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Bark-stripping Behavior of Formosan Sambar (*Rusa unicolor swinhoii*) at Tataka, Yushan National Park in Taiwan

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The bark-stripping behavior of Formosan sambar, *Rusa unicolor swinhoii*, has become conspicuous in recent years in the Tataka area of Yushan National Park in Taiwan and a cause for concern to visitors and ecologists. We conducted a monthly survey of 537 tagged trees of 21 species and monitored the abundance of sambar using camera traps from October 2018 to January 2021, aiming to interpret possible causes of the bark-stripping behavior in Tataka. We also used a generalized linear model to evaluate factors that may affect the probability of a tree having its bark stripped. Both our observations and the model predictions showed that sambar has a strong preference for bark of *Pinus armandii*, *Photinia niitakayamensis*, and *Salix fulvopubeseens* and for trees with diameter at breast height around 14 cm. Bark stripping mainly occurred between July and October when major forage was most abundant. However, sambar's need for bark surged in May when sambar abundance was moderate and decreased in October when sambar abundance was high. The seasonality of bark stripping was synchronized with the peak periods of antler development, fawn nursing, and spread of gastrointestinal parasites, suggesting that sambar strips bark to ingest minerals for their physiological needs and/or to acquire plant secondary metabolites to repel gastrointestinal parasites. Sambar abundance alone was not sufficient to predict the overall intensity of bark stripping. Rather, the product of sambar abundance and the necessity index (average wound size) were strongly correlated with the overall bark-stripping intensity. Therefore, controlling sambar abundance is essential but it alone may not be the optimal strategy for controlling bark stripping. A combination of population control and relaxing of sambar's parasite loading and/or physiological needs for minerals is an important strategy to control the overall bark stripping. Future research could use the necessity index to investigate the synchronicity of the bark-stripping behavior, deer's physiological state, environmental factors and phenology to better understand the cause of this behavior.

Key words: Deer, Plant secondary metabolites, Gastrointestinal parasites, Forest, Necessity index.

BACKGROUND

Herbivory is one of the important driving forces of plant community succession (Davidson 1993). Among vertebrate herbivores, deer exhibit a variety of behaviors that may impact plants, including browsing, bark stripping (*e.g.*, Akashi and Nakashizuka 1999), antler rubbing and trampling (Gill 1992). The extent of these impacts increases with the increasing abundance of deer at the local or regional scale (Akashi and Terazawa

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2005). While deer are increasing in abundance and distribution worldwide, *e.g.*, sika deer (*Cervus nippon*) in Japan (Kaji et al. 2000), roe deer (*Capreolus capreolus* L.) in Europe (Burbaitė and Csányi 2009), and many deer species in temperate zones (Côté et al. 2004), they play an increasingly important role in shaping the community structure of forest plants.

Compared to other forms of damage, bark stripping has stronger impacts on tree growth and survival. When stripped of bark, a tree has limited capability to recover, especially when the wounds are deep or large (Akashi and Nakashizuka 1999; Stobbe et al. 2002; Gaiser et al. 2006; Welch and Scott 2017). The capability of a bark-stripped tree to recover from damage varies with wound size, depth and tree species. Some tree species may not heal from wounds of bark stripping (*e.g.*, Akashi and Nakashizuka 1999) if the species cannot form surface calluses (Gaiser et al. 2006) or when the wounds are deep and the cambium is removed (Stobbe et al. 2002). Some trees may take 20 years for their wounds to heal if the wound size is larger than 180 cm^2 (Welch and Scott 2017). Besides causing damage that is difficult to recover from, deer tend to repeatedly strip the same individual trees (Nagaike 2020a; Welch and Scott 2017) such that wounds accumulate until the trees are completely girdled and killed. Also, deer selectively strip young trees of preferred species (Akashi and Terazawa 2005; Yen et al. 2015), which suppresses the recruitment of tree species selected by deer. Over time, bark-stripped species may decline and the tree community and succession of a forest could be altered by deer (Davidson 1993).

In Taiwan, the Formosan sambar (*Rusa unicolor swinhoii*) is widely distributed and is the only large deer species that is capable of stripping tree bark (Yen et al. 2015), apart from the Formosan sika deer (*Cervus nippon taiouanus*), which has a limited distribution in Hengchun Peninsula. Sambar abundance has increased and distribution expanded from higher altitudes in the Central Mountain Range to neighboring lower altitudes in the past 30 years (Chung 2020). Along with the population growth of sambar, bark stripping is an increasingly widespread and serious problem at altitudes over 3000 m (Yen et al. 2015). In recent years, the abundance of sambar has increased and bark stripping by sambar has become conspicuous in the Tataka area, neighboring the Central Mountain Range, of the Yushan National Park. Effective control of bark stripping damage is possible only if the causes are well understood. Therefore, the Yushan National Park initiated a monitoring project on the bark-stripping pattern of Formosan sambar in the Tataka area.

This study interprets possible causes of the bark-stripping behavior of sambar and its selectivity for tree species considering the following hypotheses. The most frequently reported cause of bark stripping is food shortage. In temperate zones, in particular where understories are covered by snow in winter, deer are believed to eat bark to compensate for low food availability when their major food source becomes less available due to thick snow cover (*e.g.*, Miquelle and Van Ballenberghe 1989; Ueda et al. 2002; Arnold et al. 2018). Therefore, this food shortage hypothesis suggests low food availability when the bark-stripping behavior occurs. The nutritional and mineral value hypothesis is also a commonly tested hypothesis to explain why deer consume bark. Jiang et al. (2005) found that the bark-stripping intensity on veitch fir (*Abies veitchii*) by sika deer was positively correlated with the crude protein concentration of bark. Ando et al. (2004) found that bark is beneficial for mineral balance compared to the major food plants of sika deer. Finally, the self-medication hypothesis (Hutchings et al. 2006) considers the medicinal effect of bark to repel internal parasites. Gastrointestinal parasites may reduce the fitness of hosts by depressing appetite, tissue deposition and skeletal growth (Sykes and Coop 2001), and could more seriously result in poor growth rate, ill-thrift and death (Min et al. 2005). Animals self-medicate by selecting and ingesting substances that may help reduce the infestations of internal parasites (Huffman 2003; Villalba et al. 2006). Bark is rich in plant secondary metabolites (PSMs), especially condensed tannins, which likely play an important role in attenuating the effect of internal parasites. Therefore, PSMs have been suggested to be the substances that herbivores actively seek out from certain plant species to repel internal parasites (*e.g.*, Hutchings et al. 2006; Saint-Andrieux et al. 2009; Lisonbee et al. 2009; Hoste et al. 2010).

This study aims to 1) document the pattern of bark-stripping behavior of Formosan sambar in the Tataka area of the Yushan National Park, 2) interpret possible causes of sambar's bark-stripping behavior, as well as its selectivity for tree species related to the three hypotheses that explain why deer strips bark, and 3) provide suggestions for the control of the bark-stripping behavior for the Yushan National Park.

MATERIALS AND METHODS

This study was conducted from October 2018 to January 2021 in the Tataka area located at the northwest corner of the Yushan National Park in Taiwan (Fig. 1). The study area covered 79 ha with an average elevation of 2720 m (2610–2850 m). Annual rainfall was 1640 mm in 2019 and 1330 mm in 2020, peaking in August for both years. Monthly average temperature ranges from 6.6 to 14.2°C, with the lowest in January and the highest in July (data provided by the Lulin Observatory, National Central University).

We tagged trees randomly along four trails in October 2018. However, trees that were less than 10 m apart from each other and trees that were located at steep slopes were not considered due to potential autocorrelation between samples and access difficulty, respectively. The four trails were 1) Dongpu pasture trail between the Tataka Visitor Center and the Yushan forestry road, 2) Yushan forestry road between the Gigantic Hemlock and Lulin trailhead and between the Gigantic Hemlock and Yushan trailhead, 3) Lulin trail between Yushan trailhead and Lulin trailhead, and 4) Black Forest trail that located on the south of the Lulin trail (Fig. 1). Diameter at breast height (DBH) and GPS fixes of each tree were recorded. The size of each wound was calculated by the product of length and width of the wound (*e.g.*, Welch and Scott 2017) because wound shape was roughly rectangular or elongated ellipse. The actual size of the wounds may be slightly smaller than our calculation. Wounds from bark stripping that already existed when this study began were measured and each wound was outlined using crayon to distinguish old wounds from new ones. From November 2018 to January 2021, this study conducted monthly surveys on all tagged trees and measured wound sizes. When wounds occurred on branches of a tree, diameters of the branches were also measured.

This study set up eight camera traps in October 2018 to monitor the relative abundance of sambar (Fig. 1). In January 2020, two more camera traps (LU4, BL4 in Fig. 1) were added for a more complete coverage of the study area. Camera traps were set up at locations along each trail where sambar footprints and pellets were abundant and also hidden from view of visitors. Camera traps were at least 100 m apart from each other to avoid autocorrelation. Photos were retrieved every two to three months from November 2018 to January 2021. This study used the abundance index for sambar proposed by Gu (2018). The index was defined as the number of consecutive photos per 1000 hours that were at least one hour apart. Individuals were not distinguished and the number of individuals in a photo

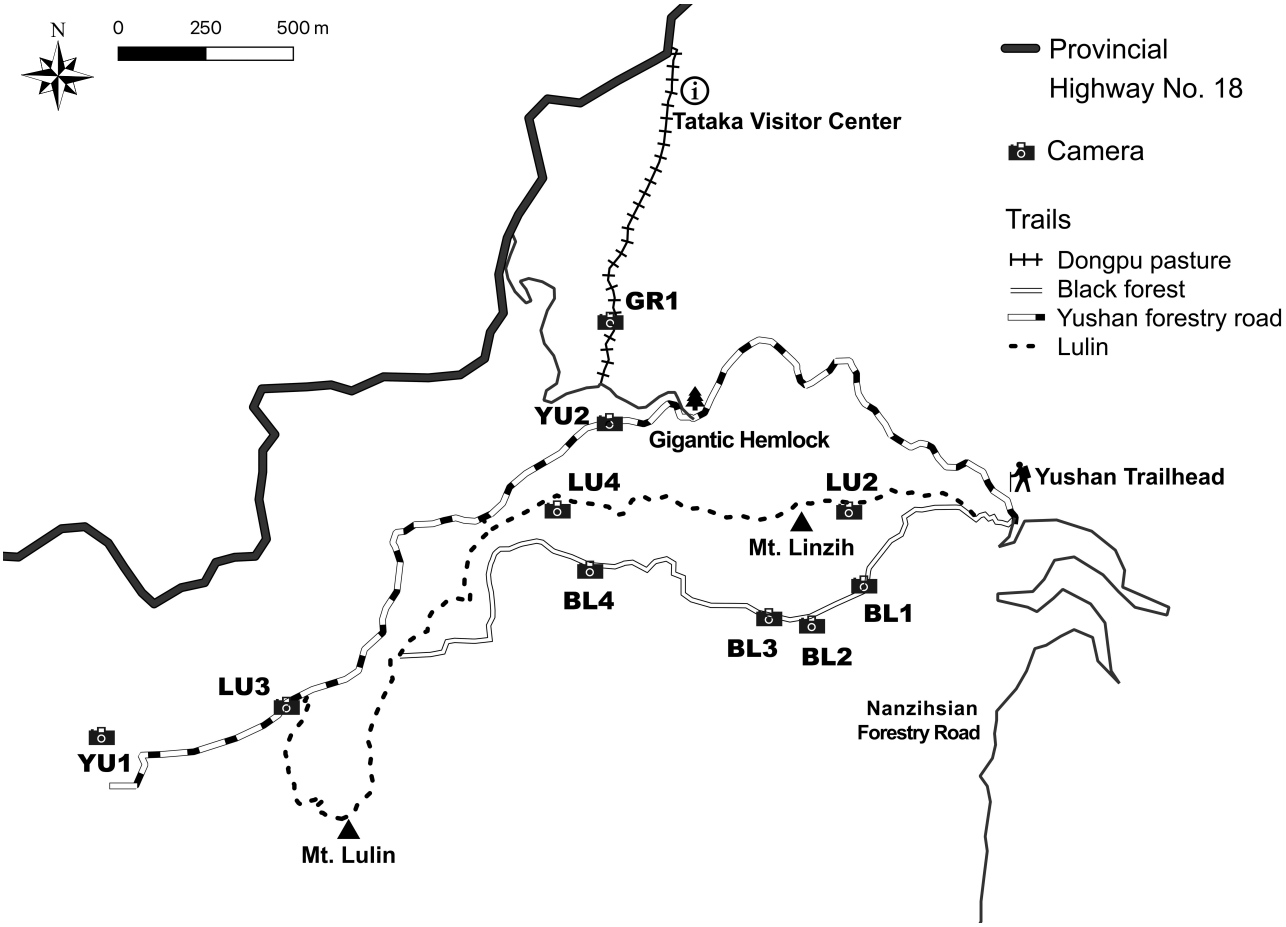

Fig. 1. Distribution of survey trails and camera traps at Tataka, Yushan National Park in Taiwan.

was ignored. This index has a Pearson's correlation coefficient of 0.764 with the estimated population size of sambar and a relatively small coefficient of variation, making the index ideal for reflecting the abundance of sambar (Gu 2018).

Two sets of indices were used to reflect the seasonality of the bark-stripping behavior in terms of monthly frequency and intensity of bark stripping. The frequency indices were the number of bark-stripped trees and the number of wounds. The intensity indices were the average size per wound and total size of wounds. Because low sample size may bias the estimated indices, only the indices from those tree species that had 20 or more individuals were interpreted. It is worth noting that the abundance of sambar and their needs for bark can both contribute to the two indexes. When the bark-stripping frequencies or intensities increased, it is difficult to attribute this increase to the increasing abundance of sambar or the increasing needs for bark by sambar. In order to disentangle the confounding factors between the abundance of sambar and their needs for bark, this study applied the Marginal Value Theorem (Charnov 1976) of the optimal foraging theory (Pyke 2019) and proposed a 'necessity index.' The Marginal Value Theorem predicts that when animals feed on a path of resources they maximize their intake of energy, nutrition, or more generally the 'currencies,' per unit time before they move to the next patch (Charnov 1976). Under this theorem, when an individual sambar is in higher needs for bark, it is expected to eat more bark and cause a larger size of wound before it moves to the next target than when it does not need bark as much. Therefore, this study defined 'necessity index' as the average size per wound to reflect the seasonality of sambar's needs for bark at an individual level. The total size of wounds, on the other hand, is an index of overall bark-stripping intensity exhibited by the whole sambar population.

Individual needs for bark multiplied by the total number of individuals would be equivalent to the total consumption of bark by the whole sambar population. In other words, if the 'necessity index' is valid, the overall intensity of bark stripping, *i.e.*, the total size of wounds, would be predicted by the product of the necessity index (needs for bark per individual sambar) and sambar abundance (index for the total number of sambar). Therefore, this study regressed the monthly total size of wounds on the necessity index, sambar abundance and their interaction term in a general linear model using GLM procedure in SAS 9.4 (SAS Institute Inc., Cary, NC, USA) to evaluate the effects of the necessity index, sambar abundance and their interaction term on the total size of wounds. The intercept was set to zero because when either sambar abundance or the necessity index was zero, the total size of wounds was expected to be zero. This study did not consider the total size of wounds per tree because the optimal foraging behavior is a strategy exhibited at the individual level and each single wound was likely to be caused by one individual, but wounds on a tree could be caused by multiple individuals.

For the preference of tree species, this study defined a 'preference index' to show which tree species sambar prefer. If sambar did not prefer any tree species for stripping bark, the percentage of trees being bark-stripped of a species was expected to be equal to the percentage of that species within all the tagged trees (expected percentage). If sambar preferred one species over others, the preferred species would be bark-stripped at a higher percentage (observed percentage) than the expected percentage when sambar did not prefer bark of any tree species. On the contrary, if sambar avoids a tree species when stripping bark, then the observed percentage would be lower than the expected percentage. Therefore, the preference index was defined as the observed percentage of a tree species being bark-stripped divided by the percentage of that species within all the tagged trees. The preferred tree species will have a preference index higher than one and the tree species avoided by sambar will have a preference index lower than one. We conducted Chi-square test of independence to examine if tree species was associated with the observed bark-stripping percentage. For a tree species to be tested, a 2 × 2 contingency table was established in which one variable was tree species and another was bark stripping incidence. Each tree was categorized as either the target tree species or not and either bark-stripped or not. For a valid Chi-square test, tree species that had less than 20 individuals were not tested to avoid any expected values lower than five. A p-value < 0.05 indicated that a tree species was significantly more preferred or avoided by the sambar than expected.

Along with season and tree species, this study used a generalized linear model to evaluate other factors that possibly have effects on the probability that a tree was bark-stripped by sambar. Earlier studies showed that the probability of a tree to be bark-stripped was related to DBH and its squared term (Yen et al. 2015) and the abundance of deer (Akashi and Terazawa 2005). Similarly, if a tree is located in a habitat preferred by sambar, then the tree would be subject to a higher probability of encountering sambar and being bark-stripped. Yen et al. (2019) described the habitat selection by Formosan sambar using a resource selection function model that included elevation, solar radiation, moisture regime, land cover type, and slope. This study used slope as the only environmental variable in the model because our study area was only 79 ha with small ranges of elevations, solar radiation, moisture regime, and a major land cover type of coniferous and broad-leaved mixed forest. Slopes in our study area are highly variable and range from 1.9 to 44.5 degrees with an average of 22.6 (SD = 10.2). Therefore, this study established a generalized linear model to evaluate the effect of month, tree species, sambar abundance, DBH, DBH^2 and slope in explaining the probability of a tree being bark-stripped. This study initially considered rainfall and temperature to be involved in the model, but these two variables were highly correlated with month. Therefore, this study used months in the model to evaluate the seasonality of bark-stripping probability (experienced by a tree) before discussing the potential effects of rainfall and temperature on the probability. The response variable of the model was the incidence of bark stripping on a tree each month (hence a binary response). For an appropriate estimate of the probability of a tree being bark-stripped, only the tree species with 20 or more individuals were used in the model. This study evaluated the model using the GENMOD procedure in SAS 9.4 with the logit link function to link the binary response and predictor variables.

Finally, this study calculated the annual damage (total size of wounds) that occurred in 2019 and 2020. The initial total size of wounds recorded in the first survey in October 2018 represents the accumulated damages of the bark-stripping behavior since this behavior occurred in Tataka. The initial total size of wounds was divided by the average annual damage of 2019 and 2020. The result was used to interpret how long ago sambar started to strip bark in Tataka.

RESULTS

Selectivity

This study tagged 536 trees of 21 species in Tataka, seven species of which had 20 or more individuals (Table 1). Tagged trees were dominated by Masters pine (*Pinus armandii*), Taiwan red pine (*P. taiwanensis*), Taiwan stranvaesia (*Photinia niitakayamensis*) and mountain willow (*Salix fulvopubeseens*) in terms of number of trees. These four species combined accounted for 65.4% of all the tagged trees. Among the tagged trees, 240 individuals of 16 species were bark-stripped (Table 1). The three most frequently bark-stripped species in terms of observed percentage of bark-stripped individuals were Masters pine (37.9%), Taiwan stranvaesia (21.7%) and mountain willow (13.3%). The number of wounds also showed the same ranking of the top three species, with Masters pine suffering the most wounds (212), followed by Taiwan stranvaesia (149) and mountain willow (73) (Table 1). Ten of the bark-stripped species had a preference index larger than one (1) (Table 1), meaning that sambar preferred bark of these species to others. Among the tree species that had more than 20 individuals, Taiwan stranvaesia has the highest preference index (1.84) followed by Taiwan cherry (*Prunus campanulata*, 1.55). The most frequently bark-stripped species, Masters pine, had the third highest preference index of 1.30 (Table 1). All the preference indexes for these three species were statistically significant at $\alpha = 0.05$ level (Table 1). Sambar significantly avoided Taiwan red pine and Taiwan red cypress whose preference indexes were significantly lower than one (Table 1).

Sambar's selectivity for tree species was also exhibited by the total size of wounds. Masters pine and mountain willow were the top two most-damaged species and were stripped to a similar total size of wounds (5.73 and 5.99 m^2, respectively), followed by Taiwan stranvaesia (4.92 m^2, Table 1). These three species combined accounted for 77.2% of the total size of wounds of all sampled trees (Table 1).

Seasonality

Frequency and intensity of bark-stripping in Tataka has a pronounced peak in summer months. The number of bark-stripped trees, number of wounds (Fig. 2a), and total size of wounds (Fig. 2b) gradually rose from May to July and stayed relatively high from July to September before descending in October and November. Sambar abundance was the lowest in February and gradually rose starting in March and peaked in September (Fig. 2c). After September, sambar abundance descended quickly over time and reached its lowest point in February. However, the necessity index (average wound size), surged to its highest value in May and stayed relatively high until September (Fig. 2b), which was different from the pattern of bark-stripping frequency (Fig. 2a), total size of wounds (Fig. 2b) and sambar abundance (Fig. 2c). The monthly total size of wounds was highly predictable based on the product of sambar abundance and necessity index ($p < 0.001$, Table 2, Fig. 3). Sambar abundance or necessity index alone did not have significant effects on the monthly total size of wounds ($p = 0.252$ and 0.903, respectively, Table 2).

All the predictive variables, except sambar abundance ($p = 0.346$), in the generalized linear model had significant effects on the probability of a tree being bark-stripped at $\alpha = 0.05$ level. Table 3 shows the coefficient estimate for each variable in the model without sambar abundance. Compared to April, the probability of bark-stripping was significantly higher between May and November than other months and the top two highest probabilities happened in July and September (Table 3). This seasonality is in accordance with the pattern shown by the number of wounds, number of bark-stripped trees (Fig. 2a) and total size of wounds (Fig. 2b), but is different from the necessity index that peaked in May (Fig. 2b).

The probability of bark-stripping differed significantly among tree species (Table 3, Fig. 4). When month, slope and DBH were set to be equal, all the species, except Taiwan red cypress, that had 20 or more individuals were predicted to experience a higher probability of bark-stripping by sambar compared to Taiwan red pine (all $p < 0.001$, Table 3). The top three species that had the highest predicted bark-stripping probability (Table 3, Fig. 4) were the same as the top three species that were most frequently bark-stripped (Table 1), but the ranking was different. Masters pine experienced the highest bark-stripping frequency but Taiwan stranvaesia was predicted to have the highest bark-stripping probability. DBH and its quadratic term both had significant effects on bark-stripping probability (both $p < 0.05$, Table 3). When all other variables were held constant, the maximum probability of bark-stripping occurred at a DBH of roughly 14 cm (Fig. 4). Slope had a significantly negative effect on bark-stripping probability (Table 3), meaning that trees at flatter areas were subject to higher probability of bark-stripping than at steeper slopes.

Sambar caused 10.7 m^2 and 9.5 m^2 of wounds from our tagged trees in 2019 and 2020, respectively, at a rate of roughly 10.1 m^2 per year. Our initial survey in October 2018 recorded 28.4 m^2 of existing wounds. If the rate of bark-stripping was constant over the years, it would take 2.8 years or 33.6 months for sambar to cause 28.4 m^2 of wounds. Therefore, the beginning of bark-stripping behavior of sambar could be dated back to January 2016 from October 2018.

Table 1. Bark stripping frequency and intensity for each sampled tree species from November 2018 to January 2021 at Tataka, Yushan National Park in Taiwan. Percentage of each tree species is the number of each species divided by the total number of trees (546). Percentage of the bark-stripped trees is the number of bark-stripped trees of the species divided by the total number of bark-stripped trees (240). Size of wounds was rounded to the second decimal place. Preference index of a tree species is the percentage of bark-stripped trees divided by the percentage of that species among all sampled trees. Significance of the preference index was tested using Chi-square test of independence for tree species that had more than 20 individuals. Tree species are ordered by the number of trees

Species	All trees		Bark-stripped trees		Wounds		Preference index	*p*-value
	N	%	*n*	%	*n*	size (m^2)		
Pinus armandii Franchet var.	156	29.1	91	37.9	212	5.73	1.3	0.002**
Pinus taiwanensis Hayata	72	13.4	8	3.3	8	0.15	0.25	< 0.001***
Photinia niitakayamensis Hayata	63	11.8	52	21.7	149	4.92	1.84	< 0.001***
Salix fulvopubescens	60	11.2	32	13.3	73	5.99	1.19	0.405
Chamaecyparis formosensis Matsum.	44	8.2	6	2.5	9	0.57	0.3	< 0.001***
Picea morrisonicola Hayata	31	5.8	12	5	18	1.19	0.86	0.267
Prunus campanulata Maxim.	23	4.3	16	6.7	28	1.15	1.55	0.036*
Pieris taiwanensis Hayata	15	2.8	0	0	0	0	0	\
Eurya glaberrima Hayata	14	2.6	1	0.4	2	<0.01	0.16	\
Tsuga formosana Hayata	12	2.2	4	1.7	5	0.11	0.74	\
Cunninghamia konishii Hayata	10	1.9	5	2.1	7	0.35	1.12	\
Rhododendron rubropilosum Hayata	10	1.9	0	0	0	0	0	\
Trochodendron aralioides Siebold & Zucc.	7	1.3	5	2.1	13	0.4	1.6	\
Juniperus formosana Hayata	5	0.9	1	0.4	1	0.01	0.45	\
Acer morrisonense Hayata	4	0.7	3	1.3	6	0.71	1.68	\
Rhododendron pseudochrysanthum Hayata	4	0.7	0	0	0	0	0	\
Schefflera taiwaniana (Nakai) Kaneh	2	0.4	2	0.8	4	0.13	2.23	\
Elaeagnus formosana	1	0.2	0	0	0	0	0	\
Pyrus kawakamii Hayata	1	0.2	1	0.4	2	< 0.01	2.23	\
Pseudotsuga wilsoniana Hayata	1	0.2	1	0.4	1	0.13	2.23	\
Elaeagnus thunbergii	1	0.2	0	0	0	0	0	\
Total	536		240	100	538	21.57		

DISCUSSION

Bark-stripping frequency, as usually measured in studies, has been related to deer abundance (*e.g.*, Akashi and Terazawa 2005), food abundance (Arnold et al. 2018), and a deer's needs for particular nutrition or mineral at particular life stage such as antler development, pregnancy, or calving (*e.g.*, Ando et al. 2004). In order to disentangle these confounding effects, this study measured bark-stripping frequency, total size of wounds, deer abundance and their needs for bark simultaneously.

This study found that sambar have a pronounced preference for bark of certain tree species. Yen et al. (2015) surveyed 83 plots in four protected areas in Taiwan and also found that sambar preferred Pinaceae

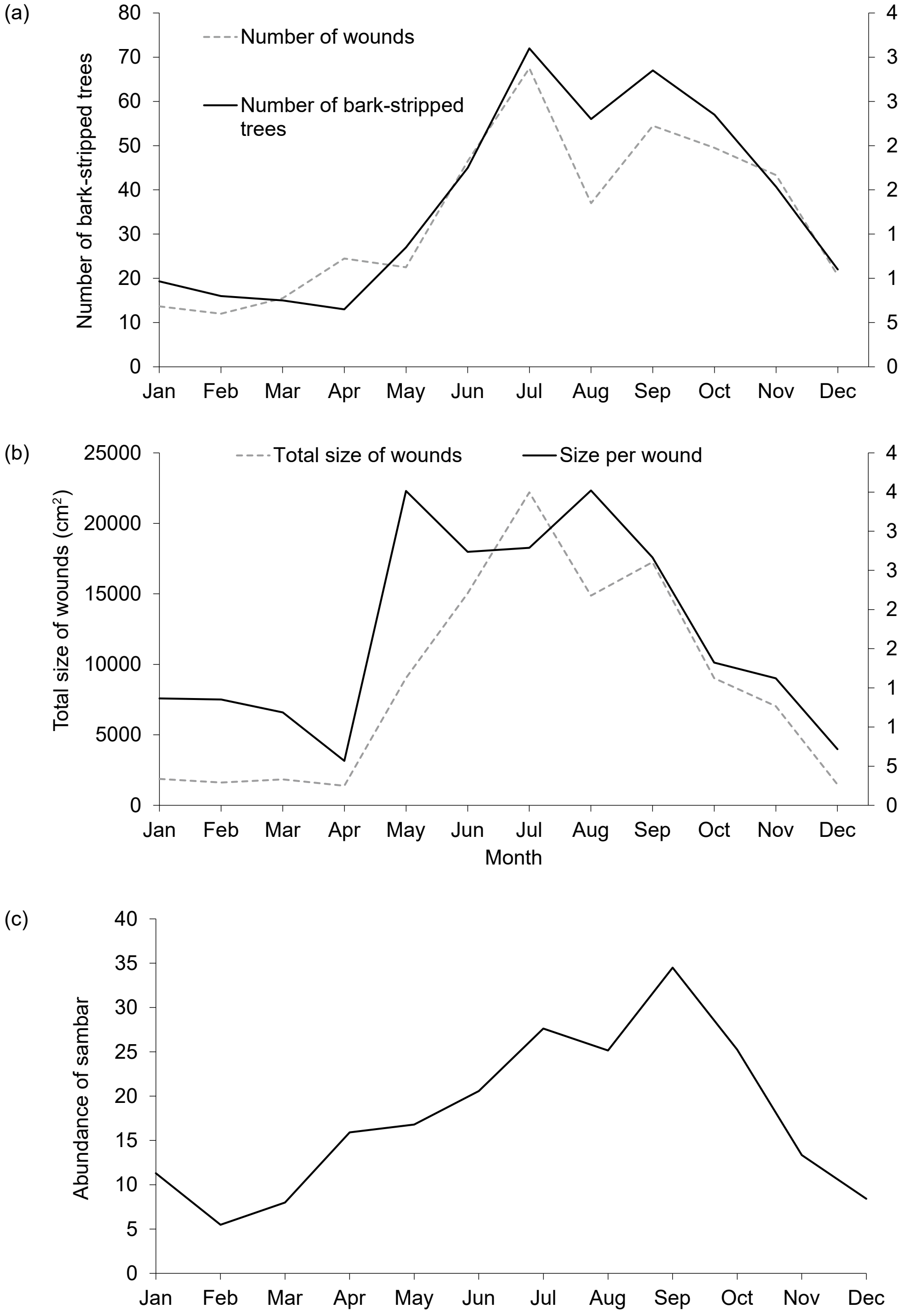

Fig. 2. Averages of indexes of (a) the bark-stripping frequency (b) bark-stripping intensity and necessity index (average size per wound) and (c) sambar abundance from November 2018 to January 2021 at Tataka, Yushan National Park in Taiwan.

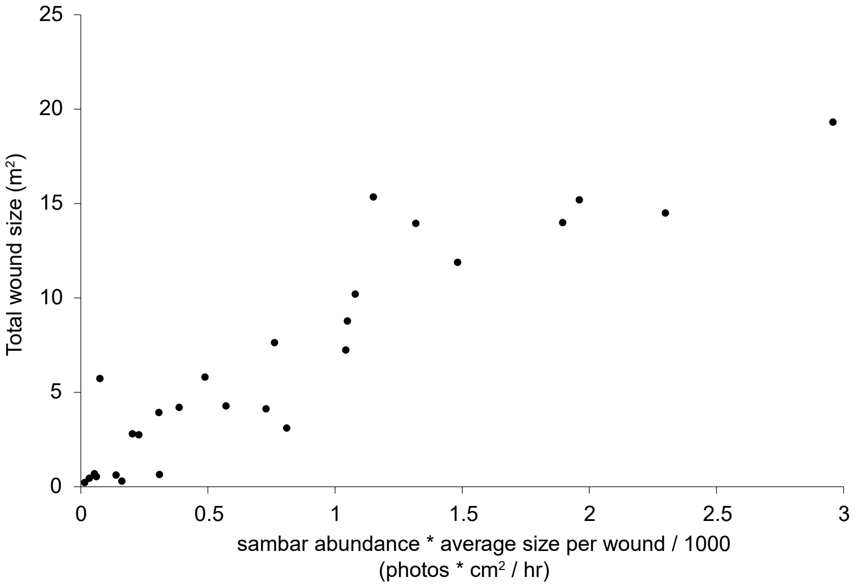

Fig. 3. Relationship between the monthly total size of wounds (overall bark-stripping intensity) and the product of sambar abundance and necessity index. Pearson's correlation coefficient was 0.925 ($p < 0.001$).

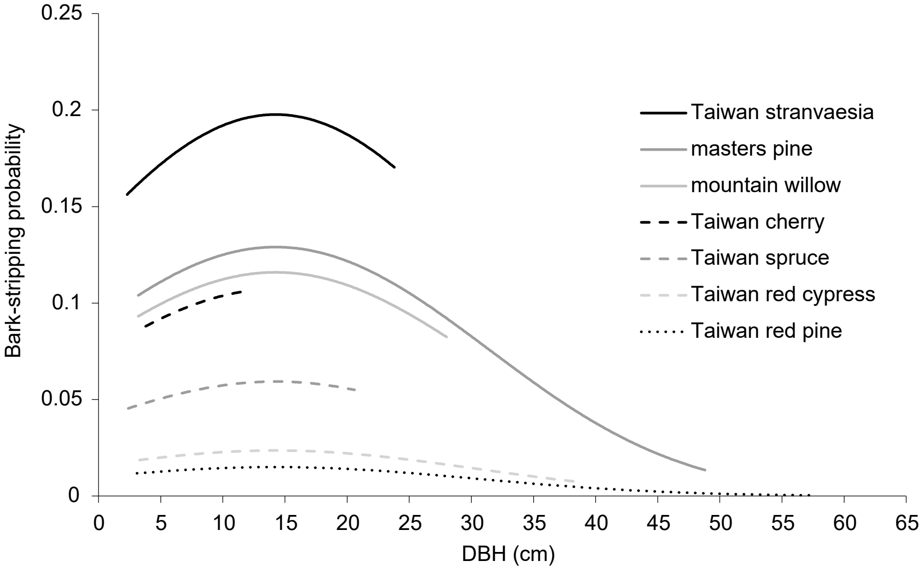

Fig. 4. Predicted probability of bark-stripping by sambar for seven tree species along the diameter at breast height (DBH) at Tataka, Yushan National Park in Taiwan. Month was set to September and slope was set to zero. Range of the DBH for each species was based on the observed values.

Table 2. Parameter estimates of the general linear model to evaluate the effects of sambar abundance, necessity index and their interaction on the overall intensity of bark stripping (total size of wounds). The intercept was set to zero because the overall intensity of bark stripping was expected to be zero when sambar abundance or necessity index was zero

Parameter	Estimate	SE	*t*	*p*-value
Sambar abundance	-0.0093	0.0079	-1.17	0.252
Necessity index	-0.0450	0.3656	-0.12	0.903
Sambar abundance * necessity index	0.1437	0.0234	6.15	< 0.001***

species, except Taiwan red pine, for bark stripping. Ando et al. (2003 2004) also found that sika deer selectively stripped bark of both coniferous and broadleaf trees. The selectivity of tree species by deer implies that the contents of bark, whether nutrition, minerals or secondary metabolites, needed by deer may vary between species.

The nutritional and mineral value hypothesis (Miquelle and Van Ballenberghe 1989) is a commonly tested hypothesis to explain why deer selectively strip bark of particular tree species. Ando et al. (2004) compared nutritional contents between bark and dwarf bamboo (*Sasa nipponica*), the main forage of sika deer in their study area, and found that bark contained less crude protein and hemicellulose but more Ca and less K/(Ca + Mg) than dwarf bamboo, suggesting that bark is poor in nutrition but beneficial for mineral balance. Saint-Andrieux et al. (2009) compared the mineral contents of bark from beech (*Fagus sylvatica*) stripped by red deer (*Cervus elaphus*) and non-stripped beech but did not find a significant difference. However, selectivity exhibited by deer observed in our study and other research (*e.g.*, Akashi and Nakashizuka 1999; Yen et al. 2015; Nagaike 2020b) was for tree species instead of individual trees of the same species. Therefore, chemical contents should be compared among tree species and the results should relate to deer preference for tree species. In our study area, bark-stripping frequency, total size of wounds, and the necessity index all rose in May (Fig. 2a b) when males started to develop antlers and females were in the peak period of nursing young (Huang 2019). Minerals, especially calcium, are crucial for both antler growth and lactation. Therefore, we hypothesize that intake of calcium and other minerals for antler growth and lactation is one of the reasons why sambar strip bark and also exhibit selectivity for tree species.

Physical properties of bark, such as hardness, thickness (Ando et al. 2004) and ease of detachment (Saint-Andrieus et al. 2009) have also proven important for the selection of tree species by deer. However, these properties are related to stem age or DBH because bark thickness generally increases with DBH (Williams et al. 2007; Zeibig-Kichas et al. 2016). In this study (Fig. 4) and Yen et al. (2015), sambar had the highest probability to strip bark of trees with DBH around

Table 3. Coefficient estimates for the predictive variables in the generalized linear model for the probability of a tree being bark stripped. Estimates for months were compared to April. Estimates for tree species were compared to Taiwan red pine

Parameter	DF	Estimate	SE	Wald Chi-square	*p*-value
Intercept	1	-6.338	0.502	159.46	< 0.001***
Month					
Jan	1	0.416	0.351	1.4	0.236
Feb	1	0.294	0.386	0.58	0.446
Mar	1	0.082	0.405	0.04	0.840
May	1	0.756	0.356	4.51	0.034*
Jun	1	1.252	0.334	14.02	< 0.001***
Jul	1	1.729	0.321	29.03	< 0.001***
Aug	1	1.470	0.327	20.17	< 0.001***
Sep	1	1.747	0.320	29.71	< 0.001***
Oct	1	1.597	0.324	24.28	< 0.001***
Nov	1	1.197	0.322	13.82	< 0.001***
Dec	1	0.623	0.341	3.33	0.068
Apr	0	0	0	.	.
Species					
masters pine	1	2.275	0.364	39.07	< 0.001***
mountain willow	1	2.153	0.385	31.26	< 0.001***
Taiwan cherry	1	2.065	0.416	24.66	< 0.001***
Taiwan red cypress	1	0.461	0.491	0.88	0.348
Taiwan spruce	1	1.421	0.434	10.73	0.001***
Taiwan stranvaesia	1	2.784	0.374	55.48	< 0.001***
Taiwan red pine	0	0	0	.	.
DBH	1	0.057	0.023	6.29	0.012*
DBH^2	1	-0.002	0.001	12.45	< 0.001***
Slope	1	-0.011	0.005	4.72	0.030*

14 cm and 20 cm, respectively, instead of younger trees with softer, thinner and easier-to-detach bark. A 35-year monitoring study by Welch and Scott (2017) also found that red deer tend to strip bark of *Picea sitchensis* with DBH around 20 cm. Therefore, physical properties are not likely to be the ultimate factor that causes the selectivity for tree species by deer for bark stripping.

The frequency and intensity indices all showed that stripping by sambar mainly occurred during May and November (Fig. 2a b, Table 3). The necessity index also surged in May (Fig. 2b). Although the food shortage hypothesis was the most frequently reported cause of bark stripping by deer in the temperate zone, summer is high in food abundance when the major forage of sambar, Yushan cane (*Yushania niitakayamensis*), was fully grown in Taiwan, making the food-shortage hypothesis unlikely. Although Yen et al. (2015) observed sambar's bark-stripping characters in 83 plots in Taiwan and suggested future research to investigate the food-shortage hypothesis, they did not monitor the bark-stripping behavior over time and did not find any seasonality for this behavior.

The strong seasonality of the bark-stripping behavior of sambar implies that physiological states of sambar significantly changed in May and remained in summer. Besides being the season of antler growth and nursing of young, summer has high temperatures and rainfall, making it the optimal season for the spread of gastrointestinal parasites (Waller 1997; Sun et al. 2018). Herbivores have been shown to self-medicate when infected with gastrointestinal parasites by consuming tannin-rich plants that they typically avoid (Min et al. 2005; Lisonbee et al. 2009; Villalba et al. 2010). Tannin has also been demonstrated *in vitro* (*e.g.*, Max et al. 2005) to be an effective parasite repellent for ruminants. Because sambar select tree species to strip bark and bark-stripping frequency, total size of wounds as well as the necessity index reached the maximum in summer, we hypothesize that, besides ingesting minerals for antler growth and lactation, sambar strip bark to acquire PSMs to attenuate burden of gastrointestinal parasites. Because contents of PSM vary among plant species (Bryant et al. 1991), future research could investigate the correlation between contents of PSM and the selectivity of sambar for tree species.

The necessity index proposed in this study is, to our knowledge, the first index to reveal that deer need bark. Conventionally, bark-stripping frequency (percentage or number of trees bark-stripped) and intensity (wound size or percentage of girth bark-stripped) are used to evaluate the seasonality of the bark-stripping behavior and interpret the possible cause of the behavior based on the seasonality. However, bark-stripping frequency and intensity are accumulated results of the behavior exhibited by the whole population. Fluctuation of population abundance could therefore affect the observed seasonality of the bark-stripping behavior. Because the need for minerals for antler growth and lactation may be factor causing deer to strip bark, sex ratio and age structure of a deer population could determine to what extent the population needs bark. Moreover, species composition and DBH structure of trees could also contribute to the observed bark-stripping frequency and intensity, depending on the cause of the behavior. Therefore, seasonality of the bark-stripping behavior revealed by frequency and intensity is likely a confounded result of all the above factors and may thus obscure the real timing of the need for bark by deer. Interpretation based solely on the seasonality of bark-stripping frequency and intensity could be biased. On the other hand, the necessity index or average wound size reveals the need for bark at individual level that is independent of deer abundance, sex/age composition, and plant species and DBH structure. This argument is supported by the results that the overall impact (total size of wounds per month) was best predicted by the product of necessity index and sambar abundance, not by any of them alone. Therefore, the necessity index is a better parameter than the bark-stripping frequency and intensity to reveal the actual period of time during which sambar needs bark. Also, management practices to control bark stripping should consider both population control and relaxing of the sambar's need for bark.

Sambar prefers to use flatter slopes (Yen et al. 2019). Our generalized linear model also showed that slope was negatively correlated with the probability of a tree being bark stripped. These results indicate that trees growing at steeper slopes would have a lower chance of being encountered by sambar and a lower probability of being bark stripped. Management practices to compensate for the loss of important tree species due to bark-stripping could consider planting trees at steeper slopes to reduce the risk of further damage by sambar. The estimated beginning year of bark stripping at Tataka is 2016 based on average annual damage. Our observations (Yin, unpublished data) before this study also showed that sambar started to strip bark at Tataka in 2016. Therefore, annual damage done by sambar seems to be stable over the past six years. However, the distribution expansion and population growth of sambar over the past 30 years have been significant (Chung 2020). We suggest that the Yushan National Park Headquarters investigate the cause of the bark-stripping behavior of sambar from the perspectives of self-medication and physiological requirement for minerals before the sambar abundance further increases.

CONCLUSIONS

Formosan sambar at Tataka, Yushan National Park strips bark significantly in summer and selectively on certain tree species. Our findings suggest that the ultimate cause of the bark-stripping behavior could be gastrointestinal parasites and/or the physiological requirement for minerals at particular life stages. Our necessity index, or the average wound size, is the first index to reveal the deer's need for bark at the individual level. Future research could use the necessity index to investigate the synchronicity of the bark-stripping behavior, deer's life stage, environmental factors and phenology to better understand the cause of this behavior. Because the overall bark-stripping impact was not determined solely by sambar abundance, controlling sambar abundance may not be the optimal strategy to control the impact of bark-stripping. A combination of population control and relaxing of sambar's needs for bark is an important strategy for the control of bark stripping.

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