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Rhinoceros Beetles Suffer Male-Biased Predation by Mammalian and Avian Predators

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Male sexually-selected traits often impose an increased risk of predation on their bearers, causing male-biased predation. We investigated whether males of the sap-feeding Japanese rhinoceros beetle *Trypoxylus dichotomus* were more susceptible to predation than females by comparing the morphology of beetles caught in bait traps with the remains of beetles found on the ground. The males of this species are larger than the females and have a horn on the head. We found that predation pressure was greater for males than for females, and that larger individuals of both sexes were more vulnerable to predation. We identified two predators, the raccoon dog *Nyctereutes procyonoides* and jungle crow *Corvus macrorhynchos*, by monitoring sap-site trees with infrared video cameras. Raccoon dogs visited sap-site trees at night, while crows came after daybreak. The highest frequency of visits by both predators was observed in the first half of August, which matches the peak season of *T. dichotomus*. Raccoon dogs often left bite marks on the remains of prey, whereas crows did not. Bite marks were found on most of the remains collected at two distant localities, which suggested that predation by raccoon dogs is common. Size- and sex-dependent differences in the conspicuousness and active period of *T. dichotomus* probably explain these biased predation patterns. Our results suggest that having a large horn/body is costly in terms of the increased risk of predation. Predation cost may act as a stabilizing selection pressure against the further exaggeration of male sexual traits.

Key words: sex-biased predation, sexual selection, weapon, sexual dimorphism, *Trypoxylus dichotomus*

INTRODUCTION

Sex-biased predation is widespread across the animal kingdom (Magnhagen, 1991; Zuk and Kolluru, 1998; Kotiaho, 2001; Christe et al., 2006). The direction of sex bias (female- or male-bias) depends on the nature of the sexual differences of prey as well as the preferences and foraging tactics of predators (Zuk and Kolluru, 1998; Christe et al., 2006; Boukal et al., 2008); however, the risk of predation is often higher for males than for females in insects, birds, amphibians, and reptiles (Magnhagen, 1991; Acharya, 1995; Zuk and Kolluru, 1998; Kotiaho, 2001; Christe et al., 2006; Costantini et al., 2007; Boukal et al., 2008). This is partly because the males of many species are more active in mate acquisition than females, which increases the risk of predation for males (Magnhagen, 1991; Kotiaho, 2001). In addition, sexually-selected morphological traits in males, such as a larger body,

weapons, and bright colors are generally conspicuous to predators and other natural enemies (Magnhagen, 1991; Zuk and Kolluru, 1998; Kotiaho, 2001; Godin and McDonough, 2003). Male-biased predation may counteract the sexual selection of male sexual traits, thereby influencing the evolutionary dynamics of these traits (Andersson, 1994; Zuk and Kolluru, 1998; Zuk et al., 2006).

The sap-feeding rhinoceros beetle *Trypoxylus dichotomus* (Coleoptera: Scarabaeidae) clearly exhibits sexual dimorphism (Fig. 1A): males are larger than females and bear one large horn on the head and another small horn on the prothorax (Fig. 1A). These beetles roost in tree canopies during the day and fly to sap sites (lesions in the tree bark that exude sap) at night to feed and mate; however, a small number of individuals remain at sap sites even after daybreak (McCullough, 2013). Large variations in the size of the body and male horn have been reported (Siva-Jothy, 1987; Karino et al., 2005; Hongo, 2007). The male horn functions as a weapon as well as an honest signal of body size and/or physiological conditions in intrasexual competition (Karino et al., 2005; Hongo, 2007; Emlen et al., 2012). Setsuda et al. (1999) examined the remains (exoskeletons) of prey individuals and found that males were more vulnerable to predation than females. Crows were suspected to be the main predator of this beetle, although predation by crows was not directly observed (Setsuda et al., 1999). Meanwhile, Hongo

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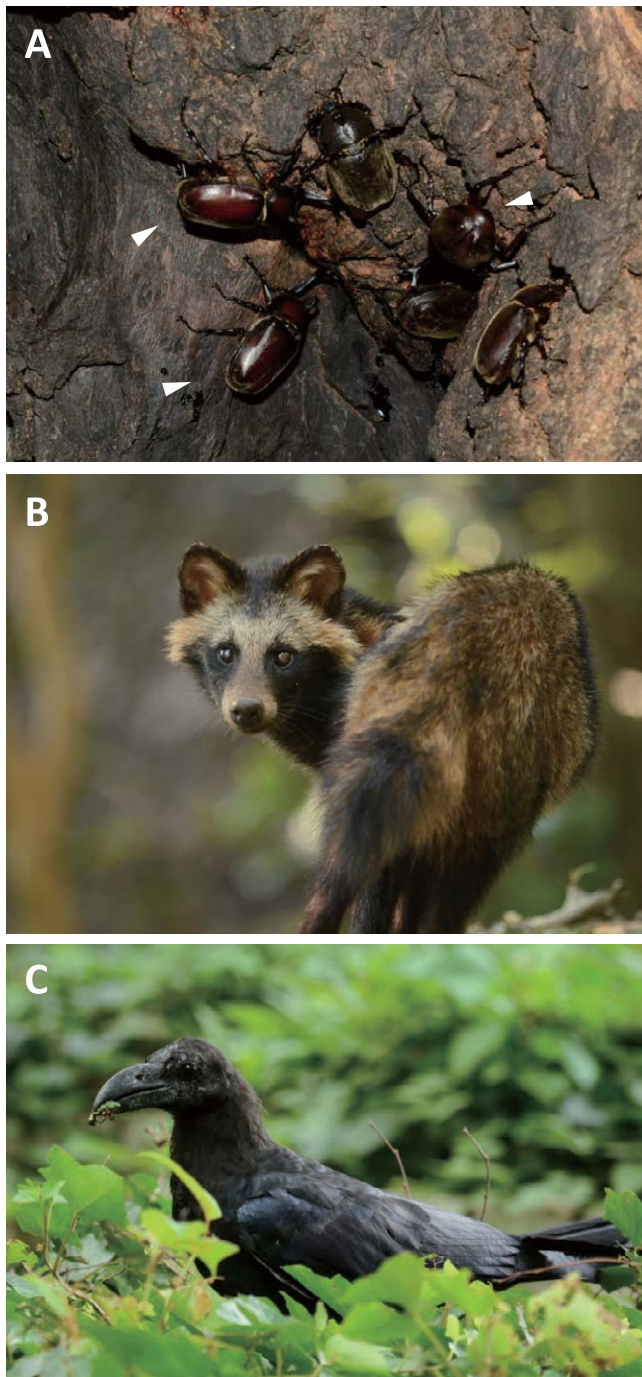


Fig. 1. Three males (indicated by arrowheads) and three females of *Trypoxylus dichotomus* feeding on the sap of a tree (A), a raccoon dog *Nyctereutes procyonoides* (B), and a jungle crow *Corvus macrorhynchos* preying on a scarab beetle *Anomala albopilosa*.

and Kaneda (2009) reported that the predation of beetles by the Ural owl *Strix uralensis* was slightly female-biased. These inconsistent findings demonstrate that the risk of predation for males differs depending on the habits of the major predators.

In the present study, we aimed to assess the relative predation pressure imposed on the males of *T. dichotomus* by different predators. We first examined if the males of *T.*

dichotomus were more susceptible to predation than the females by comparing the morphology of the remains of beetles found on the ground with that of individuals captured in a bait trap. We also attempted to identify the predators of *T. dichotomus* by monitoring sap sites with infrared video cameras.

MATERIALS AND METHODS

Study site

Studies were conducted in two secondary forests located 60 km apart: a forest in the Forestry and Forest Products Research Institute in Tsukuba, Ibaraki Prefecture (36.0°N, 140.1°E; referred to as 'Tsukuba') and another in The University of Tokyo Forest in Tanashi, Tokyo Metropolis (35.7°N, 139.5°E; 'Tanashi'). We monitored two sawtooth oaks *Quercus acutissima* standing 600 m apart in the Tsukuba forest. These trees had sap sites 1–1.5 m above the ground and *T. dichotomus* aggregated there every night. The remains of many predated insects, i.e., prothoraxes, horns, and elytra, were found on the ground near the sap-site trees. The other forest, 'Tanashi', had dozens of *Q. acutissima* and *Quercus serrata* with sap sites, and the remains of many predated *T. dichotomus* were collected in this forest.

Collection and size measurements of prey and living individuals

We investigated whether the males were more susceptible to predation than the females using the methods described by Setsuda et al. (1999). We collected the remains of *T. dichotomus* from mid-July to early September in 2011 and 2012 within a 5 m radius of the two surveillance trees in Tsukuba at intervals of 3–10 days. We determined the sex of the remains based on the presence/absence of a long horn on the head or short horn on the prothorax, and measured the length of the horn on the males with a digital caliper. The prothorax width of both sexes was also measured. The prothorax width and male horn length are common indexes of body size (Hongo, 2007). In addition, we carefully checked the prothorax of prey samples collected in 2012 for the presence of bite marks. We collected the remains of *T. dichotomus* in mid-September, the end of the activity season of this species, at Tanashi in 2012. We determined the sex of the remains and checked for the presence of bite marks.

We caught living individuals in a bait trap (a 10-L bucket containing bananas, vinegar, and soil) hung from a tree at a height of 1.5 m in Tsukuba from July to August in 2011. The trap was covered with a net (mesh size: 8 cm × 8 cm) to prevent predation by natural enemies. Five traps were placed 50–200 m apart from each surveillance tree and insects caught in traps were collected almost every day. The sex and body size of these insects were determined as described above.

Because the horn length, prothorax width, and sex ratio of prey individuals were not different between the study years (2011 and 2012) or between the two surveillance trees in Tsukuba ($P > 0.3$ by Welch's *t* test or Fisher's exact test), we combined these data in all analyses. The sex ratios of prey, prey with bite marks, prey without bite marks, and living beetles caught in bait traps were compared by Fisher's exact test. We did not investigate the sex ratio of living beetles in the Tanashi population; however, sex ratios of *T. dichotomus* adults in other populations including the Tsukuba population have been reported to be either 1 or slightly female-biased (Siva-Jothy, 1987; Setsuda et al., 1999; Hongo and Kaneda, 2001; Kiritani, 2012; present study). Thus, the sex ratio of prey, prey with bite marks, or prey without bite marks in the Tanashi population was compared with 1 by a binomial test. The horn length and prothorax width of male prey samples and the prothorax width of female prey samples were compared with those of living samples by Welch's *t* test using the Tsukuba population. We also compared the prothorax width of males between prey samples with bite marks (which were

likely to have been preyed on by raccoon dogs, see Results) and those without bite marks (which were likely to have been preyed on by crows) by Welch's *t* test.

Observation of predators with camera traps

We aimed four cameras (Trophy Cam; Bushnell, Overland Park, Kansas, USA) at the two surveillance trees in Tsukuba from 6 August to 9 October in 2012 to identify the predators of *T. dichotomus*. These cameras were concealed behind a bush or in a tree within 1–3 m of the sap-site trees to minimize predator caution. The cameras were triggered by an infrared motion sensor detecting warm-blooded vertebrates to record a digital movie (20 or 30 s per infrared reaction) with the aid of an infrared light at night.

We counted the number of visits of the two predators (Fig. 1B, C), the raccoon dog *Nyctereutes procyonoides* and the jungle crow *Corvus macrorhynchos*, per day per tree. When jungle crows were witnessed twice within a few minutes, we assumed that the same individual or different individuals in the same flock visited the site repeatedly. In this case, we counted the cohort of visits as one visit. If the interval was more than 30 min, we regarded the two visits as independent.

Experiments of predation

To identify the predator of the remains, we examined the marks that each predator left on prey exoskeletons. In August 2011, two males and two females of *T. dichotomus* were placed in a plastic container (30 cm × 20 cm × 5 cm) and placed on the ground in the Tsukuba forest, in which many crows were frequently observed. This site was between the two surveillance trees. The hind wings of the insects were cut to prevent them from flying away. We recorded the feeding behavior of crows with a video camera (Handycam, Sony, Japan) mounted on a tripod set within 2.5 m of the container. We checked the insects remaining in the container one hour later and also carefully searched for the remains of beetles within a 5 m radius of the container. This trial was repeated six times.

In August 2012, we let raccoon dogs feed on *T. dichotomus* tethered with a string to the two surveillance trees in Tsukuba. The string (ca. 1 m in length and 1.2 mm in diameter) was attached to the branch of a tree near the sap sites. Tethered insects were allowed to feed on sap from the tree *ad libitum*. White ink was painted on the prothoraxes of these insects in order to identify the remains. The feeding behavior of raccoon dogs was recorded by video cameras with infrared motion sensors, as described above. We attached 2–3 males and females to each tree and collected their carcasses 3–4 days later. We repeated the trial four times and tethered eight males and eight females in total. As the tethered insects were likely to be preyed upon by both raccoon dogs and crows, we carefully checked the movies, and matched the point we collected the carcasses of painted/tethered insects with the point raccoon dogs preyed on insects.

RESULTS

Sex ratio and size differences between prey and living individuals

The sample sizes of the remains collected in 2011 and 2012 in Tsukuba and Tanashi are summarized in Table 1. The size of some remains was not measured because of severe breaks (large bite marks) (Table 1). We collected 171 females and 154 males in the bait traps in Tsukuba in 2011. We did not measure the length of the horns when they were broken (two of 154 males). The sex ratio of prey individuals in Tsukuba was significantly skewed toward males relative to that of living individuals captured in the bait traps (Table 2, $P < 0.001$ by Fisher's exact test). The sex ratio of prey in Tanashi was also significantly different from 1 (Table

Table 1. The number of remains (male horn, male prothorax, or female prothorax) of *T. dichotomus* collected from the ground of forests in Tsukuba in 2011 and 2012 and Tanashi in 2012. The number of remains, the size of which was measurable, is shown in parentheses.

	Tsukuba		Tanashi
	2011	2012	2012
Male horn ^a	91 (90)	67 (67)	69 (45)
Male prothorax ^a	82 (62)	69 (45)	41 (20)
Female prothorax	48 (36)	43 (39)	37 (23)

^a Remains with both the head horn and prothorax are included.

Table 2. The sex ratio (proportion of males) of living individuals caught in a forest in Tsukuba in 2011, prey samples collected from the ground of the forest in Tsukuba in 2011 and 2012, and prey samples collected from the ground of a forest in Tanashi in 2012.

	Tsukuba		Tanashi
	Living insects	Prey insects	Prey insects
Male	154	160	69
Female	171	91	37
Male ratio	0.47	0.64	0.65

The bold figures indicate a significant difference from 0.47 (Tsukuba) or 0.5 (Tanashi) by Fisher's exact test ($P < 0.05$).

2, $P = 0.002$ by the binomial test). The length of the long horn and width of the prothorax of male prey individuals in Tsukuba were significantly greater than those of living individuals (Fig. 2A, $P < 0.001$ by Welch's *t* test). The width of the prothorax of female prey samples was also greater than that of living females (Fig. 2B, $P < 0.001$ by Welch's *t* test). No significant difference was observed between the prothorax widths of the two groups of remains with and without bite marks (Fig. 3, $P = 0.57$ by Welch's *t* test).

A large proportion of male prey samples at the two study sites, particularly Tanashi, had bite marks (Table 3, 62% (43/69) in Tsukuba and 88% (36/41) in Tanashi). The proportion of female prey samples with bite marks was smaller than that of male prey samples (Table 3, 47% (20/43) in Tsukuba and 62% (23/37) in Tanashi). The sex ratio of prey samples with bite marks was slightly skewed toward males in both populations (Table 3), whereas that of prey samples without bite marks was not (Table 3).

Mammalian and avian predators of prey beetles

The raccoon dog *Nyctereutes procyonoides* (Fig. 1B) and jungle crow *Corvus macrorhynchos* (Fig. 1C) were found to prey on *T. dichotomus* in Tsukuba. The raccoon dog visited sap sites at night, mainly 0 a.m.–2 a.m. (Fig. 4A). Within the observation period (August–October), the frequency of its visits peaked in early August and then gradually decreased (Fig. 4A). Raccoon dogs mostly visited the site alone; however two adult individuals visited together on one occasion. Since we were unable to identify individuals, the number of raccoon dogs that visited the sap sites was undetermined. They typically wandered around the sap-exuding tree for a few minutes, and preyed on *T. dichotomus* at the tree without carrying them away (Supplementary Movies S1, S2 online). The body length of raccoon dogs was

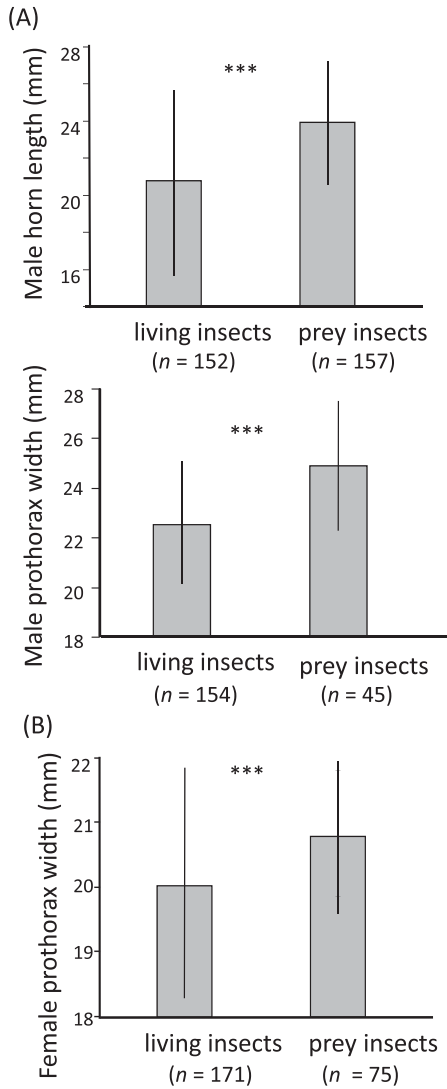


Fig. 2. Size comparisons between living and prey samples. The horn length and prothorax width of males (A) and prothorax width of females (B) were compared between living insects captured in bait traps in a forest in Tsukuba in 2011 and preyed individuals collected from the ground of the same forest in 2011 and 2012. *** $P < 0.001$. Bar: SD.

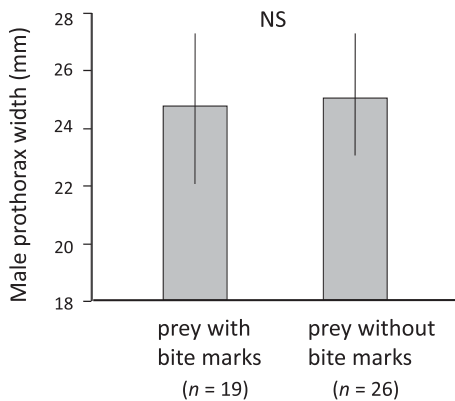


Fig. 3. Size comparisons between prey samples with and without bite marks. Prey samples were collected from the ground of a forest in Tsukuba in 2012. NS: not significant. Bar: SD.

Table 3. The number of prothoraxes with or without bite marks collected from the ground of forests in Tsukuba and Tanashi in 2012.

	Tsukuba		Tanashi	
	With bite marks	Without bite marks	With bite marks	Without bite marks
Male	43	26	36	5
Female	20	23	23	14
Male ratio	0.68	0.53	0.61	0.26

The bold figure indicates a significant difference from 0.47 (Tsukuba) by Fisher's exact test ($P < 0.05$).

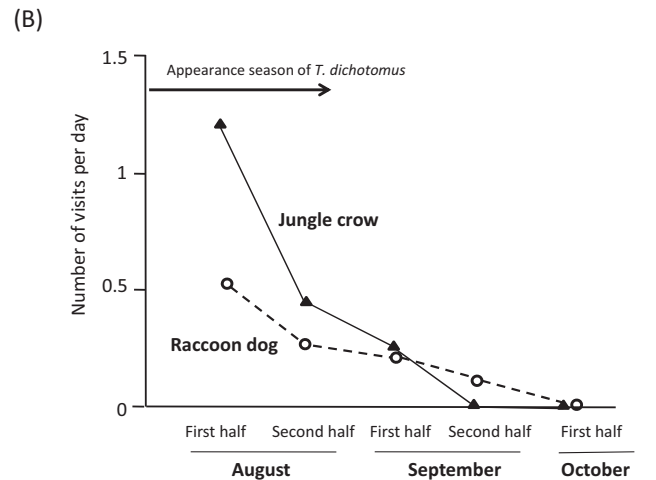
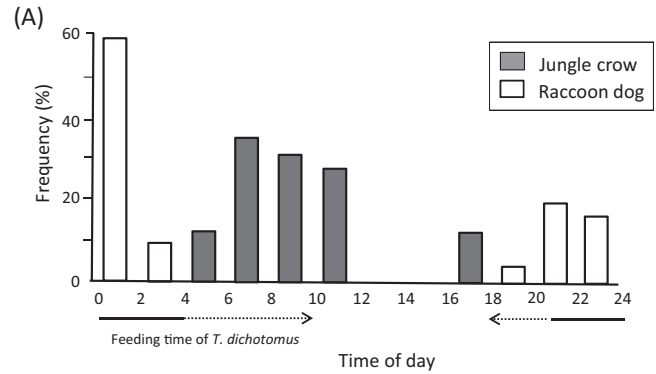


Fig. 4. Changes in the frequency of predator visits to sap sites. (A) Diurnal changes in visits by the two predators. The double-headed arrow indicates the feeding period of *T. dichotomus*. The solid line shows the active feeding time reported by Siva-Jothy (1987), and the dotted line shows the time at which a small number of individuals were observed at sap sites in Tsukuba (Kojima, unpublished data). (B) The number of visits of raccoon dogs and (a flock of) crows per day per sap-site tree during the observation period (6 August–9 October 2012) in Tsukuba. The arrow indicates the appearance season of *T. dichotomus*, which was adopted from Hongo (2007) and Kiritani (2012).

estimated to be 60–70 cm. Although they did not climb the tree, they were able to reach insects > 1 m above the ground by stretching their body (Supplementary Movies S1, S2 online).

Jungle crows visited the sap sites after daybreak in small flocks (at least two individuals), mainly between 6 a.m.

and 12 p.m. The visiting time of crows never overlapped with that of raccoon dogs (Fig. 4A). As with raccoon dogs, the frequency of visits peaked in early August and then rapidly decreased (Fig. 4B). Each flock of jungle crows was estimated to stay near the sap site trees for approximately 10–20 min because crows were recurrently recorded on cameras during this period. Crows searched for *T. dichotomus* from the ground or from a tree branch near the sap (Supplementary Movie S3 online). Crows ate *T. dichotomus* on the ground (Supplementary Movie S3 online) or on a branch.

Other mammals (the masked palm civet *Paguma larvata*, housecat *Felis silvestris catus*, and Japanese badger *Meles meles anakuma*) and birds (Japanese pygmy woodpecker *Dendrocopos kizuki* and Chinese bamboo partridge *Bambusicola thoracicus*) were also recorded on the cameras. Although a masked palm civet was observed catching an orthopteran insect at a sap site, none of these mammals preyed on *T. dichotomus*.

Bite marks of predators on the remains

We used 16 tethered beetles (eight males and eight females) to investigate the relationship between bite marks and predation by raccoon dogs in the field. After an observation for 3–4 days, six beetles (three males and three females) were determined to be eaten by raccoon dogs. Three (two males and one female) were preyed on by jungle crows, three (one male and two females) were eaten by unidentified predators, and four died without being eaten. Most parts of the mesothorax, metathorax, and abdomen were consumed by raccoon dogs (Fig. 5A, B). The remaining prothoraxes of two females and three males had clear bite marks of > 3 mm in length (Fig. 5A, B); however, no bite marks were found on the remaining prothorax of one female.

We also examined whether jungle crows left bite marks on beetles at predation (Supplementary Movie S5 online). A total of 16 beetles (nine males and seven females) of the 20

beetles used in this experiment were preyed on by crows. We recovered the remains of 15 prey beetles (eight males and seven females), the mesothorax, metathorax, and abdomen of which were mostly consumed (Fig. 5C, D). No bite marks were found on the remaining prothoraxes of any prey individuals (eight males and seven females).

DISCUSSION

An examination of the remains of predated beetles and beetles caught in bait traps at sap sites in Tsukuba revealed that predation pressure is greater for males of *T. dichotomus* than for females and that larger individuals of both sexes are more vulnerable to predation. It is likely that male-biased predation also occurred at Tanashi. Similar sex- and size-biased predation of *T. dichotomus* was reported previously at another location in Gifu Prefecture (Setsuda et al., 1999). Thus, this predation pattern probably occurs in a wide area.

Our study confirmed that the jungle crow is an important predator of *T. dichotomus*, as was speculated previously (Setsuda et al., 1999; Kiritani, 2012). Jungle crows visited sap sites almost every day to prey on *T. dichotomus* during the prevalent period (the first half of August). We showed that the raccoon dog is also an important predator of *T. dichotomus* during the night, although the raccoon dog has been known to eat various insects including *T. dichotomus* (Koike et al., 2012). In our study, both jungle crows and raccoon dogs selectively preyed on *T. dichotomus* from the insect species that gathered around the sap (e.g., the scarab beetles *Protaetia orientalis*, *Rhomborrhina japonica*, and *R. polita*; the longicorn beetle *Massicus raddei*; the stag beetles *Prosopocoilus inclinatus* and *Dorcus rectus*; and the cockroach *Periplaneta fuliginosa*). These predators appear to visit sap sites in synchrony with the prevalence of *T. dichotomus* (early August). Since *T. dichotomus* has the largest body size and biomass among the insect species found at sap sites, it appears to be the favored food of the two predators. Hongo and Kaneda (2009) reported the predation of *T. dichotomus* by Ural owls in another area of Japan (Kyoto Prefecture). Although we frequently observed a family of Ural owls at night near the surveillance trees in Tsukuba, *T. dichotomus* was not preyed on by this family.

We found that raccoon dogs often left bite marks on the prothorax of *T. dichotomus*, whereas crows did not (Fig. 5). Therefore, it is possible to estimate the frequency of predation by raccoon dogs based on the proportion of remains with bite marks. At least 58% of prey were estimated to have been preyed on by raccoon dogs in Tsukuba. Similar bite marks were also observed on 76% of prey beetles in Tanashi, in which predators were not identified. This result suggests that the predation of *T. dichotomus* by raccoon dogs is common in the central part of Japan. Although raccoon dogs visited

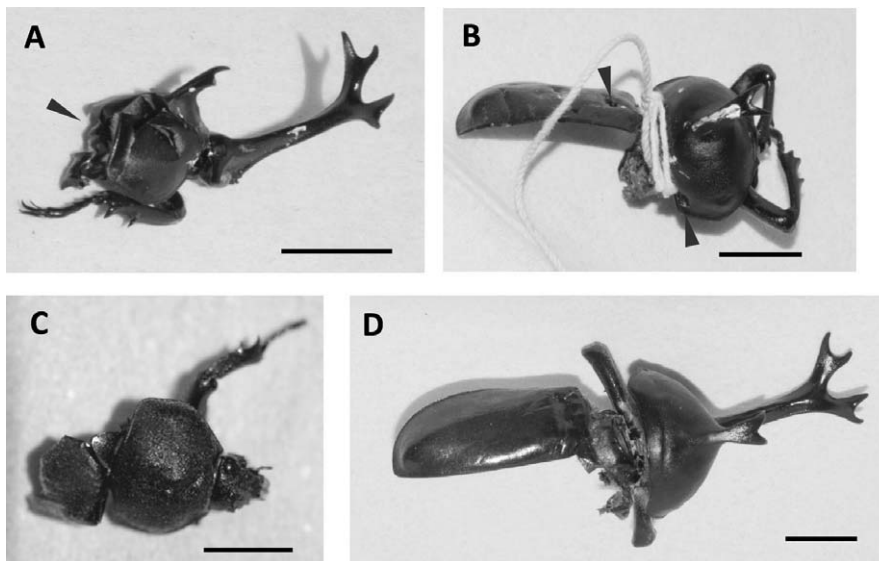


Fig. 5. Typical examples of the remains of *T. dichotomus* preyed on by raccoon dogs (A, B) and jungle crows (C, D). Bite marks are indicated by arrowheads in (A) and (B). Males were tethered and marked with white paint in the predation experiment. (C) A female. (D) A male. Scale bar = 1 cm.

the sap sites less frequently than jungle crows in Tsukuba during the peak season of *T. dichotomus* (August), they preyed on more beetles than the crows at each visit. Raccoon dogs would be able to catch *T. dichotomus* more efficiently than crows because raccoon dogs visited sap sites after midnight (Fig. 4A) when many *T. dichotomus* actively fed on the sap (Siva-Jothy, 1987), while crows visited the sap sites after daybreak (approximately 6 a.m.) (Fig. 4A) when most insects had already left. Although raccoon dogs are unable to climb trees to catch insects, sap exudation from *Quercus* trees in Japan generally occurs at a height of 1.5 m or less (Takakuwa, 2007; Ichikawa and Ueda, 2009), which is reachable by raccoon dogs. In addition, raccoon dogs are likely to have many chances to prey on *T. dichotomus* because *T. dichotomus* and raccoon dogs often share habitats in the 'Satoyama' (a mosaic of rice paddy fields, grassland, and secondary forests) or riparian forests (Hirasawa et al., 2006).

Which predator is responsible for sex- and size-dependent predation? The sex ratio of the remains with bite marks was skewed toward males (68 and 61%) in both Tsukuba and Tanashi, while that of the remains without bite marks was not (53 and 26%). This result appears to suggest male-biased predation by raccoon dogs. The lack of a difference in size between male remains with and without bite marks implies that predation by both raccoon dogs and crows is dependent on size; however, further studies are needed to accurately evaluate sex- and size-dependent predation pressure by each predator.

How do the size- and sex-dependent predation patterns of *T. dichotomus* occur? Predators may ingest the entire body of small individuals and females but leave part of the exoskeleton of large individuals and males unconsumed. Such a differential ingestion behavior would lead to the apparent size- and sex-dependent patterns; however, we do not have any concrete evidence for differential ingestion by jungle crows or raccoon dogs. Multiple factors are considered to be involved in size- and sex-dependent predation. First, a temporal overlap between the feeding of beetles and foraging of predators may lead to a biased predation pattern. The numbers of smaller males of *T. dichotomus* feeding at sap sites peaks at 10 p.m., while that of larger males peaks at 12 a.m.–3 a.m. (when the foraging activity of raccoon dogs is high) and they often stay at sap sites after sunrise (when the foraging activity of crows is high) (Siva-Jothy, 1987; Setsuda et al., 1999, and Kojima unpublished data). In addition, larger males are likely to stay at sap sites longer than females and smaller males in order to defend their territory and wait for mates (Siva-Jothy, 1987). Therefore, predators have a larger opportunity to prey on larger males than smaller ones or females. Second, larger males may be more conspicuous to predators than females or small males. Third, predators may prefer and choose larger males if they are more nutritious or palatable than smaller male and females.

Predation pressure is greater for males of *T. dichotomus* than for females, and larger individuals of both sexes are also more vulnerable to predation. Sexual traits are suggested to incur various costs including increased predation risk, increased energy expenditure, and immunosuppression (Zahavi, 1975; Andersson, 1994; Grafen, 1990; Kotiaho,

2001). While producing and carrying a large horn is known to impose no or little cost on *T. dichotomus* (McCullough et al., 2012; McCullough and Emlen, 2013; McCullough and Tobalske, 2013), our results of size- and sex-biased predation suggest that the male horn is costly in terms of the increased risk of predation by mammalian and avian predators. If the size of the horn is heritable in *T. dichotomus*, predation cost will act as a stabilizing selection pressure on this trait, constraining its further enlargement. The trade-off between predation risk and the benefit in acquiring mates is likely to have had a significant impact on the evolution of this exaggerated sexual trait in this species.

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