greater knowledge of the feeding habits of babirusas in the cultivated areas.

Our recent investigation of the animal's response to coconut palm trees and intact whole coconuts revealed 1) that babirusas are able to crack open fallen immature coconut fruits and 2) that as coconut fruits develop, animals spend more time attempting to open fruits but largely fail to crack the mature coconuts used as raw material in copra production. In addition, we reported the possibility that babirusas eat fallen staminate flowers, broken pieces of coconut kernel, and haustorium scattered over coconut groves as wastes after copra production (Ito et al. 2020).

During behavioural observations (Ito et al. 2020), we noticed that babirusas tended to eat the basal part of the mesocarp of young coconuts that had not yet formed solid endosperm or kernels. Thus, we questioned 1) whether the babirusa's selection of the basal part of the young coconut mesocarp is opportunistic, and if not, 2) whether there are differences between the basal part and other parts of the young mesocarp perceived by the babirusa.

Hence, the objectives of this study were 1) to better understand the babirusa's feeding behaviour based on direct observation and video analysis, in particular the apparent preference for the basal part of young coconut mesocarp by the comparison of the size of feeding marks on the basal and apical ends, and 2) to explore the potential physicochemical factors influencing the preference for the basal coconut mesocarp by measuring the breaking load or hardness and performing nutritional and gas chromatography-mass spectrophotometry (GC-MS) analyses.

## Materials and methods

### *Study site and period*

The observations of the feeding behaviour and experiments were carried out at the Bali Zoo in Singapadu Village, Bali, Indonesia. These were intermittently conducted for a total of 36 days between 26 August 2017 and 30 August 2018.

### *Animals, enclosure and husbandry*

Two female zoo-based Sulawesi babirusas (*B.*

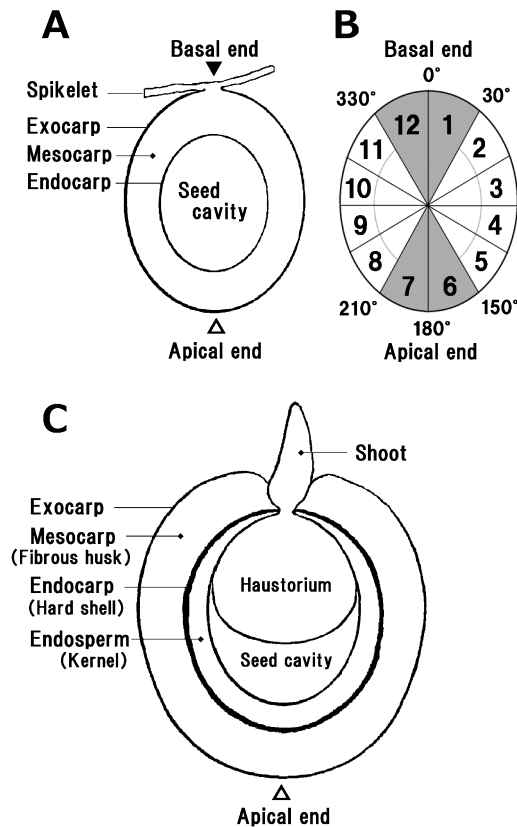
*celebensis*), 13 and 14 years of age at the onset of observations, were observed in this study. Both animals had been familiar with coconut palm trees and their fruits since they were one year old (Ito et al. 2019a, 2019b, 2020). They were kept in a 100 m<sup>2</sup> enclosure with a ground surface of hard soil and gravel. Two simple shelters, a water pool and mud wallow, were provided for the animals. In the centre of the enclosure, a coconut palm tree provided shade. During the study period, animal handling was kept to a minimum. Keepers fed the animals twice a day in the morning and late afternoon, with additional tree leaf fodder given at mid-day.

### *Plant material*

A total of 147 fresh immature coconut fruits were obtained from a local coconut grove. Of these, 29 coconuts were used for an initial test of feeding behaviour. The next 111 coconuts were used to identify and compare the feeding marks of babirusas. The remaining seven coconuts, weighing 1.0 kg each, were delivered to laboratories within three days of harvesting for physicochemical analyses. Of these seven coconuts, three were used for the breaking load measurement, three for the nutrition analyses, and one for the GC-MS analysis. The coconuts used in this study consisted of seeds and three layers: a thin smooth exocarp (outermost layer), a thick fleshy mesocarp (middle layer), and a thin, soft endocarp (inner layer surrounding the seed). The basal part of the mesocarp was mainly composed of non-fibrous parenchyma tissue, whereas the apical part was composed of still visibly young fibres embedded in the parenchyma. These coconuts had not yet formed kernels in the seeds (Fig. 1A). In morphological term, the coconut surface attached to the spikelet (branch of the inflorescence) was designated as the basal end, and the opposite end was designated as the apical end.

### *Plant tissue sampling*

Tissue sampling for the nutritional analysis and GC-MS analysis was conducted as follows: First, the whole coconut was split with a stainless-steel knife into a basal half and an apical half. This was to avoid the cross-contamination of the two distinct samples taken from the same mesocarp layer. Second, the exocarp and endocarp layers were completely removed from each half. Third, a sample was cut out of each end of the mesocarp. These were immediately placed in individual containers, sealed and kept frozen at -20°C until analysis.



**Fig. 1.** Diagram of the longitudinal sections of coconut fruits, modified from Ito et al. (2020). A: Immature coconut fruit. The basal end is attached to the coconut palm via a spikelet. B: Twelve radial partitions on the split coconut halves to determine the position and total surface area of feeding marks. The shaded areas indicate the target of the evaluation. C: Mature (germinating) coconut fruit.

### Behavioural observations

Twenty-nine young coconuts with a mean weight of 996 g ( $SD = 200.4$ , range: 530 g to 1310 g) were cut longitudinally from the basal end to the apical end with a stainless-steel knife. An average of 4.5 coconut halves ( $SD = 1.5$ ) per day were placed on the ground in the shade of the palm tree for the babirusas at the time of the morning feeding. For 13 days, between 26 August 2017 and 19 April 2018, the animals' feeding behaviour and responses to the split coconut halves, such as sniffing, manipulating with snout or forelimbs, and biting or scooping with teeth, were observed from the moment of approach until leaving. These behaviours were also video-recorded from outside the enclosure. The total video-recording time was about 1 h 15 min.

### Feeding mark sampling

To determine the position and surface area ( $\text{mm}^2$ ) of the coconut parts eaten by the babirusas, a feeding exper-

iment was conducted for 23 days between 26 July 2018 and 30 August 2018. A total of 111 young coconuts with a mean size of 13.2 cm ( $SD = 1.1$ )  $\times$  11.0 cm ( $SD = 0.9$ ) and mean weight of 839 g ( $SD = 172.3$ , range: 520 g to 1280 g) were prepared for the experiment. The coconuts were cut longitudinally. One split half was used as a test food, and the other half was kept untouched as a reference. An average of 4.8 coconut halves ( $SD = 1.4$ ) per day were placed on the ground at the time of the morning feeding at approximately one metre intervals. Once the feeding was over, the leftovers were immediately collected and gently rinsed with running water. The surface with feeding marks was then photographed together with the reference half.

### Gypsum moulding of feeding marks

In the photographs of the leftover coconuts, the boundaries between the parts eaten and uneaten were too uncertain to accurately evaluate the position and surface area of the eaten parts, even though the eaten areas tended to turn dark brown in colour. In addition, the parts that had been fed on shrank unevenly over time due to the natural dryness of the enclosure. To overcome these complications and obtain better three-dimensional evidence, the internal surface structure of 106 pairs of the coconut halves (sample nos. 1 to 106) with feeding marks were moulded with plaster (Gypsum casting, Aplus Pacific, Indonesia) within two hours of being fed on. The remaining five pairs of halves (sample nos. 107 to 111) were immersed in ethanol to preserve them. Prior to the moulding process, a piece of duct tape was placed around the lateral edge of the cut surface of each halved coconut to accommodate the moulding material. Then, a gypsum slurry was prepared in accordance with the manufacturer's instructions and poured into the chamber. After solidification, the plant tissue was removed to expose the gypsum impression. The surfaces of all impressions of the feeding marks were then photographed again under the same conditions.

### Image analysis

The position and surface area ( $\text{mm}^2$ ) of the feeding marks on the photographs of the gypsum impressions were assessed using ImageJ software (ImageJ, v1.51j8, National Institutes of Health, USA). Based on the preliminary observational finding that babirusas tended to eat from the middle of the seed cavity towards the peripheral edge, a polar grid was superimposed on each photographed image to create 12 radial sections, each  $30^\circ$

(Fig. 1B). The pole of the grid was positioned at the centre of the coconut seed cavity. The polar axis ( $0^\circ$ ) was drawn vertically upwards from the pole to the basal end of the coconut, and the 12 radial sections were numbered clockwise, with the first section covering  $0^\circ$  to  $30^\circ$ . The total area covered by the feeding marks in each radial section of each test coconut was then measured. The basal area was defined as a symmetrical pair of sections, nos. 1 and 12, corresponding to the range between  $330^\circ$  and  $30^\circ$ , whereas the apical area was defined as the pair of sections on the opposite side, nos. 6 and 7, corresponding to the range between  $150^\circ$  and  $210^\circ$ . To determine significant differences in the mean total area ( $\text{mm}^2$ ) of the feeding marks between the basal area (section nos. 1 and 12) and apical area (nos. 6 and 7) of the same coconut halves ( $n = 106$ ), a paired sample *t*-test was conducted.

#### *Breaking load measurement*

To investigate whether there was a relationship between the hardness of the basal and apical parts of the mesocarp and the babirusas' feeding pattern, the breaking load (stress level sufficient to break a material in Newtons [N]) of the mesocarp layer was measured using a creep meter RE33005 (Yamaden, Tokyo, Japan) equipped with a brass plunger (Yamaden catalog No. 67, compress surface:  $1 \text{ mm} \times 5 \text{ mm}$ ). Of the seven coconuts prepared for physicochemical analyses, three coconuts were used. Each coconut was split in half longitudinally with a stainless-steel knife to create a total of six flat surfaces. Then, the spherical end of the split coconut halves was cut off parallel to the cut surface in order to flatly place the sample on the table of the creep meter. The axis of the compress surface of the plunger was positioned at a right angle to the longitudinal axis of the coconut sample above the centre of the targeted part. A single measurement was taken of the basal and apical parts of each flat surface at a constant speed of  $1 \text{ mm/s}$ . Welch's *t*-test was applied to compare the mean breaking loads (N) of the two parts of the coconut mesocarp.

#### *Nutritional analysis*

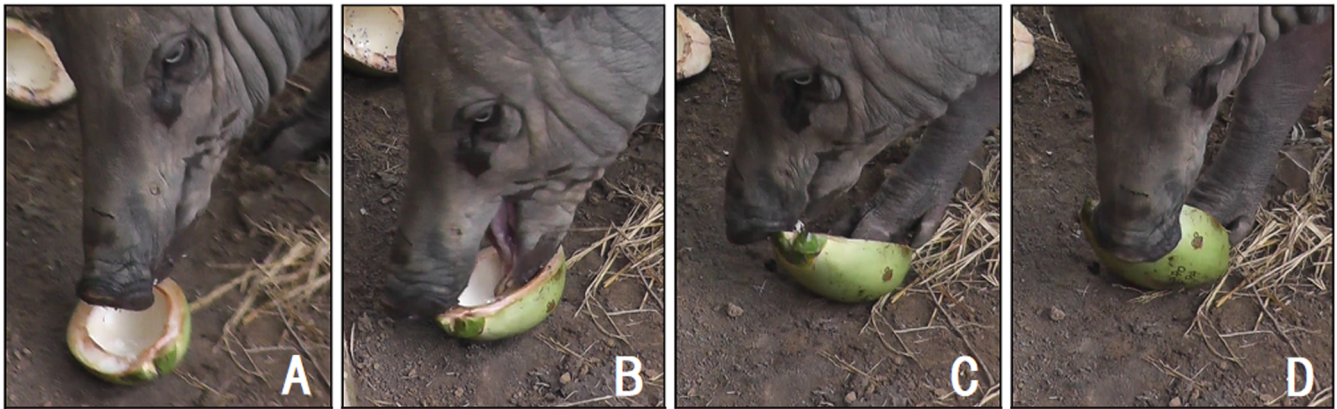
To investigate the potential nutritional differences between the basal and apical parts of the young mesocarp, the quantity of macronutrients in each part was determined by certified methods of nutritional analysis. A total of  $100 \text{ g}$  of pooled samples from three coconuts was analysed. The water content was determined by the ambient pressure drying method at  $135^\circ\text{C}$  for  $2 \text{ h}$ . The crude protein content was analysed by the Dumas com-

bustion method, multiplying the determined nitrogen content by a nitrogen-to-protein conversion factor of 6.25. The crude fat was determined by the Soxhlet extraction method using diethyl ether. The total quantity of reducing sugar was determined by the modified Somogyi method (Kobayashi and Tabuchi 1954) after acid hydrolysis of the tissue in a boiling water bath with 2.3% HCl for  $2.5 \text{ h}$ . The insoluble, soluble and total dietary fibre contents were determined using the enzymatic-gravimetric procedure (modified Prosky method; Prosky et al. 1988). The determination of the dietary fibre contents was performed three times, and those of the other nutritional components was performed twice. The means were used as the final values.

#### *GC-MS analysis*

To explore the potential chemical factors behind the babirusa's preference for the basal part of coconuts, the dynamic headspace GC-MS technique was employed to separate and identify volatile compounds in the basal and apical parts, and the volatile profiles were compared. The analysis was conducted with an Agilent 7890 GC coupled to an Agilent 5977A MSD (Agilent Technologies, Palo Alto, CA, USA) equipped with a GERSTEL MPS 2 auto sampler and GERSTEL TDU-CIS 4 injection system (GERSTEL, Mülheim an der Ruhr, Germany). Samples of both plant tissues were taken from the same mesocarp layer of one coconut fruit and thawed to a room temperature of  $24^\circ\text{C}$ . Then,  $2.5 \text{ g}$  of each tissue was placed in an individual  $10\text{-mL}$  vial. Based on the ambient temperature  $25^\circ\text{C}$  recorded during feeding at the Bali Zoo, the extraction temperature was set to the same  $25^\circ\text{C}$ . The following temperature programme for the TDU was used:  $30^\circ\text{C}$  was held for  $0.5 \text{ min}$  and then increased to  $250^\circ\text{C}$  at  $720^\circ\text{C/min}$  and held for  $5 \text{ min}$ . The temperature programme for the CIS was as follows:  $10^\circ\text{C}$  was held for  $0.5 \text{ min}$  and then increased to  $250^\circ\text{C}$  at  $720^\circ\text{C/min}$  and held for  $20 \text{ min}$ . The TDU was operated in the splitless mode. Separation was carried out on an Agilent DB-WAX UI column ( $60 \text{ m} \times 0.25 \text{ mm i.d.}$ ,  $0.25\text{-}\mu\text{m}$  film thickness; Agilent Technologies) with the following oven temperature programme:  $40^\circ\text{C}$  was held for  $3 \text{ min}$  and then increased to  $250^\circ\text{C}$  at  $5^\circ\text{C/min}$  and held for  $5 \text{ min}$ . Helium was used as the carrier gas at a constant flow rate at  $2.11 \text{ mL/min}$ . MS analysis was carried out by electron ionization at  $70 \text{ eV}$ . The ion source and quadrupole temperatures were set at  $230^\circ\text{C}$  and  $150^\circ\text{C}$ , respectively. The analytical conditions were identical for both samples. The major volatile components were identified





**Fig. 2.** Images of a female Sulawesi babirusa eating a longitudinally sectioned immature coconut from the basal side (taken from video). Whole coconut size and weight: 12.5 cm  $\times$  10.0 cm, 680 g. A: Sniffing the cut surface of the immature coconut. B: Onset of eating the inside of the immature coconut. Scooping the basal part of the coconut with her mandibular incisor teeth. C: Holding down the apical part with the hoof of her forelimb. D: Continuing to eat the basal part of the immature coconut.

by matching the mass spectra obtained with those in the NIST 14 Library (National Institute of Standards and Technology, Gaithersburg, MD, USA) (<http://webbook.nist.gov/chemistry/>). The quantitative differences between the two samples were then evaluated by comparing the peak areas of the chromatograms.

#### Statistical analyses

All analyses were carried out in R version 2.8.1 (R Development Core Team 2008), with  $P < 0.05$  indicating statistical significance.

## Results

#### Feeding behaviours

Independently of the size and weight of coconuts, the babirusas demonstrated the following pattern of feeding behaviour. Prior to the first bite, the animals examined the cut surface of the coconut half with their noses while wiggling both the right and left ends of the nasal disc on the snout without exception (100%, 58 of 58 halves; Fig. 2A). Then, they placed their mandibular incisor teeth on the internal surface of the seed cavity and scooped the immature endocarp and mesocarp layers towards the peripheral edge of the coconut half with their teeth (Fig. 2B). When the animals manipulated the coconut with their snout, or their teeth touched the surface, the split half would spin on the ground or begin to wobble. When this happened, they frequently held down one end of the split half with the hoof of their forelimb (Fig. 2C). The first few bites were almost always taken from the basal

side of the young mesocarp (87.9%, 51 of 58 halves; Fig. 2B–D). The babirusas appeared to consume more of the basal side of the young mesocarp layer (Figs. 2D and 3).

#### Position and surface size of feeding marks

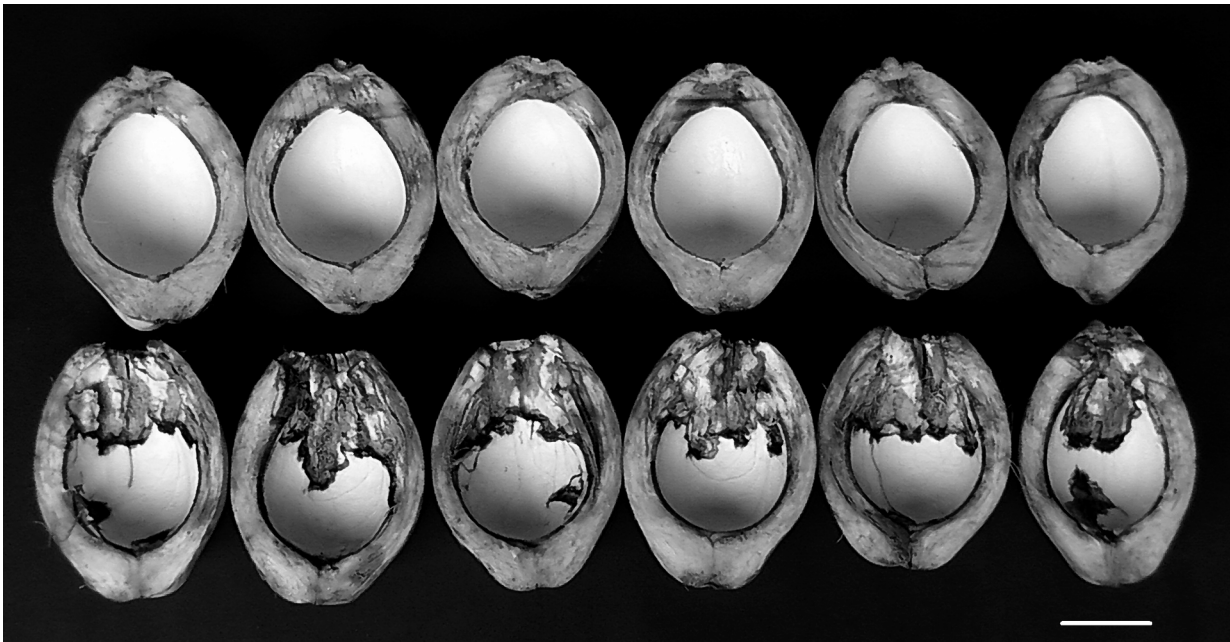
The mean total area ( $\text{mm}^2$ ) of the feeding marks in each radial section is shown in Table 1. The paired sample *t*-test indicated that there was a statistically significant difference between the eaten basal area (radial section nos. 1 and 12,  $M = 2034$ ,  $SD = 761$ ,  $n = 106$ ) and the corresponding area in the apical part (section nos. 6 and 7,  $M = 267$ ,  $SD = 338$ ,  $n = 106$ ;  $t [105] = 23.75$ ,  $P < 0.001$ ). On average, the eaten basal area was 7.6 times larger than the corresponding area in the apical part (Fig. 4). Even when the analysed sections were expanded to include section nos. 1, 2, 11, and 12 as the basal area ( $M = 2932$ ,  $SD = 1122$ ,  $n = 106$ ) vs. section nos. 5 to 8 as the apical area ( $M = 467$ ,  $SD = 579$ ,  $n = 106$ ), a significant difference was still detected (paired sample *t*-test,  $t [105] = 23.88$ ,  $P < 0.001$ ).

#### Hardness

As shown in Fig. 5, the apical part of the young mesocarp had a significantly higher breaking load ( $M = 43.8$ ,  $SD = 6.4$ ,  $n = 6$ ) than the basal part ( $M = 19.5$ ,  $SD = 2.5$ ,  $n = 6$ ; Welch's *t*-test,  $t [6.51] = 8.71$ ,  $P < 0.001$ ).

#### Nutritional content

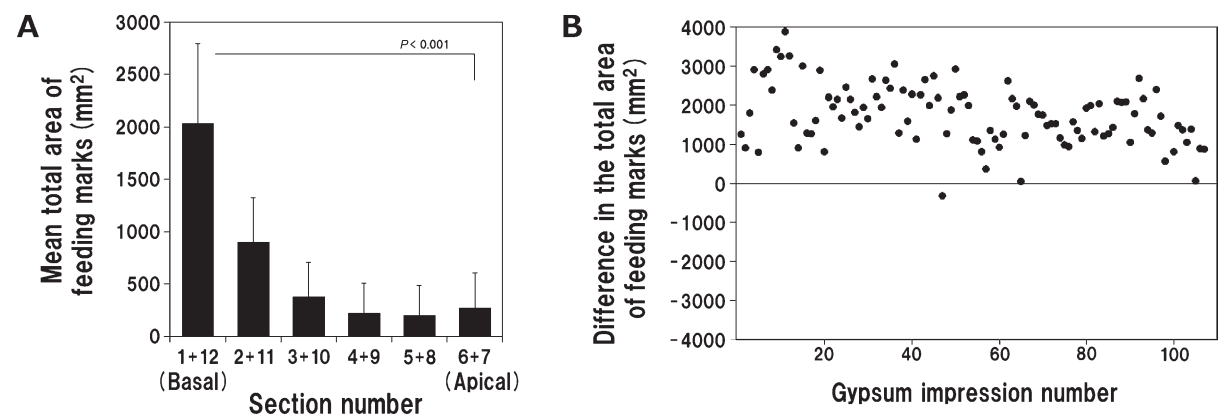
The results of the nutritional analysis are presented in Table 2.



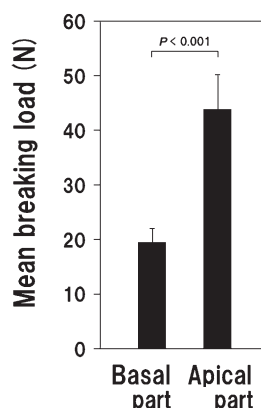
**Fig. 3.** The reference half of the coconut (upper row) and the leftover half of the test coconut with feeding marks (lower row). The basal end of the halves is directed upward. The feeding marks on the experimental halves are located on the basal side. Plant tissue crushed by teeth tends to quickly turn dark brown. From left to right: coconut nos. 49 to 54 with a whole coconut weight of 810 g, 790 g, 750 g, 740 g, 730 g, and 650 g, respectively. The scale bar indicates 5 cm.

**Table 1.** Mean and standard deviation (*SD*) of total area (mm<sup>2</sup>) of the feeding marks in the 12 radial partitions on the longitudinally cut surface of the young coconut fruits

	Radial section number											
	1	2	3	4	5	6	7	8	9	10	11	12
Mean	989	393	167	105	106	144	123	95	116	211	505	1045
<i>SD</i>	415	249	176	153	162	181	168	150	161	189	232	379



**Fig. 4.** Total surface areas of the feeding marks made by the Sulawesi babirusas on the split halves of young coconut fruits. A: Mean total area (mm<sup>2</sup>) of the feeding marks on six symmetrical pairs of young coconut fruits with radial partitions marked on the longitudinally cut surface (*n* = 106). Error bars indicate 1 *SD*. The total surface area of the feeding marks on the basal area (“1 + 12”) was significantly larger than that on the apical area (“6 + 7”; paired sample *t*-test, *P* < 0.001). B: Difference in the total area (mm<sup>2</sup>) of feeding marks on the basal and apical areas of young coconut fruits (*n* = 106). Numerical values on the Y axis are calculated as “the basal part minus the apical part”, and “0” on the Y axis means that the values of both areas are equal.

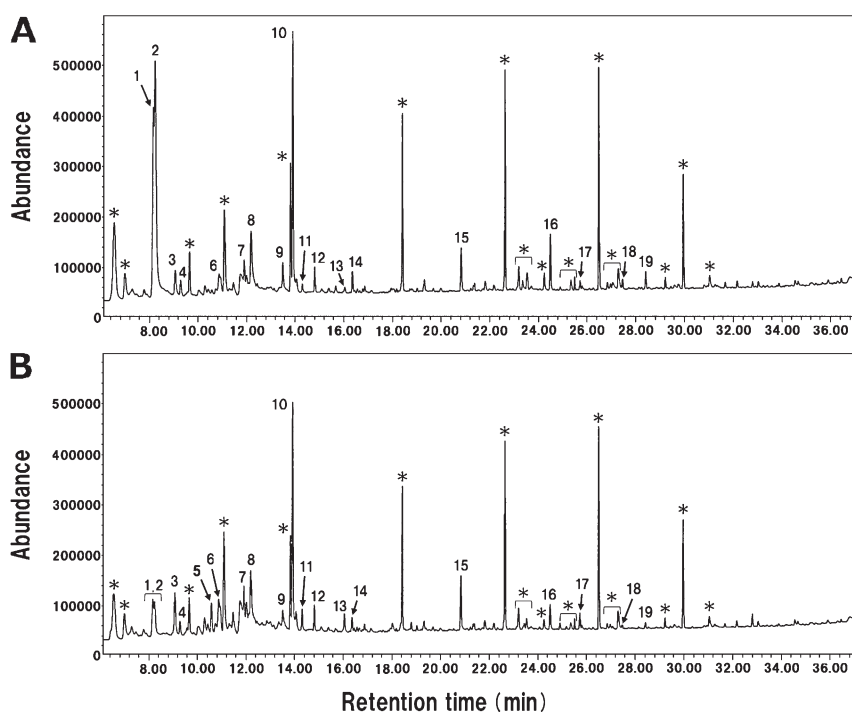


**Fig. 5.** Mean breaking load of the basal and apical parts of immature coconut mesocarp ( $n = 6$ ). Error bars indicate 1 *SD*. The breaking load of the basal part was significantly lower than that of the apical part (Welch's *t*-test,  $P < 0.001$ ).

**Table 2.** Nutritional content of the basal and apical parts of the immature coconut mesocarp

Nutrients	Content (g / 100 g)	
	Basal part	Apical part
Water	90.3	87.9
Crude protein	0.9	0.3
Crude fat	0.5	0.5
Total dietary fibre	5.4	7.3
Soluble fibre	0.6	< 0.5
Insoluble fibre	4.8	7.3
Total sugars*	3.1	5.1

\*: Total sugars gained from acid hydrolysis are expressed in terms of glucose equivalent.



**Fig. 6.** Total GC-MS chromatogram of the immature coconut mesocarp. A: The basal part of the immature mesocarp. B: The apical part of the immature mesocarp. Numbered peaks are identified in Table 3. Peaks marked with an asterisk (\*) are background peaks found in the blank runs.

### Volatile compounds

The total GC-MS chromatogram of the immature mesocarp samples revealed the presence of 19 main compounds, 14 of which were identified (Fig. 6; Table 3). The most dominant compound in the basal part of the mesocarp was 3-methylbutanal (peak 2, retention time: 8.23), and there was an eightfold difference relative to the

apical part (peak area value, 1013 vs. 123, respectively). Also, four times more 2-methylbutanal (peak 1, retention time: 8.15) was detected in the basal part than in the apical part (peak area value, 564 vs. 119, respectively). 1-Butanol (peak 10, retention time: 13.90) was recorded in both samples with a similar peak area (597 vs. 476).



**Table 3.** Volatile profiles of the basal and apical parts of the immature coconut mesocarp

Peak No.* <sup>1</sup>	Retention times (min)* <sup>1</sup>	Compound	Peak area values* <sup>2</sup>	
			Basal part	Apical part
1	8.15	2-Methylbutanal	564	119
2	8.23	3-Methylbutanal	1013	123
3	9.06	Aliphatic hydrocarbons	94	164
4	9.26	Unidentified	51	41
5	10.56	1-Penten-3-one	—	95
6	10.86	Aliphatic hydrocarbons	111	211
7	11.90	Butyl acetate	100	139
8	12.18	Hexanal	250	254
9	13.50	1-Methoxy-2-propanol	105	67
10	13.90	1-Butanol	597	476
11	14.29	1-Penten-3-ol	24	55
12	14.80	Unidentified	56	56
13	16.04	2-Hexenal	18	51
14	16.35	2-Pentylfuran	43	29
15	20.82	Nonanal	96	127
16	24.48	2-Nonenal	116	56
17	25.71	2,6-Nonadienal	16	31
18	27.45	2,4-Nonadienal	25	12
19	28.40	2,4-Nonadienal	39	15

\*1: Peak numbers and retention times correspond to labels in Fig. 6.

\*2: Peak area per gram of each sample measured ( $\times 10^4$ ).

The identity of peaks 4 and 12 could not be determined.

## Discussion

### *Food preference of babirusas*

Leus (1994, 1996) published an extensive list of potential food sources for babirusas in the wild, highlighting the importance of the fruits of fruit-bearing trees in their natural habitat. Babirusas have also been observed to consume leaves, roots, invertebrates, and animal matter with careful selection of food items (Leus et al. 1992; Leus and Vercammen 1996).

Interestingly, even if the coconut hemisphere wobbled and sometimes spun around on the ground, babirusas almost always began to eat the mesocarp from the basal side of the young coconuts (Fig. 2B–D). In addition, the total surface area of the feeding marks on the basal area was 7.6 times larger than that on the apical area (Fig. 4A). These behavioural and geometric findings indicate that babirusas are able to discriminate between the basal and apical parts of the young coconut fruit and that the basal part is the more preferred part.

### *Hardness*

The basal sample had a significantly lower breaking

load ( $M = 19.5$  N) compared to the apical sample ( $M = 43.8$  N) (Fig. 5). This difference is consistent with the difference in the degree of accumulation of lignocellulosic fibres, known as coir fibres, which is visible on the two sides of the cut surface of the mesocarp. The lower hardness of the basal part may play an important role in making it easier to bite it off and may also have a better texture for mastication. In more mature coconuts, the breaking load of the basal side of the mesocarp would probably be higher and lead to a reduction in the amount of consumed mesocarp even on the basal side.

### *Nutritional contents*

The nutritional data shown in Table 2 should be interpreted with caution. Unfortunately, only a single pooled sample was used for the nutritional analysis of three young coconuts due to the limited number of coconuts. Hence, to demonstrate that the observed differences in the nutritional content (Table 2) are the potential key factors influencing the preference for the basal part, further analyses with sufficient replications are required.

### Volatile compounds

The distinctive mild, sweet smell of lactones has been reported as an important flavour component of mature coconut kernels (Lin and Wilkens 1970; Saittagaroon et al. 1984). However, these compounds were not found in the GC-MS chromatogram of the coconuts evaluated herein. Rather, we found two large peaks (Fig. 6) corresponding with 2-methylbutanal and 3-methylbutanal in the basal sample (Table 3), although our results were based on the analysis of a single coconut. This can probably be attributed to the differences in the plant tissues and their stage of maturity given that we examined the mesocarp, or the outer layer of the seed, of immature coconuts in an early stage before the kernels had developed (Fig. 1).

The 2- and 3-methylbutanals are important flavour compounds in foods (Smit et al. 2009) and have been found in a wide variety of fresh foods and food products, such as meat, fish, cheese, olive oil, cacao beans, tomato, malts, baked potatoes, truffles, and certain alcoholic beverages (Woffenden et al. 2001; Duckham et al. 2002; Cserhádi and Forgács 2003; Splivallo et al. 2011; Wang et al. 2017). The organoleptic properties of 2-methylbutanal are described as musty, chocolate, nutty, furfural, and isovaleraldehyde-like with malty and fermented nuances (Moscianno 1998). Similarly, 3-methylbutanal is described as ethereal, aldehydic, chocolate, peach, malty, and fatty (Miller et al. 1974; Cserhádi and Forgács 2003; The Good Scents Company 2009).

Meanwhile, the peak of 1-butanol was relatively large in the chromatogram of the basal sample, but appeared to have a similar peak area to the apical sample (597 vs. 476). Thus, this compound may not be characteristic of basal tissue.

Taking into account the behavioural findings and differences in the GC-MS chromatogram between the basal and apical samples, it is likely that the babirusas' selection of the basal part of the immature coconut mesocarp can be attributed to the emission of volatile substances such as 2- and 3-methylbutanal. However, we cannot discount the possibility that the quantitative differences in other components, along with the complex mixture of volatile components present in young coconuts, were important contributory factors that attracted the babirusas.

In any case, further comparative analyses between the two parts are necessary to confirm the preference for the basal part of young coconuts and to acquire more conclusive evidence that would link the presence of specific volatile compounds with the selection of the basal part by the babirusa.

### Applications in the natural habitat

The time interval from pollination to maturation of coconut fruits is approximately 12 months (Fandiño 1928; Chan and Elevitch 2006). The onset of the development of plant tissues in coconuts varies among the internal layers and parts of the coconut: The expansion of the seed cavity along with the storage of coconut water occurs first, and the maturation of the pericarp and development of the kernel occur afterwards (Fandiño 1928; Jayasuriya and Perera 1985). Hence, even if a fallen young coconut appears to be large in size, unless the kernel has stored fat, the young coconut has no economic value for the Togian people who produce copra or the dried kernels of mature coconuts (Ito et al. 2020). Clearly, it is unreasonable to consider an animal eating a fallen young coconut (that has not yet formed a kernel), to be a coconut pest. Instead, the actual predators decreasing coconut yields might be arboreal animals, such as rodents and Tonkean macaques (*Macaca tonkeana*), on the Malenge Island in the Togian Archipelago (Ito et al. 2020), and plantain squirrels (*Callosciurus notatus*) at the study site (Kitchener et al. 1990).

The babirusas studied herein have much in common with the babirusas on the Togian Islands in terms of environmental conditions, such as tropical climate and vegetation, and foraging experience in coconut groves. We speculate that the preference for a specific part of immature coconuts would also be shared by the babirusas on the Togian Islands. The dissemination of the experimental findings of this paper to the local people of those islands might help to remove the common misconception that babirusas crack open whole mature coconuts and destroy the economic value of copra crops.

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